Diversité et fonction des communautés d'oiseaux et de lépidoptères dans les paysages forestiers fragmentés : réponses multi-échelles et interactions trophiques

Luc L. Barbaro

▶ To cite this version:

Luc L. Barbaro. Diversité et fonction des communautés d'oiseaux et de lépidoptères dans les paysages forestiers fragmentés : réponses multi-échelles et interactions trophiques. Sciences du Vivant [q-bio]. Université des Sciences et Technologies (Bordeaux 1), 2013. tel-02810764

HAL Id: tel-02810764

https://hal.inrae.fr/tel-02810764

Submitted on 6 Jun 2020

Diplôme d’Habilitation à Diriger des Recherches

(HDR)

Présenté à
L’UNIVERSITÉ BORDEAUX 1
Ecole Doctorale Sciences et Environnements (SE)
Spécialité Ecologie évolutive, fonctionnelle et des communautés

Par

Luc Barbaro

Chargé de Recherches

UMR 1202 BIOGECO INRA-Université Bordeaux 1 - Equipe Ecologie des Communautés

Diversité et fonction des communautés d’oiseaux et de lépidoptères dans les paysages forestiers fragmentés : réponses multi-échelles et interactions trophiques

Soutenue le 25 juin 2013 devant la commission d’examen formée de :

Françoise	BUREL	Directrice de Recherches CNRS, Rennes	Rapporteur
Gérard	BALENT	Directeur de Recherches INRA, Toulouse	Rapporteur
Jean-Louis	MARTIN	Directeur de Recherches CNRS, Montpellier	Rapporteur
Philippe	CLERGEAU	Professeur Muséum National d’Histoire Naturelle, Paris	Examinateur
Lluis	BROTONS	Directeur de Recherches CTFC, Solsona, Espagne	Examinateur
Didier	ALARD	Professeur, Université de Bordeaux 1	Examinateur

Il suffit que nous parlions d’un objet pour nous croire objectifs.

Gaston Bachelard. - La psychanalyse du feu.

Table des matières

Remerciements

Le parcours dôun chercheur est marqué à la fois par lôinnovation et la permanence. Aussi, je suis reconnaissant à Gérard Balent dôavoir accompagné mon parcours quasiment depuis ses débuts jusquôà aujourdôhui, en tant que rapporteur de ce travail. Je remercie également chaleureusement les membres du jury, Françoise Burel, Jean-Louis Martin, Didier Alard, Lluis Brotons et Philippe Clergeau pour avoir accepté de le juger à lôaune de leurs propres recherches, qui ont été et sont toujours pour moi une source dôinspirations multiples.

Le parcours dôun chercheur est également à la fois un exercice solitaire et un projet collectif sans cesse revivifié par les étudiants et les autres chercheurs que lôon côtoie. Je suis donc particulièrement reconnaissant à Hervé Jactel et Emmanuel Corcket pour avoir accompagné mes recherches au cours de la décennie écoulée, notamment via lôencadrement collaboratif de différents travaux qui se sont avérés centraux pour mon évolution personnelle. Je dois ici beaucoup aux trois doctorants que jôai co-encadré ces dernières années, Inge van Halder, Brice Giffard et Yohan Charbonnier qui môont chacun à leur manière apporté un souffle nouveau en môintéressant à de nouveaux objets, de nouveaux concepts et de nouvelles méthodes, voire en rafraîchissant des intérêts anciens.

La créativité de la recherche étant régulièrement réamorcée par la mise en commun de connaissances permettant à chacun de franchir de nouveaux paliers, je remercie les chercheurs, mi-érudits et mi-explorateurs, avec qui jôai eu la chance dôéchanger au sein de plusieurs projets collectifs enthousiasmants qui ont fourni la matière centrale du présent mémoire. Je pense en particulier à Marc Dufrêne, Marc Deconchat, Ecki Brockerhoff, Vincent Bretagnolle, Arndt Hampe, Andrea Battisti, Jean-Charles Bouvier, Frédéric Archaux et Jean-Yves Barnagaud, qui môont apporté à un moment ou à un autre des éléments essentiels pour mes propres recherches. Merci également à Fabien Anthelme, Christophe Bouget, Jean-Michel Carnus, Frédéric Gosselin, Dominique Guyon, José Antonio Hódar, Christian Kerbiriou, Sylvie Ladet, Jean-Marc Louvet, Jean-Claude Martin, Pierre Menassieu, Tim Nuttle, Annie Ouin, Steve Pawson, Dominique Piou, Aurélien Plichon, Alain Roques, Adrien Rusch, Sonia Said et Corinne Vacher pour leur aide, leur soutien ou leur collaboration.

La recherche en écologie passe, quoiquôon puisse lire ou entendre ici ou là, par le recueil de données de qualité selon des protocoles rigoureux, sur le terrain. Sur le terrain, cela signifie en forêt, en montagne, dans les dunes, les champs, les vignes ou les prairies, les pieds dans lôeau, dans le froid ou sous une chaleur de plomb. Cela génère des moments difficiles, mais aussi des observations quelquefois inoubliables. Je remercie ici mes compagnons de terrain les plus réguliers, Fabrice Vétillard, Julien Nezan, Olivier Lannès, Gilles Trochard et lôindispensable et infatigable Sébastien Blache. Un grand merci aussi aux (ex)-étudiant(e)s avec qui jôai travaillé et partagé de bons moments ces dernières années, en particulier Laurent, Bruce, Laurène, Fabrice, Estelle, Manon, Karine, Jean-Charles, Maïmiti, Antoine, Amélie, Jorge, Elsa, Jean-Sébastien, Guillaume, Pierre et Nathalie. Bonne route à tous.

Enfin, jôadresse un remerciement tout particulier à Alan et Kaye Leckie à Christchurch, pour nous avoir récupérés, hébergés et préparé de délicieuses gauffres ómaisonô le lendemain du séisme. Merci aussi pour lôéchasse noire, le disque de Tim Buckley et ton best-of des meilleures chansons à écouter après un tremblement de terre, Alan !

Curriculum vitae

Luc Barbaro

né le 8 octobre 1971 à Marseille (13), nationalité française

Adresse professionnelle :
INRA UMR1202 BIOGECO
Ecologie des communautés
69 route d'Arcachon, 33612 Cestas cedex,
téléphone : +335 57 12 27 40
courriel : **luc.barbaro@pierroton.inra.fr**

Formation universitaire

2013 : Habilitation à Diriger Des Recherches de lõUniversité de Bordeaux 1 : *Diversité et fonction des communautés dõoiseaux et de lépidoptères dans les paysages forestiers fragmentés : réponses multi-échelles et interactions trophiques.* Soutenue le 25 juin 2013.

1999 : Doctorat de Biologie de lõUniversité de Grenoble 1 **:** *Dynamique agro-écologique des communautés de pelouses sèches calcicoles du Vercors méridional: application à la gestion conservatoire de la biodiversité par le pastoralisme.* Soutenue le 27 octobre 1999, mention très honorable avec félicitations du jury.

1995 : DEA *Gestion des Espaces Montagnards*, Université Grenoble 1

1994 : Maîtrise de Géographie Physique, Université Paris 7

1993 : Licence de Géographie Physique, Université Paris 7

1992 : Deug de Géographie, Université Paris 12

1989 : Baccalauréat D, Lycée de Dourdan (91)

Activités professionnelles, missions et stages

Poste actuel : Chargé de Recherches de 1ère classe dans l'Equipe **Ecologie des Communautés,** UMR BIOGECO, INRA et Université de Bordeaux (33)

2014 : Mission de 3 semaines à lõ**Universidad Mayor de San Andrès,** La Paz, Bolivie dans le cadre du projet IRD BIO-THAW (collaboration avec F. Anthelme, K. Naoki et O. Dangles)

2011 : Mission de 8 semaines à **SCION Forest Research Institute,** Christchurch, Nouvelle-Zélande, dans le cadre du projet TRANZFOR (collaboration avec E. Brockerhoff)

2005 : Mission de 6 semaines à **SCION Forest Research Institute,** Christchurch, Nouvelle-Zélande (collaboration avec E. Brockerhoff et M. Deconchat)

2004 : Chargé de Recherches de 1ère classe dans l'Equipe **Entomologie Forestière et Biodiversité,** UMR BIOGECO, INRA-Pierroton (33)

2000 : Chargé de Recherches de 2ème classe dans l'Equipe **Entomologie Forestière et Biodiversité,** UMR BIOGECO, INRA-Pierroton (33)

2000 : Chargé de mission au **Centre Ornithologique Rhône-Alpes**, Romans sur Isère (26)

1995-1999 : Doctorant dans **lõUnité de Recherches *Agricultures et Milieux Montagnards,*** Cemagref Grenoble (38), sous la direction de P. Cozic et J.P. Peltier

1994-1995 : Stages de 2 et 3e cycle au service scientifique du **Parc Naturel Régional du Vercors** (38)

Production scientifique (H-index=10 avec 269 citations Scopus)

Articles scientifiques ISI (23 articles)

Barnagaud J.Y., **Barbaro L.**, Papaïx J., Deconchat M., Brockerhoff E.G. **2014** Habitat filtering by landscape and local forest composition in native and exotic New Zealand birds. *Ecology* 95: 78-87.

Barbaro L., Giffard B., Charbonnier Y., van Halder I., Brockerhoff E.G. **2014** Bird functional diversity enhances insectivory at forest edges: a transcontinental experiment. *Diversity and Distributions* 20: 149-159.

Martin-Garcia J., **Barbaro L.**, Diez J.J., Jactel H. **2013** Contribution of poplar plantations to bird conservation in riparian landscapes. *Silva Fennica* 47(4): 1043.

Barnagaud J.Y., **Barbaro L.**, Hampe A., Jiguet F., Archaux F. **2013** Speciesô thermal preferences affect forest bird communities along landscape and local scale habitat gradients. *Ecography* 36: 1218-1226.

Baeten L., Verheyen K., Wirth C., Bruelheide H., Bussotti F., Finér L., Jaroszewicz B., Selvi F., Valladares F., Allan E., Ampoorter E., Auge H., AvŁcŁriei D., **Barbaro L.**, BŁrnoaiea I., Bastias C., Bauhus J., Beinhoff C., Benavides R., Benneter A., Berger S., Berthold F., Boberg J., Bonal D. et al. **2013** A novel comparative research platform designed to determine the functional significance of tree species diversity in European forests. *Perspectives in Plant Ecology, Evolution and Systematics* 15: 281-291.

Giffard B., **Barbaro L.**, Jactel H., Corcket E. **2013** Plant neighbours mediate bird predation effects on arthropod abundance and herbivory. *Ecological Entomology* 38: 448-455.

Barbaro L., Dulaurent A.M., Payet K., Blache S., Vetillard F., Battisti A. **2013** Winter bird numerical responses to a key defoliator in mountain pine forests. *Forest Ecology and Management* 296: 90-97.

Barbaro L., Brockerhoff E.G., Giffard B., van Halder I. **2012** Edge and area effects on avian assemblages and insectivory in fragmented native forests. *Landscape Ecology* 27: 1451-1463.

Giffard B., Jactel H., Corcket E., **Barbaro L.** **2012** Influence of surrounding vegetation on insect herbivory: a matter of spatial scale and herbivore specialisation. *Basic and Applied Ecology* 13: 458-465.

Giffard B., Corcket E., **Barbaro L.**, Jactel H. **2012** Bird predation enhances tree seedling resistance to insect herbivores in contrasting forest habitats. *Oecologia* 168: 415ï 424.

van Halder I., **Barbaro L.**, Jactel H. **2011** Conserving butterflies in fragmented plantation forests: are edge and interior habitats equally important? *Journal of Insect Conservation* 15: 591-601.

Barbaro L., Battisti A. **2011** Birds as predators of the pine processionary moth (Lepidoptera: Notodontidae). *Biological Control* 56: 107-114.

Deconchat, M., Brockerhoff E.G., **Barbaro L.** **2009** Effects of surrounding landscape composition on the conservation value of native and exotic habitats for native forest birds. *Forest Ecology and Management* 258S: S196-S204.

Barbaro L., van Halder I. **2009** Linking bird, carabid beetle and butterfly life-history traits to habitat fragmentation in mosaic landscapes. *Ecography* 32: 321-333.

van Halder I., **Barbaro L.,** Corcket E., Jactel H. **2008** Importance of semi-natural habitats for the conservation of butterfly communities in landscapes dominated by pine plantations. *Biodiversity and Conservation* 17: 1149-1169.

Barbaro L., Couzi L., Bretagnolle V., Nezan J., Vetillard F. **2008** Multi-scale habitat selection and foraging ecology of the eurasian hoopoe (*Upupa epops*) in pine plantations. *Biodiversity and Conservation* 17: 1073-1087.

Barbaro L., Rossi J.P., Vetillard F., Nezan J., Jactel H. **2007** The spatial distribution of birds and carabid beetles in pine plantation forests: the role of landscape composition and structure. *Journal of Biogeography* 34: 652-664.

Barbaro L., Pontcharraud L., Vetillard F., Guyon D., Jactel H. **2005** Comparative responses of bird, carabid, and spider assemblages to stand and landscape diversity in maritime pine plantation forests. *Ecoscience* 12: 110-121.

Barbaro L., Dutoit T., Anthelme F., Corcket E. **2004** Respective influence of habitat conditions and management regimes on prealpine calcareous grasslands. *Journal of Environmental Management* 72: 261-275.

Anthelme F., Michalet R., **Barbaro L.,** Brun J.J. **2003** Environmental and spatial influences of shrub cover (Alnus viridis DC.) on vegetation diversity at the upper treeline in the inner western Alps. *Arctic, Antarctic and Alpine Research* 35: 48-55.

Barbaro L., Dutoit T., Grossi J.L. **2003** Influence des facteurs agro-écologiques sur les assemblages dôorchidées dans les pelouses calcicoles du Vercors (Préalpes, France). *Botanica Helvetica* 113: 63-79.

Barbaro L., Dutoit T., Cozic P. **2001** A six-year experimental restoration of biodiversity by shrub-clearing and grazing in calcareous grasslands of the French Prealps. *Biodiversity and Conservation* 10: 119-135.

Barbaro L., Corcket E., Dutoit T., Peltier J.P. **2000** Réponses fonctionnelles des communautés de pelouses calcicoles aux facteurs agro-écologiques dans les Préalpes françaises. *Canadian Journal of Botany* 78: 1010-1020.

Chapitres d'ouvrages (11 chapitres)

Barbaro L., Couanon V., Lannès O. **2014** Bruant fou, Bruant jaune, Crave à bec rouge, Huppe fasciée, Merle à plastron, Tarier des prés, Mésange huppée, Locustelle tachetée, Pipit farlouse, Roitelet huppé. In: LPO Aquitaine (ed.) Atlas des oiseaux nicheurs dôAquitaine, Delachaux & Niestlé.

Jactel H., **Barbaro L**., Brockerhoff E.G., Castagneyrol B., Dulaurent A.M., Samalens J.C., Schlyter F.E. **2014** Effect of tree species diversity on *Thaumetopoea pityocampa* infestations. In: Roques A. (ed.). Processionary moths and global change: an update. Springer Verlag.

Barbaro L., Charbonnier Y., Vetillard F., Blache S., Battisti A. **2014** Numerical and functional responses of predatory vertebrates to the pine processionary moth. In: Roques A. (ed.). Processionary moths and global change: an update. Springer Verlag.

Trochard G., Blache S., Kayser Y., **Barbaro L. 2013** La Chevêchette dôEurope *Glaucidium passerinum*: premiers éléments de son régime alimentaire sur les Hauts Plateaux du Vercors. In : FRAPNA (ed.) Actes du colloque ôLa prédationô, 22-23 mars 2013, ENS Sciences, Lyon: 67-72.

Jactel H., **Barbaro L. 2009** Impacts de la production intensive de biomasse sur la biodiversité dans les forêts de plantations: lôexemple des futaies à courte révolution de Pin maritime. In: Landmann G., Gosselin F., Bonhême I. (eds). Bio2, Biomasse et biodiversité forestières. Paris, MEEDDM-Ecofor: 89-97.

Giffard B., Corcket E., **Barbaro L**., Jactel H. **2008** Variations dans les interactions tritrophiques lors de la régénération dôessences feuillues. In: Bonis A. (ed) Actualité de la recherche en écologie des communautés végétales : actes du 4e colloque Ecoveg, Rennes, 12-14 mars 2008, Lavoisier, Tec & Doc, Paris: 87-93.

Jactel H., **Barbaro L.**, Brockerhoff E. **2007** Contribution of plantation forests to biodiversity conservation: the landscape perspective. In: Martres J.L. (ed), Proceedings of the International Congress on Cultivated Forests, USSE, Spain: 336-337.

van Halder I., **Barbaro L.**, Corcket E., Jactel H. **2007** Butterfly diversity in pine plantation landscapes. In: Martres J.L. (ed), Proceedings of the International Congress on Cultivated Forests, USSE, Spain: 338-339.

Jactel H., **Barbaro L. 2004** Projet ISLANDES: évaluation de la méthode des îlots de feuillus en mélange pour restaurer la biodiversité de lôécosystème simplifié de pin maritime des Landes de Gascogne. In: Millier C., Barre V., Landeau S. (eds), Biodiversité et Gestion Forestière. GIP Ecofor, Paris: 18-26.

Barbaro L. **2003** Bergeronnette printanière, Accenteur mouchet, Rougequeue à front blanc, R. noir, Tarier des prés, Rousserolle verderolle, Roitelet huppé, R. triple-bandeau, Mésange nonnette, M. boréale, M. huppée, Moineau soulcie. In: CORA Drôme (ed.) Atlas des oiseaux nicheurs de la Drôme, Romans: pp 127 à 223.

Barbaro L., Blache S., Ladet A. **2003** Moineau soulcie (*Petronia petronia*). In: CORA (ed) Oiseaux nicheurs de Rhône-Alpes, Centre Ornithologique Rhône-Alpes, Lyon: p 259.

Articles non-indexés (11 articles)

Blache S., Trochard G., **Barbaro L. 2014** Distribution spatiale et densité de la Chevêchette dôEurope *Glaucidium passerinum* sur la Réserve Biologique Intégrale des Hauts-Plateaux du Vercors : état des lieux 2009-2011. *Le Bièvre*, sous presse.

Barbaro L. **2010** Note sur les observations de Coucou-geai *Clamator glandarius* en Aquitaine et Charente-Maritime. Online at www.faune-aquitaine.org, réf. n°0003_FA2009.

Barbaro L. **2009** La Huppe fasciée, alliée du forestier. *La Gazette des Forêts* 12: 3.

Barbaro L., Plichon A. **2009** Les Coléoptères carabiques (Coleoptera, Carabidae) des habitats humides de la Réserve Naturelle de lôEtang de Cousseau (Lacanau, Gironde). *Bulletin de la Société Linnéenne de Bordeaux* 144/37: 85-93.

Barbaro L., Vetillard F., Menassieu P., van Halder I. **2006** Liste commentée des Coléoptères carabiques (Coleoptera Carabidae) de la forêt des Landes de Gascogne (Landes et Gironde). *Bulletin de la Société Linnéenne de Bordeaux* 141/34: 197-210.

Barbaro L., Vetillard F. **2005** Les Coléoptères carabiques bioindicateurs de la gestion forestière dans les Landes de Gascogne. *Sud Ouest Nature* 129: 26-28.

Barbaro L., Grisser P., Nezan, J. **2004** Phénologie et effectifs des plongeons en période internuptiale sur le littoral aquitain de 1993 à 2004. *Le Courbageot* 24: 24-27.

Barbaro L., Nezan J., Bakker M., Revers F., Couzi L., Vetillard F., Le Gall O. **2003** Distribution par habitats des oiseaux nicheurs à enjeu de conservation en forêt des Landes de Gascogne. *Le Courbageot* 21/22: 12-23.

Barbaro L. 2000 Gestion de la biodiversité par le pastoralisme: exemple des pelouses calcicoles sèches du Vercors méridional. *La Fayolle* 2: 18-27.

Barbaro L., Boyer P. **1999** Observations sur la nidification et l'évolution récente du Moineau soulcie (Petronia petronia L.) dans les Préalpes du sud. *Le Bièvre* 16: 27-36.

Barbaro L., Cozic P. **1998** Organisation agro-écologique des pelouses et landes calcicoles du Parc Naturel Régional du Vercors. *Ecologie* 29: 443-457.

Communications dans des congrès et colloques (49 communications)

Barbaro L., Battisti A., Charbonnier Y., Dulaurent A.M., Jactel H. **2014** Trophic interactions between vertebrate insectivores and a climate-driven expanding forest moth. IUFRO World Congress, Salt Lake City, USA, 5-11th October 2014 (communication orale).

Barbaro L. 2014 Comparaison de lôavifaune nicheuse et migratrice dans un réseau de prairies humides girondines. Séminaire ôRestauration dôune prairie humide alluviale en Girondeö, Univ. Bordeaux, 17 janvier 2014 (communication orale).

Voinopol-Sassu J., Brockerhoff E.G., Hock B., **Barbaro L. 2013** Functional habitat connectivity for the Rifleman *Acanthisitta chloris* on Banks Peninsula, New Zealand. EcoTas13, 5th joint conference of New Zealand Ecological Society and Ecological Society of Australia, Auckland, New Zealand, 24-29th November 2013 (communication orale).

Blache S., **Barbaro L.,** Trochard G., de Lacoste N., Kayser Y. **2013** Ecologie du domaine vital et régime alimentaire de la Chevêchette dôEurope dans une Réserve Biologique Intégrale préalpine. 1ères rencontres nationales du réseau LPO-ONF ôPetites chouettes de montagneô 8-10 novembre 2013, Sarrebourg (communication orale).

Barbaro L., Battisti A. **2013** Stratégies de prédation dôun lépidoptère urticant par les oiseaux insectivores : lôexemple de la processionnaire du pin. 7èmes Rencontres du Groupe des Entomologistes Forestiers Francophones, Brens, 22-24 octobre 2013 (communication orale).

Charbonnier Y., **Barbaro L.,** Theillout A., Jactel H. **2013** Réponses numériques et fonctionnelles de chauves-souris insectivores à la processionnaire du pin. 7èmes Rencontres du Groupe des Entomologistes Forestiers Francophones, Brens, 22-24 octobre 2013 (communication orale).

van Halder I., **Barbaro L.,** Jactel H. **2013** Effet de la taille, lôisolation et la qualité des îlots de feuillus sur les cortèges de papillons de jour. 7èmes Rencontres du Groupe des Entomologistes Forestiers Francophones, Brens, 22-24 octobre 2013 (communication orale).

Barbaro L. 2013 Les traits de vie comme indicateurs de réponses multi-taxa à la fragmentation des paysages forestiers. Atelier scientifique ôIntérêts et limites des approches multi-taxonomiques de la biodiversitéö, programme BGP, GIP Ecofor, Maison de la Forêt, Bordeaux, 26 juin 2013 (communication orale).

Barbaro L. 2013 Relier conservation de la biodiversité et interactions trophiques : les communautés dôoiseaux et de lépidoptères dans les mosaïques de paysages forestiers. Soutenance dôHabilitation à Diriger des Recherches, INRA Bordeaux, 25 juin 2013.

Barbaro L., Brockerhoff E.G., Giffard B., Charbonnier Y., van Halder I., Deconchat M. **2013** Insectivorie et diversité fonctionnelle des communautés dôoiseaux dans les lisières forestières. Séminaire de lôUMR Biogeco, INRA Pierroton, 5 avril 2013 (communication orale).

Giffard B., Corcket E., **Barbaro L**., Prudôhomme R., Jactel H. **2013** Composition du peuplement forestier et voisinage végétal modulent les interactions trophiques dans la régénération forestière. Colloque ECOVEG 9, Tours, 3-5 avril 2013 (communication orale).

Charbonnier Y., **Barbaro L**., Theillout A., Jactel H. **2013** Numerical and functional responses of foraging forest bats to a key pine defoliator. 3rd International Berlin Bat Meeting: Bats in the Anthropocene, 1st - 3rd March 2013, Berlin, Germany (communication affichée).

Barbaro L., Deconchat M., Terraube J., Archaux F., van Halder I., Charbonnier Y. **2012** Réponses de lôavifaune et de lôinsectivorie avienne aux lisières forestières. Réunion annuelle du projet GIP Ecofor BILISSE, Toulouse, 13 décembre 2012 (communication orale).

Corcket E., **Barbaro L**., Jactel H. **2012** Régulation biologique dans les forêts. Conférences du pôle de compétitivité Xylofutur, Bordeaux Sciences Agro, Gradignan, 25 septembre 2012 (communication orale).

Barbaro L., Brockerhoff E.G., Giffard B., Terraube J., Charbonnier Y., van Halder I. **2012** Edge effects on bird functional diversity and insectivory in mosaic forest landscapes: a transcontinental comparison. 2d IUFRO Conference, Biodiversity in forest ecosystems and landscapes, University College, Cork, Ireland, 28-31 August 2012 (communication orale).

Giffard B., Corcket E., **Barbaro L**., Jactel H. **2012** Neighbouring vegetation influences tritrophic interactions between insectivorous birds, herbivorous insects and tree seedlings. Ecology and Behaviour, 8th Annual Meeting (SERL), 2 April ï 6 April 2012, CEBC CNRS Chizé (communication orale).

van Halder I., **Barbaro L.,** Jactel H. **2012** Conserving butterflies in plantation forests. International Butterfly Congress, Future of Butterflies in Europe III, Wageningen, Nederland, March 2012 (communication orale).

Barbaro L., Brockerhoff E.G., Giffard B., van Halder I. **2011** Effets des lisières et de la fragmentation forestière sur la prédation par les oiseaux insectivores dans les forêts natives néo-zélandaises. 5èmes Journées dôEcologie du Paysage IALE France, 7-10 novembre 2011, Aix en Provence (communication orale).

Samalens J.C., Dulaurent A.M., **Barbaro L.,** Piou D., Jactel H. **2011** Epidémiologie du paysage : le cas de la chenille processionnnaire du pin (*Thaumetopoea pityocampa*). 5èmes Journées dôEcologie du Paysage IALE France, 7-10 novembre 2011, Aix en Provence (communication orale).

Barbaro L., Charbonnier Y., Dulaurent A.M., Battisti A., Vetillard F., Jactel H. **2011** Functional and numerical responses of predatory vertebrates to the pine processionary moth: a synthesis. Final meeting, ANR Urticlim, 17-19 November 2011, Belgodère, Corsica (communication orale).

Terraube J., Giffard B., Charbonnier Y., van Halder I., **Barbaro L. 2011** Effet de la prédation par les oiseaux sur les populations dôinsectes forestiers et ses implications pour les communautés végétales. 6èmes Rencontres du Groupe des Entomologistes Forestiers Francophones, Le Teich, 12-14 octobre 2011 (communication orale).

Brockerhoff E., Ecroyd C., Hock B., Pawson, S., Paul T., **Barbaro L.,** Deconchat M., Jactel H. **2010** The role of plantation forests in biodiversity conservation in New Zealand. Biodiversity: 2010 and beyond, New Zealand Ecological Society Conference, 22-25 November 2010, Dunedin, New Zealand (communication orale).

Giffard B., Corcket E., **Barbaro L**., Prudhomme R., Louvet J.M., Jactel H. **2010** Effet indirect des oiseaux insectivores sur les dommages foliaires dôinsectes phytophages: influence de lôespèce de plantule forestière et du type de peuplement. Colloque Ecologie 2010, 2-4 septembre 2010, Montpellier (communication affichée).

Barbaro L. **2010** Biodiversité dans les lisières forestières: comment gérer les interfaces entre forêts et milieux ouverts pour la biodiversité ? Conseil Scientifique du pôle de compétitivité Xylofutur, 25 mars 2010, Pierroton (communication orale).

Barbaro L., Derouault A., Payet K., Blache S., Vetillard F., Jean F. **2009** Insectivorous bird assemblages along an elevation gradient of *T. pityocampa* expansion in the southern Alps. Annual meeting, ANR Urticlim, INRA Orléans, 12-13 november 2009 (communication orale).

Giffard B., Corcket E., **Barbaro L**., Jactel H. **2009** Variations de réponse des dégâts dôinsectes aux cascades trophiques lors de la régénération dôessences feuillues. 4èmes Rencontres du Groupe des Entomologistes Forestiers Francophones, Semur en Auxois, 20-22 octobre 2009 (communication orale).

Barbaro L. 2008 Les oiseaux insectivores prédateurs de la processionnaire du pin. Colloque Insectes et changement climatique, Micropolis (Aveyron) 14-15 novembre 2008 (communication orale).

Barbaro L., Blache S., Payet K., Vetillard F., Jean F. **2008** Mise en place du dispositif de suivi de l'avifaune prédatrice. Colloque Insectes et changement climatique, Micropolis (Aveyron) 14-15 novembre 2008 (communication orale).

Barbaro L., van Halder I., Vetillard F., Nezan J. **2008** Life-history traits indicate bird, beetle and butterfly responses to landscape fragmentation in plantation forests. IUFRO Conference, Kamloops, British Columbia, Canada, 4-9 aout 2008 (communication orale).

Brockerhoff E., Deconchat M., **Barbaro L.,** Paul T., Luecht S., Muir J., Henley D. **2008** Effects of land cover on indigenous forest birds in Canterbury, New Zealand. IUFRO Conference, Kamloops, Canada, 4-9 aout 2008 (communication orale).

van Halder I., **Barbaro L.,** Jactel H. **2008** Quel est lôintérêt dôéchantillonner les lisières pour évaluer la diversité des papillons de jour en forêt de plantation ? 3èmes Rencontres du Groupe des Entomologistes Forestiers Francophones, Bedoin, 27 mars 2008 (communication orale).

Giffard B., Corcket E., **Barbaro L**., Jactel H. **2008** Impact des oiseaux insectivores et du couvert arboré sur les variations d'herbivorie lors de la régénération des essences feuillues. Colloque ECOVEG 4, Rennes, mars 2008 (communication orale).

Brockerhoff E., Deconchat M., **Barbaro L.,** Luecht S., Muir J., Henley D. **2007** Effects of land cover type on indigenous forest birds in Canterbury. New Zealand Ecological Society Conference, novembre 2007, Christchurch, New Zealand (communication orale).

Deconchat M., **Barbaro L.,** Brockerhoff E. **2007** Les plantations exotiques peuvent-elles favoriser la conservation des oiseaux forestiers indigènes dans des paysages fragmentés de Nouvelle Zélande ? 4èmes Journées dôEcologie du Paysage IALE France, INRA Toulouse, novembre 2007 (communication orale).

Barbaro L., Couzi L., Nezan J., Vetillard F., Bretagnolle V. **2007** Complémentation entre habitats à lôéchelle du paysage pour la Huppe fasciée (*Upupa epops*) en forêt de plantation. 4èmes Journées dôEcologie du Paysage IALE France, INRA Toulouse, novembre 2007 (communication orale).

Barbaro L., Corcket E., van Halder I., Burlett R., Witte I., Vetillard F. **2007** Réponse des plantes vasculaires, des papillons de jour, des coléoptères carabiques et des oiseaux nicheurs au microclimat en forêt de plantation. Colloque ECOVEG 3, Bordeaux, mars 2007 (communication affichée).

Barbaro L., Couzi L., Nezan J., Vetillard F., Bretagnolle V. **2006** Rôle fonctionnel et conservation de la Huppe fasciée *Upupa epops* en forêt des Landes de Gascogne. 3èmes Rencontres Naturalistes de la LPO Aquitaine, Belin-Beliet, juin 2006 (communication orale).

Jactel H., **Barbaro L.,** Brockerhoff E. **2006** Contribution of plantation forests to biodiversity conservation: the landscape perspective. IUFRO Conference, Ecosystem goods and services from planted forests, Bilbao, October 2006 (communication orale).

Jactel H., **Barbaro L.,** van Halder I. **2006** Vers des indicateurs dõhabitat pour la biodiversité des forêts ? Séminaire Indicateurs de Biodiversité Forestière, GIP ECOFOR, Paris, mai 2006 (communication orale).

van Halder I., **Barbaro L.,** Corcket E., Jactel H. **2006** Butterfly diversity in pine plantation landscapes. IUFRO Conference, Ecosystem goods and services from planted forests, Bilbao, October 2006 (comm. orale).

van Halder I., Jactel H., **Barbaro L.,** Corcket E., Vetillard F**. 2006** Towards indirect, management oriented indicators for biodiversity in plantation forests. IUFRO Conference, Indicators for sustainable forest management in cultivated forests, Porto, 11-13 December 2006 (communication orale).

Barbaro L., Dupuich M., Corcket E., van Halder I., Witte I., Burlett R., Vetillard F., Brunet Y. **2005** Approche multi-taxa des relations microclimat-biodiversité en forêt de plantation. Colloque ECCO, Programme National coordonné ANR, 5-7 Dec. 2005, Météo France, Toulouse, France (communication affichée).

Barbaro L., Vetillard F., Nezan, J., Sin F. **2005** The scale-dependent effect of spatial heterogeneity on biodiversity in pine plantation landscapes. IUFRO Conference, Biodiversity and conservation biology in plantation forests, 26-29 April 2005, Bordeaux, France (communication orale).

van Halder I., **Barbaro L.,** Lugot A., Jactel H. **2005** Butterfly community structure in maritime pine plantation landscapes. IUFRO Conference, Biodiversity and conservation biology in plantation forests, 26-29 April 2005, Bordeaux, France (communication affichée).

Jactel H., Rossi J.P., **Barbaro L**., Piou D., Vetillard F., Barthelemy B., Menassieu P. **2004** Landscape diversity reduces processionary moth infestations in pine plantations. IUFRO Conference, Forest diversity and resistance to native and exotic pest insects, 10-13 August 2004, Hanmer Springs, New Zealand (communication orale).

Barbaro L. **2003** Bird and ground-beetle diversity along the sand deposition gradient in south-western French coastal dunes. Workshop IMPACS, Integrated Management of Pressures Affecting Coastal Sand Dunes, Carcans, 19-22 June 2003 (communication orale).

Jactel H., **Barbaro L. 2003** Biodiversity indicators at stand and landscape scales in pine plantation forests. IUFRO Conference, Monitoring and indicators of forest biodiversity in Europe, 12-15 November 2003, Florence, Italie (communication orale).

Barbaro L., Jactel H., Tavernier A., Menassieu P., Vetillard F., Balent G., Cornic J.F., Couzi L., Goulard M., Guinberteau J., Guyon D., Lung B., Revers F., Timbal J. **2002** Les îlots de feuillus en forêt des Landes de Gascogne: effet sur la biodiversité et lõétat sanitaire des plantations de Pin maritime. Séminaire Biodiversité et Gestion Forestière, GIP Ecofor, Engref Paris, février 2002 (communication orale).

Barbaro L., Corcket E., Dutoit T., Peltier J.P. **1999** Réponses fonctionnelles des communautés de pelouses calcicoles aux facteurs agro-écologiques dans les Préalpes françaises. Journées dõEcologie Fonctionnelle, La Grande Motte, 15 au 17 mars 1999 (communication affichée).

Mémoires et rapports de recherche (20 rapports)

Barbaro L., Ouin A., Jactel H., Deconchat M., van Halder I. **2013** Biodiversité dans les lisières forestières : comment gérer les interfaces entre forêts et milieux ouverts pour la biodiversité ? Rapport final du projet Biolis, Action interrégionale Aquitaine - Midi-Pyrénées: 13 p.

Barbaro L. 2013 Linking biodiversity conservation to trophic interactions: avian and lepidopteran communities in mosaic forest landscapes. Mémoire dõHabilitation à Diriger des Recherches, Univ. de Bordeaux 1: 136 p.

Barbaro L. 2013 Evaluation de lõindicateur óDéplacement des espèces lié au changement climatiqueô de lõObservatoire National de la Biodiversité pour la Fondation pour la Recherche sur la Biodiversité, mars 2013.

Jactel H**., Barbaro L.,** Vetillard F., Nezan J., Charbonnier Y., Terraube J., van Halder I., Rigot T., Roques A., Tavares C., Branco M. **2012** Lutte biologique contre la cochenille du pin maritime *Matsucoccus feytaudi* en Corse 2009-2012. Rapport final du programme quadriennal, Lutte biologique contre la cochenille du pin maritime, Région Corse: 50 p.

Barbaro L., Terraube J., Duphil E., Deconchat M., Charbonnier Y., Ouin A., van Halder I., Corcket E., Alard D., Jactel H. **2012** Biodiversité dans les lisières forestières. Bilan scientifique du projet BIOLIS, INRA - Régions Aquitaine et Midi-Pyrénées: 25 p.

Trochard G., Blache S., **Barbaro L. 2012** La Chevêchette dõEurope *Glaucidium passerinum* sur la Réserve Biologique Intégrale des Hauts Plateaux du Vercors : bilan de trois années de recherche sur lõécologie et la biologie de lõespèce (2009-2010-2011). Rapport final LPO Drôme, ONF, Réserve Naturelle des Hauts Plateaux du Vercors: 51 p.

Barbaro L., Vetillard F., Payet K., Derouault A., Blache S. **2011** Etude de lõimpact de lõexpansion de la processionnaire sur la biodiversité interspécifique des zones néo-colonisées : avifaune prédatrice. Rapport final, ANR Urticlim, INRA Biogeco: 7 p.

Barbaro L., Jouandoudet F. **2008** Bilan préliminaire de lõinventaire des Orthoptères de la Réserve Naturelle de lõEtang de Cousseau. Rapport INRA Biogeco - RN Etang de Cousseau: 19 p.

Barbaro L. 2008 Ecologie de la recherche alimentaire de la Huppe fasciée *Upupa epops* en forêt des Landes de Gasxcogne. Bilan de programme personnel n°142, CRBPO, MNHN: 6 p.

Rossi J.P., Jactel H., van Halder I., **Barbaro L.**, Corcket E., Alard D. **2007** Indicateurs indirects de biodiversité en forêt de plantation. Rapport final, GIP ECOFOR, Les indicateurs de biodiversité en milieu forestier: 19 p.

Barbaro L. 2006 Action 3.1. Pratiques sylvicoles et diversité. In: Kremer A. (coord.), Rapport dôévaluation de lôUnité Mixte de Recherche BIOGECO, INRA -Univ. Bordeaux 1.

van Halder I., **Barbaro L.,** Corcket E., Jactel H. **2006** Rapport final du projet FORSEE. Indicateurs de biodiversité. Projet INTEREGIIIB Espace Atlantique: 24p.

Barbaro L., Brunet Y. **2005** FORMICA (FORêts, MICroclimat et Assemblages dôespèces): une approche hiérarchisée des relations entre microclimat, biodiversité et fonctionnement des paysages forestiers. Rapport dôactivité 2004-2005 du Programme National - ACI ECCO: 8 p.

Barbaro L. 2004 Critère 4: conservation et amélioration appropriées de la biodiversité dans les écosystèmes forestiers. In: Carnus J.M. (coord), GIS Observatoire des Forêts d'Aquitaine, Document d'orientations 2004-2007, INRA Pierroton: 20-23.

Jactel H., **Barbaro L. 2004** Biodiversité spécifique et fonctionnelle des îlots de feuillus en pinède de plantation (Landes de Gascogne). Rapport final du projet ISLANDES, programme Biodiversité et gestion forestière 2001-2003, GIP Ecofor: 95 p.

Barbaro L., Jactel H. **2002** Projet ISLANDES. Les îlots de feuillus en forêt des Landes de Gascogne: relations entre la biodiversité forestière et lôétat sanitaire des plantations de Pin maritime. Rapport d'étape du programme Biodiversité et gestion forestière, GIP Ecofor: 18 p.

Barbaro L. 2002 Action 3.1. Pratiques sylvicoles et diversité; Action 5.1. Conservation de la diversité. In: Kremer A. (coord.), Demande de reconnaissance d'une Unité Mixte de Recherche óDiversité Biologique des Ecosystèmes Terrestresô, INRA-Univ. Bordeaux 1: pp 56 et 61-62.

Jactel H., **Barbaro L**., Lung B., Guyon D., Timbal J., Guinberteau J. **2000** Projet ISLANDES : évaluation de la méthode des îlots de feuillus en mélange pour restaurer la biodiversité de l'écosystème simplifié de Pin maritime des Landes de Gascogne et améliorer sa résistance aux insectes ravageurs et champignons pathogènes. Projet de recherche GIP Ecofor, Biodiversité et gestion forestière, INRA Pierroton: 39 p.

Barbaro L. 1999 Dynamique agro-écologique des communautés de pelouses sèches calcicoles du Vercors méridional: application à la gestion conservatoire de la biodiversité par le pastoralisme. Thèse de Biologie, Université Joseph Fourier Grenoble 1: 185 p.

Boyer P., **Barbaro L. 1996** Passereaux nicheurs et pratiques pastorales: contribution au suivi écologique de l'Article 19 en Ariège. Ministère de lôEnvironnement, Cemagref Grenoble: 96 p.

Produits à vocation pédagogique destinés à un large public

2014 Interview dans le documentaire óDiscrète chevêchetteô, réalisation Yoann Périé, production Vue sur Terre, septembre 2013 (http://www.vuesurterre.com/)

2013 Interview dans le documentaire óLes conquérants: la processionnaire du pinô, réalisation Vincent Amouroux, production Arte-Zed, diffusion 2^{e} semestre 2013.

2010 Interview dans le film óLa biodiversité et la santé des forêtsô, INRA - Salon de lôAgriculture. (http://www7.bordeaux-aquitaine.inra.fr/layout/set/print/toute_l_actu/videos/video_biodiv_foret)

2007 Interview pour le magazine dôinformation jeunesse en Gironde óPetiôpotinô, n°11, printemps 2007.

Travaux encadrés ou co-encadrés (3 thèses, 2 post-docs, 8 masters, 6 autres)

Voinopol-Sassu J. 2013 Effect of native forest connectivity on rifleman *Acanthisitta chloris* in Banks Peninsula, New Zealand. MSc project, University of Lincoln, New Zealand (co-encadrement E. Brockerhoff).

De Lacoste N. 2013 Sélection de lôhabitat forestier de la Chevêchette dôEurope *Glaucidium passerinum* par analyse des domaines vitaux dans une Réserve Biologique Intégrale de montagne. Master 1, Ecologie, Biodiversité, Evolution, Univ. Paris Sud Orsay (co-encadrement S. Blache).

Gaüzère P. 2012 Effects of forest composition on activity and structure of bat communities. Master Pro, Biodiversité et Développement Durable, Université de Perpignan (co-encadrement Y. Charbonnier).

Barnagaud J-Y. 2012 Effets de la fragmentation des forêts natives sur lôavifaune native et exotique de Nouvelle-Zélande. Chercheur post-doctoral, INRA Pierroton.

Charbonnier Y. 2011- Diversité fonctionnelle des forêts et des communautés de chiroptères et dôoiseaux insectivores sur un gradient latitudinal en Europe. Thèse de doctorat en cours (co-direction H. Jactel).

Terraube J. 2011 Réponses de lôavifaune aux lisières forestières dans des paysages fragmentés. Chercheur post-doctoral, INRA Pierroton.

Derouault A. 2009 Comparaison des communautés dôoiseaux insectivores sur des gradients dôexpansion en latitude et en altitude processionnaire du pin. Contrat dôIngénieur de Recherches, ANR Urticlim.

Giffard B. 2008-2011 Rôle des interactions tri-trophiques complexes dans la régénération dôessences feuillues. Thèse de doctorat soutenue le 3/10/2011 (co-direction E. Corcket et H. Jactel).

Payet K. 2008 Analyse quantitative de la structure et de la composition des paysages forestiers sur le versant Nord-Ouest du Mont Ventoux. Contrat dôIngénieur de Recherches, ANR Urticlim.

Giffard B. 2007 La prédation par les oiseaux sur les insectes herbivores : effets indirects sur la régénération dôespèces feuillues. Master 2, Univ. Bordeaux 1 (co-encadrement E. Corcket).

Nezan J. 2006 Etude par radiopistage des domaines vitaux et des sites de recherche alimentaire de huppes fasciées en forêt de plantation. Contrat dôIngénieur de Recherches, ANR ECCO.

van Halder I. 2005- Effets de la connectivité fonctionnelle des paysages de plantations de pin maritime sur la biodiversité des lépidoptères rhopalocères associés aux îlots de feuillus. Thèse de doctorat en cours, suspendue pour recrutement professionnel (co-direction H. Jactel).

Dupuich M. 2005 Distribution spatiale et effet des lisières sur les déplacements de deux coléoptères carabiques (Coleoptera Carabidae) en forêt landaise. Master 2, Univ. Bordeaux 1.

Grillon X. 2004 Protocole du premier inventaire araignées de la Réserve Naturelle de l'Etang de Cousseau (Lacanau-Gironde). Stage de DESS, RN Etang de Cousseau, SEPANSO (co-encadrement A. Plichon).

Sin F. 2004 Relations spatiales prédateur-proie en forêt de plantation: la huppe fasciée *Upupa epops* et la processionnaire du pin *T. pityocampa* dans les Landes de Gascogne. Master 1, Univ. Bordeaux 1.

Le Mouel S. 2003 Cartographie numérique dôun paysage forestier hétérogène: le bassin-versant du Tagon en Gironde. Contrat dôIngénieur de Recherches, ANR Ecologie Quantitative.

Claudel L. 2003 Ecologie et gestion conservatoire d'un papillon menacé *Coenonympha oedippus* à la Réserve Naturelle de l'Etang de Cousseau (Gironde). Stage volontaire, RN Etang de Cousseau-Univ. Bordeaux 1 (co-encadrement B. Touzard).

Pontcharraud L. 2002 Structure du paysage et biodiversité en forêt landaise. Stage de DESS SIGMA, ENSAT-Univ. Toulouse Le Mirail (co-encadrement D. Guyon).

Vetillard F. 2001 Des feuillus au secours des résineux: projet de restauration de la biodiversité par lôimplantation de feuillus dans la forêt monospécifique des Landes de Gascogne. Stage de BTSA GPN, (co-encadrement H. Jactel).

Jurys et comités de thèses

Jurys de thèse et de diplômes EPHE

Miguet P. 2013 Influence of crop heterogeneity in farmlands on population dynamics and distribution, CNRS Chizé, INRA AMAP (dir. V. Bretagnolle & C. Gaucherel, déc. 2013)

Haquart A. 2013 Référentiel dôactivité des chiroptères : éléments pour lôinterprétation des dénombrements de chiroptères avec les méthodes acoustiques en zone méditerranéenne française. Diplôme Ecole Pratique des Hautes Etudes, Univ. Montpellier 2 (dir. C. Kerbiriou, J.F. Julien et A. Besnard).

Gillis H. 2011 Changement global et dynamique de sélection dôhabitat de reproduction dôun oiseau nichant au sol: cas du busard cendré en milieu agricole intensif. Thèse de Doctorat, Univ. Pierre et Marie Curie, CNRS Chizé (dir. V. Bretagnolle).

Giffard B. 2011 Rôle des interactions tri-trophiques complexes dans la régénération dôessences feuillues. Thèse de Doctorat, Univ. de Bordeaux (dir. H. Jactel, E. Corcket et L. Barbaro).

Avon C. 2010 Influences de la composition et de la structure actuelles de la mosaïque paysagère sur la diversité de la flore en forêt. Thèse de Doctorat, Univ. dôOrléans (dir. J.L. Dupouey et L. Bergès).

Debras J.F. 2007 Rôles fonctionnels des haies dans la régulation des ravageurs: le cas du psylle *Cacopsylla pyri* L. dans les vergers du sud-est de la France. Thèse de Doctorat, Univ. dôAvignon (dir. T. Dutoit et R. Rieux).

Blache S. 2005 La Chevêche *Athene noctua* en zone d'agriculture intensive: habitat, alimentation, reproduction. Diplôme Ecole Pratique des Hautes Etudes, Univ. Montpellier 2 (dir. M. Thévenot).

Richard E. 2004 Conversion en futaie régulière et diversité des Coléoptères carabiques: aspects méthodologiques et réponse des communautés. Thèse de Doctorat, Engref Paris (dir. F. Gosselin).

Principaux projets scientifiques

2013-2017 - BIO-THAW, Modeling Biodiversity and land use interactions under changing glacial water availability in Tropical High Andean Wetlands, IRD - Fondation pour la Recherche sur la Biodiversité

2013-2015 - LEVANA, Influence de lôorganisation des paysages agricoles sur la distribution, la stabilité et la dispersion des papillons, programme DIVA 3 Agriculture et Biodiversité

2012-2014 - Restauration écologique en zone humide fluviatile fortement dégradée: l'Ile de Raymond en basse Garonne (Gironde), FRB Stratégie Nationale pour la Biodiversité 2011-2020

2011-2014 - FunDivEUROPE, Functional significance of forest biodiversity in Europe, Programme FP7, Union Européenne
2011-2013 - BILISSE, Biodiversité et services écosystémiques dans les lisières forestières, GIP ECOFOR (coordinateur de WP)
2011-2012 - BIOLIS, Biodiversité dans les lisières forestières, Action inter-régionale Aquitaine-Midi-Pyrénées (coordinateur)
2010-2013 - Lutte biologique contre la cochenille du pin maritime en Corse, Région Corse (coordinateur de WP)
2008-2011 - URTICLIM, Anticipation des effets du changement climatique sur l'impact écologique, sanitaire et social d'insectes forestiers urticants, ANR Biodiversité (coordinateur de WP)
2006-2007 - Indicateurs indirects de biodiversité en forêt de plantation, GIP Ecofor programme BGF
2005-2008 - Ecologie et adaptation des insectes phytophages et gestion de leurs populations, ANR ECOGER
2005-2008 - Ecologie de la recherche alimentaire de la huppe fasciée, programme personnel CRBPO-MNHN
2005-2006 - FORMICA, Forêts, microclimat et assemblages d'espèces, ANR ECCO - PNBC (coordinateur)
2004-2006 - FORSEE, Indicateurs de gestion durable des forêts, INTERREG III A
2002-2003 - Spatialisation et dynamique des processus écologiques à l'échelle de paysages forestiers hétérogènes, ACI Ecologie Quantitative (co-coordinateur)
2001-2003 - ISLANDES, Biodiversité des îlots feuillus en forêt de plantation, GIP ECOFOR (co-coordinateur)

Reviewing scientifique

Ecologie: Journal of Applied Ecology, Ecology, Journal of Animal Ecology, Journal of Biogeography, Ecography, Oikos, Plant Ecology, Biological Journal of the Linnean Society, Bird Study, Landscape and Urban Planning, Acta Oecologica, Biologia.
Entomologie et Forêt: Forest Ecology and Management, Biological Control, Agricultural and Forest Entomology, European Journal of Forest Research, Annals of Forest Science, Revue Forestière Française.

Activités d'enseignement

Master 2 Recherche Fonctionnement des Ecosysytèmes Terrestres, Université Bordeaux 1, UE Interactions biotiques : óPrédation et insectivorie avienneô

Activités administratives et expertises

Evaluation de lôindicateur óDéplacement des espèces lié au changement climatiqueô de lôObservatoire National de la Biodiversité pour la FRB (Fondation pour la Recherche sur la Biodiversité) en 2013
Présentation du bilan scientifique óConservation de la biodiversitéô devant la commission dôévaluation de lôUMR Biogeco par lôAERES en novembre 2009
Correspondant INRA pour lôentretien des collections entomologiques cédées à la Société Linnéenne de Bordeaux (Musée dôHistoire Naturelle de Bordeaux) par lôINRA Bordeaux
Responsable du groupe de travail AQR óDocumentationô de lôUMR Biogeco
Participation à la rédaction du rapport dôévaluation et du projet quadriennal de lôUMR Biogeco en 2006 et 2009
Participation au groupe de travail óBiodiversitéô du GIS Observatoire des Forêts d'Aquitaine et à la rédaction du document d'orientations 2004-2007

Participation à des comités scientifiques

Membre du Conseil Scientifique du Conservatoire Régional Espaces Naturels dôAquitaine
Membre du Comité dôHomologation Régional des observations dôoiseaux rares en Aquitaine
Co-organisateur des 3èmes Rencontres Naturalistes organisées par la LPO Aquitaine en juin 2006

Qualifications complémentaires

Stage de formation du CNRS Chizé óModélisation spatio-temporelle et utilisation des SIG dans les études d'écologie évolutiveô - novembre 2001
Stages de formation du Muséum National d'Histoire Naturelle (CRBPO) óTechniques de capture, de manipulation et de mesures biométriques d'oiseauxô - avril 2001, sept. 2003, aout 2005
Stage de formation GIP Ecofor ï Irstea óAtelier de formation aux statistiques bayésiennesô - décembre 2012

1ère partie :

Introduction générale

Astronomy was a respected science long before ecology, and Copernicus and Galileo never moved a star.

Robert MacArthur. - Geographical ecology.

1.1. Préambule

Mon parcours de recherche se situe à l'interface de la **biogéographie et de l'écologie des communautés**, dont j'ai progressivement assimilé les concepts et les outils au cours de ma formation universitaire initiale de géographe jusqu'à mon doctorat sur les communautés végétales prairiales de montagne. Depuis une dizaine d'années, mes recherches se sont peu à peu centrées sur le **rôle de l'hétérogénéité des mosaïques paysagères dans la conservation de la biodiversité multi-taxonomique** dans les forêts de plantation. Le niveau d'organisation du paysage s'est naturellement avéré comme le plus pertinent pour aborder des questions relevant à la fois de la biogéographie de la conservation et de l'écologie des communautés. J'ai ainsi travaillé, souvent dans le cadre de collaborations, sur plusieurs taxa de vertébrés et d'arthropodes prédateurs (araignées, coléoptères carabiques, chiroptères), mais tout particulièrement sur les oiseaux insectivores et les lépidoptères herbivores, dans une perspective finalisée **de contrôle biologique des insectes ravageurs forestiers par conservation de la diversité** des ennemis naturels.

Le présent travail s'organise en trois parties, comprenant d'abord une introduction des concepts et des méthodes essentiels à la compréhension des patrons et des processus écologiques étudiés. L'introduction générale de ce mémoire présente le contexte théorique et méthodologique dans lequel mes recherches se situent : une **approche hiérarchique multi-niveaux d'organisation** des systèmes écologiques, une approche des mosaïques paysagères comme des **continuums d'habitats** plutôt que des fragments isolés dans une matrice de non-habitat, et une utilisation des **guildes trophiques et des traits d'histoire de vie** des espèces comme des facteurs explicatifs de la réponse des communautés à la structure et à la composition des habitats. La diversité fonctionnelle des communautés permet en effet de relier des questions d'écologie de la conservation à des questions de fonction de la biodiversité dans les paysages forestiers, et de **services écosystémiques rendus par les oiseaux insectivores** en forêt de production. Cependant, les changements globaux placent ces interactions trophiques entre oiseaux et lépidoptères dans un climat d'incertitude rendant nécessaire l'utilisation de concepts et méthodes issus de la **biogéographie évolutive et de l'écologie expérimentale**, notamment des outils spécifiques d'analyse des données, qui sont détaillés dans la deuxième partie de l'introduction générale.

Cette introduction est suivie d'une sélection de travaux publiés depuis 2007, rédigés pour une grande partie en collaboration avec les doctorants que j'ai encadrés durant cette période. Ces travaux s'intéressent d'abord aux **réponses multi-échelles des communautés d'oiseaux et de lépidoptères** à l'hétérogénéité et à la fragmentation des paysages forestiers, puis aux **interactions trophiques entre oiseaux prédateurs et lépidoptères proies** vues comme un élément structurant les réponses des espèces à cette hétérogénéité. Enfin, une discussion générale synthétise les principales contributions de mes travaux à la construction de ce lien entre conservation de la diversité et fonction des communautés d'oiseaux, tout en dessinant mes perspectives de recherche future autour de trois questions structurantes : (1) la compréhension des mécanismes sous-tendant les patrons de **réponses des oiseaux forestiers aux méso- et macro-échelles**, (2) l'analyse de la relation existant entre **magnitude de l'insectivorie et métriques de diversité fonctionnelle** des communautés et (3) la question plus finalisée de la complémentarité fonctionnelle des taxa prédateurs pour assurer un **contrôle biologique durable dans les mosaïques de paysages** dominées par la forêt.

1.2. Introduction : diversité, échelles et processus

1.2.1. Une approche multi-niveaux des systèmes écologiques

La complexité naissant des interactions entre niveaux hiérarchiques dôorganisation dans lôespace et dans le temps est une composante essentielle des systèmes écologiques (Allen & Starr 1982, Larrère & Larrère 1997). Les patrons et les processus sont intrinsèquement liés en écologie du paysage, et cette relation est dépendante du niveau dôorganisation et de lôéchelle spatiale et temporelle considérés (Burel & Baudry 1999, Whittaker et al. 2005). Lôhétérogenéité spatio-temporelle des systèmes écologiques nécessite des approches multi-niveaux dôorganisation tenant compte de facteurs explicatifs emboîtés agissant comme des ôfiltres écologiquesô (Allen & Starr 1982, Wiens 1995, Cushman & McGarigal 2002). Les niveaux dôorganisation généralement retenus en biogéographie et en écologie du paysage correspondent à des hétérogénéités de structure à différentes échelles spatiales ou temporelles (Tews et al. 2004, Schweiger et al. 2005, Wu 2013). Par exemple, pour lôanalyse de la fragmentation forestière, les facteurs explicatifs peuvent être hiérarchisés aux niveaux de la parcelle, du fragment forestier et du paysage environnant le fragment (Deconchat & Balent 1996). Ce niveau du paysage à méso-échelle sôemboîte lui-même dans le niveau à macro-échelle du biome ou de la région biogéographique (Jenkins & Ricklefs 2011). A chacun de ces niveaux correspond un niveau dôorganisation de la diversité biologique (Ŭ, ɓ, ɔ) ayant chacun des ôdriversô spécifiques, environnementaux, biotiques, stochastiques et historiques (Whittaker et al. 2001, Meynard et al. 2011, Svenning et al. 2011). Le pouvoir explicatif des facteurs historiques a été globalement moins étudié que celui des facteurs environnementaux ou stochastiques (Larrère & Larrère 1997, Svenning et al. 2011). Sôils sôavèrent parfois inopérants en raison dôune absence de corrélation claire entre patterns actuels et passés (Mac Nally and Horrocks 2002, Ernoult et al. 2006), ils sont souvent essentiels dans la compréhension des dynamiques actuelles de la biodiversité dans les paysages hétérogènes (Petit et Burel 1998, Knick & Rotenberry 2000, Hermy & Verheyen 2007, Sirami et al. 2010, Bonthoux et al. 2013). Plus généralement, les approches multi-échelles en écologie du paysage permettent de mettre en évidence les facteurs responsables de la distribution des espèces et des communautés à chaque niveau dôorganisation de la biodiversité, en particulier dans les études multi-taxa (Burel et al. 1998, Cushman & McGarigal 2002, Herrando & Brotons 2002, Mac Nally et al. 2004, Bossenbroek et al. 2005, Schweiger et al. 2005, Coreau & Martin 2007, Kissling et al. 2008, Sirami et al. 2010).

Les analyses spatialement explicites permettent en particulier dôisoler la composante environnementale de la variabilité purement liée à la dimension spatiale dans la distribution des espèces et des communautés (Heikkinen et al. 2004, Legendre et al. 2005, Dormann et al. 2007, Keil et al. 2012). Une part essentielle des patrons de distribution peut sôexpliquer par les facteurs environnementaux sous-jacents aux structures spatiales mesurées à large échelle, en particulier la quantité et la distribution spatiale des habitats dans la mosaïque paysagère (Cushman & McGarigal 2002, Heikkinen et al. 2004, Knick et al. 2008, Fahrig et al. 2011, **chap. 2.1.1**). Cependant, des structures spatiales indépendantes de lôhabitat peuvent subsister, quôon attribue en général à des interactions de compétition ou dôaggrégation inter- ou intra-spécifiques, des facteurs historiques de dispersion et recolonisation dôespèces, voire des interactions hôtes-pathogènes à large échelle (Wiens 1995, Svenning et al. 2011, Ricklefs 2013). Pour une espèce donnée, on peut considérer que la persistance dôune population est déterminée par lôinteraction entre la dispersion et lôhétérogénéité spatio-temporelle de lôenvironnement (Holt 2009). La mesure de la multi-dimensionnalité de la niche écologique le long des principaux facteurs environnementaux permet alors de mieux comprendre les patrons de distribution des communautés dôespèces au sein de paysages hétérogènes dans le temps et dans lôespace (Prodon & Lebreton 1981, Balent & Courtiade 1992, Clavero & Brotons 2010, Barnagaud et al. 2012). Il sôagit alors dôanalyser dans un degré de complexité supplémentaire, comment la biodiversité est organisée dans des paysages hétérogènes et fragmentés.

1.2.2. Biodiversité dans les paysages hétérogènes

Dans les paysages terrestres, plusieurs visions de lôhétérogénéité spatiale des habitats se sont succédé historiquement selon trois principaux paradigmes : la théorie de la biogéographie des îles, celle des métapopulations, et celle du continuum dôhabitats, que nous adoptons préférentiellement dans le présent travail (MacArthur & Wilson 1967, Dunning et al. 1992, Wiens 1995, Hanski 1999, Manning et al. 2004). Selon les deux premières, les paysages sont vus de manière binaire comme des mosaïques dôhabitats et de non-habitat tandis que la troisième les considère comme des matrices dôhabitats de différentes qualités distribués en mosaïques spatialement hétérogènes (Wiens 1995, Brotons et al. 2003, Kupfer et al. 2006). Ce changement progressif de paradigme a beaucoup influencé les recherches en écologie du paysage ces dernières années, notamment en mettant lôaccent sur le lien entre fragmentation du paysage et mécanismes de sélection de lôhabitat et de mobilité des espèces. Il a également considérablement précisé la notion de fragmentation des habitats en isolant les effets inter-reliés de ses différentes composantes : la perte dôhabitat (óhabitat lossô), la fragmentation *sensu stricto* (réduction de la taille des fragments) et les effets de lisière (Fahrig 2003, Ewers & Didham 2006, Fletcher et al. 2007, **chap. 2.1.2 et 2.4.1**). Il a aussi souligné lôinfluence parfois prépondérante des processus écologiques intervenant dans la matrice paysagère sur les processus intra-fragment dôhabitat (Dunning et al. 1992, Wiens 1995, Brotons et al. 2003). Cette influence de la matrice se traduit notamment par une réduction ou une augmentation de la fréquence et de la magnitude des processus intra-fragments (Norton et al. 2000, Laurance 2002, Tscharntke et al. 2012).

Une complexité ou une hétérogénéité accrue dans les mosaïques paysagères a généralement un effet positif marqué sur la biodiversité des communautés occupant ces paysages (Balent & Courtiade 1992, Tews et al. 2004, Fahrig et al. 2011, Haslem & Bennett 2011). De plus, opérer une distinction entre hétérogénéité fonctionnelle (nombre et proportions des types dôhabitat) et hétérogénéité de configuration (arrangement spatial des types dôhabitat) permet de répondre aux interrogations sur le devenir de la biodiversité dans les paysages de production (Fahrig et al. 2011). En agissant directement sur les composantes des mosaïques paysagères, les pratiques de gestion influencent directement la dynamique des paysages hétérogènes (Balent & Courtiade 1992, Baudry et al. 2003, Benton et al. 2003, Aviron et al. 2005). La mise en évidence de mécanismes de complémentation et de supplémentation de ressources entre habitats dans les paysages en mosaïques représente un bon exemple du rôle joué par lôhétérogénéité fonctionnelle sur la persistance de certaines espèces (Dunning et al. 1992, Ouin et al. 2004, Tubelis et al. 2004, Ethier & Fahrig 2011, **chap. 2.3.1**). La présence dôéléments structurants clés (ókeystone structuresô) comme les haies, les arbres isolés, et les fragments dôhabitats semi-naturels (corridors et continuités) permet en effet dôaugmenter la connectivité, tant structurelle que fonctionnelle, dans les paysages hétérogènes (Clergeau et Burel 1997, Tews et al. 2004, Fischer et al. 2006, Haslem & Bennett 2011). Cette connectivité fonctionnelle du paysage permet dôinférer les mouvements dôune espèce donnée entre fragments dôhabitats à différentes échelles de temps, mais également les processus dôextinction et de recolonisation locale à lôorigine de la persistance des espèces dans ces fragments (Petit & Burel 1998, Hanski 1999, Boulinier et al.

2001, Baudry et al. 2003, Brotons et al. 2005, Baguette & Van Dyck 2007, Sirami et al. 2008). Nous franchissons un degré de plus dans lôanalyse de la complexité des mosaïques de paysages en nous intéressant maintenant aux interactions trophiques existant entre les espèces et les communautés occupant ces mosaïques, donc à la fonction occupée par ces espèces organisées en réseaux au sein de ces systèmes complexes.

1.2.3. Fragmentation et interactions biotiques

Le rôle structurel joué par les interactions inter-spécifiques au sein des réseaux écologiques dans la réponse des espèces et des communautés à la fragmentation des habitats a été souligné récemment (Hagen et al. 2012). La fragmentation augmente en effet la fréquence et la magnitude des processus écologiques (óhyperdynamismeô), comme les interactions biotiques (Laurance 2002). Dôautres travaux montrent que lôeffet de la fragmentation au sens strict peut être contradictoire (Fahrig 2003), voire être un facteur de stabilité des interactions biotiques à des niveaux de fragmentation intermédiaires (Cooper et al. 2012). Les interactions biotiques peuvent être également modifiées par des effets de lisières indépendants des effets de surface dans les habitats fragmentés (Ewers et al. 2013). De manière plus générale, il nôest pas établi dans quelle mesure les interactions biotiques se traduisent par des signaux macro-écologiques à large échelle (Gotelli et al. 2010, Kissling et al. 2012). Par exemple, nous manquons singulièrement de connaissances sur la manière dont les réseaux trophiques sont reliés dans lôespace (Brooks et al. 2012). Pourtant, lôabsence dôinteractions biotiques limitantes avec des compétiteurs, consommateurs ou pathogènes, la présence de ressources alimentaires localisées ou la facilitation sociale intra-spécifique peuvent influencer les relations espèces-habitats de manière significative (Ricklefs 2013). Coexistence et coévolution dôespèces en interaction forte comme les prédateurs et leurs proies, ou herbivores et plantes-hôtes, déterminent leur sélection de lôhabitat à de multiples échelles spatiales et temporelles (Morris 2003).

Lôherbivorie par les grands ongulés en forêt est par exemple régulièrement invoquée comme le facteur principal déterminant la composition de la végétation du sous-bois (Nuttle et al. 2011, Suzuki et al. 2013). Des cascades trophiques peuvent apparaître dans les écosystèmes terrestres par effet de régulation ótop-downô des prédateurs sur le niveau trophique inférieur des herbivores, en affectant indirectement le niveau des producteurs primaires (Mooney et al. 2010, Eisenberg et al. 2013). Dans les forêts tempérées, plusieurs études expérimentales ont permis de mettre en évidence de telles interactions tri-trophiques entre oiseaux insectivores, insectes herbivores et végétation (Marquis & Whelan 1994, Mäntylä et al. 2011, **chap. 2.4.2**). Des effets óbottom-upô négatifs de lôherbivorie par les grands ongulés sur les oiseaux insectivores ont aussi été démontrés, par le biais dôune modification des ressources alimentaires affectant les plantes-hôtes des insectes-proies (Nuttle et al. 2011, Chollet & Martin 2012, Eisenberg et al. 2013). La distribution des proies disponibles à large échelle peut en effet influencer celle des espèces dôoiseaux prédateurs (Bretagnolle & Gillis 2010, Aragon & Sanchez-Fernandez 2013), voire celle des communautés dôoiseaux dans leur ensemble (Jonsson et al. 2011). Lôinfluence de la disponibilité des proies est pourtant fortement dépendante, à des échelles plus fines, de deux de ses composantes que sont lôaccessibilité et la détectabilité de la ressource alimentaire (Almenar et al. 2013, **chap. 2.3.1**). Il semblerait que certains oiseaux insectivores soient néanmoins capables de prédire dans une certaine mesure cette disponibilité à lôéchelle régionale grâce à leur mobilité pendant une phase nomade post-migratoire (Barber et al. 2008) et à lôutilisation dôindices visuels (vision Ultra-Violet) et/ou olfactifs (Composés Organiques

Volatils) (Mäntylä et al. 2008). Ainsi la sélection multi-échelles de lôhabitat par les espèces et leurs assemblages est au moins en partie fonction des interactions biotiques tissées par les espèces au sein des réseaux trophiques (Hagen et al. 2012). Comme le soulignent Gotelli et al. (2010), on peut alors se demander *óà quel point du continuum spatial allant des territoires individuels aux paysages à lôéchelle continentale, la signature des interactions entre espèces cesse-t-elle dôêtre visible ?*ô

1.2.4. Traits de vie et structure du paysage

La prise en compte des traits dôhistoire de vie des espèces paraît fondamentale pour mieux comprendre la réponse des réseaux trophiques à la surface et à lôisolement des fragments dôhabitats, à la composition de la mosaïque paysagère, et aux effets de lisière entre habitats adjacents (Henle et al. 2004, Hagen et al. 2012). Lôhomogénéisation biotique et fonctionnelle à large échelle qui est observée de manière répétée dans des communautés dôespèces et des situations biogéographiques variées fait de la diversité fonctionnelle un élément majeur des études actuelles en biogéographie et écologie de la conservation (McKinney & Lockwood 1999, Clergeau et al. 2006, Devictor et al. 2008, Clavero & Brotons 2010, Clavel et al. 2011). Parmi les questions-clés de recherche sur la diversité fonctionnelle se trouvent le rôle de la complémentarité et de lôappariement des traits de vie, la redondance fonctionnelle et le conservatisme de niche, c'est-à-dire la tendance des traits de vie à rester similaires au cours du temps (Petchey & Gaston 2006, Flynn et al. 2009, Philpott et al. 2009, Wiens et al. 2010, Hagen et al. 2012). En outre, la comparaison des distributions spatiales de la diversité fonctionnelle et des diversités taxonomiques ou phylogénétiques à large échelle montre à la fois des zones de congruence et de divergence (Gaston et al. 2008, Cumming & Child 2009, Devictor et al. 2010, Meynard et al. 2011). A lôéchelle des paysages et des régions biogéographiques, les travaux qui sôintéressent à la distribution spatiale des traits de vie dans des paysages hétérogènes apportent une importante contribution à lôidentification des mécanismes sous-jacents à la distribution des espèces et des communautés (Hausner et al. 2003, Fischer et al. 2007, Fonderflick et al. 2013, Newbold et al. 2013, Samas et al. 2013, , **chap. 2.2.2**). En effet, lôappartenance à une guilde trophique donnée est souvent indicatrice de la réponse des espèces de vertébrés insectivores à la structure et à la composition du paysage (Tscharntke et al. 2008, Clough et al. 2009, Frey-Ehrenbold et al. 2013). Enfin, guildes trophiques et traits de vie sont également de bons prédicteurs de la probabilité dôoccurrence des espèces à échelle plus fine (Wells et al. 2012, **chap. 2.2.1**) et de leur capacité invasive (Blackburn et al. 2010, Allen et al. 2013).

Nous pouvons donc envisager lôexistence dôun lien étroit entre conservation de la diversité fonctionnelle et persistance de la fonction occupée par les espèces partageant certains traits dôeffets dans les communautés, comme le prédit la théorie (Jax 2005, Mason et al. 2005). Ce lien pourrait être mieux mis en lumière par une exploration approfondie des relations entre métriques de diversité fonctionnelle et rôle fonctionnel des communautés mesuré expérimentalement (Philpott et al. 2009, Laliberté & Tylianakis 2012, Butterfield & Suding 2013). Comme élément pilote des processus écosystémiques, la diversité fonctionnelle influence en effet la fonction et la résilience des systèmes écologiques (Mason et al. 2005, Fischer et al. 2007). En filtrant sélectivement le pool régional dôespèces en fonction de leurs traits de vie, la fragmentation forestière, lôintensification des usages du sol et la simplification structurelle des mosaïques paysagères réduit la diversité fonctionnelle globale, et singulièrement celle des taxa vertébrés supérieurs comme les oiseaux insectivores (Tscharntke et al. 2008, Clough et al. 2009, Najera & Simonetti 2010). Les services écosystémiques rendus par les oiseaux insectivores pourraient sôen trouver alors considérablement réduits (Whelan et al. 2008, Cumming & Child 2009, Flynn et al. 2009), en accord avec les hypothèses de ómodération de la sélection des traits fonctionnels par le paysageô et de ómodération de lôassurance spatiale et temporelle par la complexité du paysageô (Tscharntke et al. 2012). Les oiseaux remplissent en effet des services écosystémiques variés comme la pollinisation, la prédation dôinsectes ou la dispersion des semences végétales dans les écosystèmes terrestres, et lôextinction fonctionnelle locale de certains traits peut conduire à une sévère diminution de certaines fonctions (Zamora et al. 2010, Anderson et al. 2011, Wenny et al. 2011, Albrecht et al. 2012). Parmi ces services écosystémiques, le contrôle biologique des insectes ravageurs agricoles et forestiers est une importante fonction assurée par les oiseaux insectivores (Whelan et al. 2008, Sekercioglu 2012). La prédation par les oiseaux insectivores contribue à maintenir les populations dôinsectes ravageurs à des niveaux dôabondance bas, et permet de diminuer les dégâts aux productions végétales de manière significative (Mols & Visser 2002, Glen 2004, Jedlicka et al. 2011, Mäntylä et al. 2011).

1.2.5. Diversité fonctionnelle des oiseaux insectivores

La diversité fonctionnelle des communautés dôoiseaux est sans doute un facteur-clé pilotant lôintensité dôinsectivorie avienne, via la complémentarité des traits de vie au sein des assemblages dôoiseaux prédateurs (Philpott et al. 2009, Barbaro & Battisti 2011). En particulier, lôéquitabilité fonctionnelle des prédateurs pourrait jouer un rôle majeur dans lôintensité de prédation par les oiseaux et la réduction associée des dégâts dôinsectes (Mason et al. 2005, Hillebrand et al. 2008, Crowder et al. 2010). Certaines espèces dôoiseaux seraient ainsi des óinsectivores fonctionnelsô assurant une régulation biologique efficace dans les agro-ecosystèmes (Jones et al. 2005, Jedlicka et al. 2011, Sinu 2011). Cette efficacité repose sur la densité-dépendance des relations entre oiseaux insectivores prédateurs et insectes herbivores proies, qui sont souvent des lépidoptères dans les habitats agricoles et forestiers tempérés (Glen 2004). Le type de réponses numérique et fonctionnelle des oiseaux insectivores à la densité des lépidoptères dépendra alors de la forme et de la magnitude de la relation prédateur-proie et du degré de spécialisation alimentaire du prédateur (Crawford & Jennings 1989, Abrams & Ginzburg 2000, Klemola et al. 2002, Dupuy et al. 2009, **chap. 2.3**).

Le rôle évolutif majeur joué par la prédation avienne sur les Lépidoptères forestiers est connu de longue date (Buckner 1967, Dempster 1983, Holmes 1990). Les passereaux insectivores utilisent une gamme dôindices visuels et olfactifs pour localiser leurs proies, comme la vision Ultra-Violet et les Composés Organiques Volatils émis par les plantes attaquées par les insectes herbivores (Mäntylä et al. 2008). Ils sôassocient aussi en groupes mixtes de recherche alimentaire (ómixed-species foraging flocksô) permettant dôaugmenter lôefficacité de cette recherche (Forsman et al. 2009, Sinu 2011). Lôintensité de óforagingô et dôinsectivorie dépendent également de la structure et de la composition du paysage, en particulier du niveau de fragmentation forestière et des effets de lisière entre forêts et milieux ouverts (Brotons & Herrando 2003, Gonzalez-Gomez et al. 2006, Skoczylas et al. 2007, **chap. 2.4.1**). Lôefficacité de la prédation avienne sur les insectes herbivores est de lôordre de 20 à 100% selon les études (Crawford & Jennings 1989, Battisti et al. 2000, Mols & Visser 2002, Glen 2004). Un tel service de prédation rendu par les oiseaux insectivores nôen rend que plus crucial la conservation de communautés dôoiseaux en équilibre fonctionnel, dôautant que le nombre total dôoiseaux estimé nôest que de 200-300 milliards, soit 40 à 60 oiseaux pour un humain sur la planète (Gaston & Blackburn 1997).

1.3. Changements globaux et incertitude des données écologiques

1.3.1. óPatterns and processesô: lier observation et experimentation en écologie

Biogéographie et macro-écologie ont connu ces dernières décennies une accumulation de données sans précédent. Celles-ci ont permis de mettre en évidence des patrons de distribution dôespèces et de communautés de valeur presque universelle (Jenkins & Ricklefs 2011), même si beaucoup de ces patrons étaient déjà connus et décrits, par exemple par Robert MacArthur, dès les années 60 (Brown 1999). Cependant, les progrès dans la compréhension des mécanismes sous-jacents à ces patrons de distribution, et de manière plus générale à lôétablissement de lois à valeur générale en écologie, sont encore minces, faisant de ces patrons ódes puzzles agaçantsô, selon lôexpression de James H. Brown (Brown 1999, McGill & Nekola 2010). Ceci explique sans doute la quête presque obsessionnelle pour les mécanismes que manifestent beaucoup dôécologues et de biogéographes confrontés à la complexité de leur discipline (McGill & Nekola 2010). En effet, même si les échelles macro-écologiques sont généralement considérées comme trop larges pour pouvoir expérimenter, écologie du paysage et biogéographie de la conservation ont également besoin dôapproches plus expérimentales (Whittaker et al. 2005, Jenerette & Shen 2012, Tscharntke et al. 2012), couplées à des méthodes dôéchantillonnage et dôanalyse des données permettant de contrôler différents facteurs explicatifs emboîtés, hiérarchisés ou colinéaires (Cushman & McGarigal 2002, Legendre et al. 2005, Fletcher et al. 2007, Svenning et al. 2011).

Lôexpérimentation en écologie du paysage peut en particulier être utilisée pour 1) identifier la structure des paysages ; 2) identifier la variation des processus écologiques au sein de différents paysages ; 3) identifier la sensibilité des processus à la structure des paysages ; et 4) identifier les facteurs à lôorigine de la formation des patrons paysagers (Jenerette & Shen 2012, voir aussi Tscharntke et al. 2012). Lôabsence de prise en compte des processus écologiques sous-tendant les patrons dôoccurrence dôespèces, par exemple dans la construction des modèles de distribution dôespèces (óspecies distribution modelsô) peut conduire à un faible pouvoir prédictif de ces modèles, notamment en situation de non-équilibre entre disponibilité de lôhabitat favorable et patrons dôoccurrence dôune espèce donnée (Brotons et al. 2012, Kissling et al. 2012). Lier observation et expérimentation aux échelles multiples de lôécologie du paysage et de la biogéographie est donc un challenge important pour permettre de répondre aux principales hypothèses soulevées par ces disciplines (Tscharntke et al. 2012).

1.3.2. Un climat dôincertitude

Le changement global tel quôil est mesuré actuellement place les écosystèmes terrestres dans un climat dôincertitude accru (Whittaker et al. 2005, Berggren et al. 2009). Intensification des modes dôoccupation du sol, homogénéisation biotique à lôéchelle de paysages ou régions, urbanisation, reboisement ou déforestation à larges échelles, invasions dôespèces et réchauffement climatique ont un impact profond et durable sur la biodiversité (Clergeau et al. 2006, Didham et al. 2007, Flynn et al. 2009, Brockerhoff et al. 2010, Clavel et al. 2011, Clavero et al. 2011, Pautasso et al. 2011, Jongsomjit et al. 2013, Pawson et al. 2013). Ce dernier est au centre des préoccupations en matière de conservation depuis plus dôune décennie, en raison de la difficulté à conserver des espèces sous un climat qui ne leur conviendrait plus dans le futur (Huntley et al. 2008, Settele et al. 2008). Il y a en effet une coïncidence entre rareté des espèces et rareté des conditions climatiques dans lesquelles elles évoluent (Ohlemüller et al. 2008), et cette relation est encore renforcée par la nécessaire coïncidence entre espèces et leurs plantes-hôtes, par exemple pour les lépidoptères (Schweiger et al. 2008). De fait, une des conséquences les moins prédictibles et pourtant les plus importantes du changement climatique est l’impact à moyen et long terme sur les interactions biotiques comme les relations plantes-insectes et prédateur-proie (Preston et al. 2008, Bretagnolle & Gillis 2010). Si l’effet des interactions entre niche d’habitat et niche climatique sur la réponse au réchauffement commence à être connu (Warren et al. 2001, Schweiger et al. 2008, Clavero et al. 2011, Pe’er et al. 2011, Barnagaud et al. 2012, Jongsomjit et al. 2013), une incertitude considérable subsiste sur l’évolution des interactions inter-spécifiques dans un tel contexte (Berggren et al. 2009, Bretagnolle and Gillis 2010, Auer & Martin 2013).

En particulier, des disparités spatiales et temporelles entre prédateurs et proies pourraient affecter l’efficacité de la régulation biologique dans les paysages de production (Thomson et al. 2010, Visser et al. 2012). Ces disparités auront également des conséquences pour la conservation des espèces les plus sensibles au changement climatique, comme les passereaux migrateurs trans-sahariens (Gordo et al. 2005, Both et al. 2010, Salido et al. 2012). Une augmentation de la fréquence et de la magnitude des pullulations d’insectes défoliateurs est aussi une conséquence probable de ces disparités spatio-temporelles entre prédateurs et leurs proies (Klemola et al. 2002, Klapwijk et al. 2012), même si les prédateurs généralistes peuvent dans une certaine mesure suivre rapidement l’expansion de leurs proies (Dupuy et al. 2009, Kaunisto et al. 2012). Couplées à une augmentation de la mortalité des arbres forestiers par sècheresses répétées, ces pullulations accrues d’insectes herbivores et xylophages auront un rôle fonctionnel clé en affectant la dynamique des perturbations en forêt et ses conséquences, positives et négatives, sur la biodiversité (Müller et al. 2008, Klapwijk et al. 2012). Les effets en cascade du changement global sur les réseaux trophiques se traduisent aussi par des déclins trans-continentaux à large échelle pour les passereaux insectivores forestiers soumis à l’importante augmentation des populations d’ongulés sauvages et à ses conséquences sur la végétation (Nuttle et al. 2011, Chollet & Martin 2012, Auer & Martin 2013). Un tel climat d’incertitude risque en outre d’avoir des conséquences évolutives importantes sur les populations de passereaux insectivores confrontées à des disparités phénologiques et spatiales avec leurs insectes-proies (Salido et al. 2012, Visser et al. 2012).

1.3.3. Apports de la biogéographie évolutive

En effet, en agissant sélectivement sur les traits de vie des espèces, le changement global risque de modifier à long terme la coexistence d’espèces actuellement en équilibre. Les traits associés à la tolérance thermique, les modes d’utilisation des ressources, la phénologie et la dispersion sont les plus significativement influents sur les aires de distribution géographique des espèces (Carnicer et al. 2012). Pour les oiseaux, la productivité (taille des pontes) a par exemple été modifiée en une centaine d’années, entre l’aire de distribution native et l’aire d’introduction de certains passereaux (Samas et al. 2013). Un autre trait susceptible d’être modifié par le réchauffement climatique est la phénologie de la reproduction (Visser et al. 2012). Si la désynchronisation phénologique entre les oiseaux et leurs proies a une valeur adaptative, les conséquences évolutives pourraient être une sélection pour une plus petite taille des œufs ou des adultes, même si la plasticité phénotypique peut aussi réduire cette désynchronisation (Charmantier et al. 2008, Visser et al. 2012). Le récent intérêt pour le conservatisme de niche, c'est-à-dire la tendance de beaucoup de traits écologiques à rester similaires au cours du temps, a mis en évidence son rôle important en biogéographie évolutive (Holt 2009, Wiens et al. 2010, Strubbe et al. 2013). Le conservatisme de niche peut par exemple être associé à un déclin démographique à long terme (Lavergne et al. 2012), ou conduire les espèces exotiques à nôoccuper quôune partie de lôhabitat disponible dans leur aire dôintroduction (Brockerhoff et al. 2010, Strubbe et al. 2013). Dôautre part, les traits adaptatifs définissent aussi les limites dôaires de distribution (Carnicer et al. 2012), et les caractéristiques écologiques des populations en limite dôaire climatique peuvent différer de celles qui occupent le cœur de lôaire de distribution (Hampe & Petit 2005, Hargrove & Rotenberry 2011, Peôer et al. 2011).

Un nouvel indice mesurant les préférences thermiques des communautés (CTI : Community Thermal Index) a permis de quantifier la ódette climatiqueô des communautés dôoiseaux et de Lépidoptères en Europe sur la période 1990-2008 (Clavero et al. 2011, Devictor et al. 2012). Il apparaît que la capacité de dispersion des espèces est un trait fonctionnel majeur pour expliquer les patrons de distribution dôespèces, les dynamiques dôextinction-colonisation locales et les tendances dôévolution à long terme des communautés (Boulinier et al 2001, Holt 2009, Carnicer et al. 2012, Stevens et al. 2012). Les traits de dispersion sont en outre corrélés à dôautres traits comme la fécondité, la spécialisation écologique et la taille des individus (Brotons et al. 2005, Samways & Lu 2007, Stevens et al. 2012) et déterminent la réponse des espèces à la fragmentation des habitats, par le biais de la connectivité du paysage (Petit & Burel 1998, Warren et al. 2001, Hanski 1999, Henle et al. 2004, Baguette & Van Dyck 2007, Gil-Tena et al. 2013). Enfin, un dernier trait déterminant les dynamiques évolutives de la biodiversité est lôorigine biogéographique des espèces, en particulier leur caractère natif ou exotique. Les introductions et invasions dôespèces permettent de tester des hypothèses sur le conservatisme de niche (Wiens et al. 2010, Strubbe et al. 2013), les traits de vie prédicteurs du succès dôétablissement (Blackburn et al. 2010, Allen et al. 2013), lôimpact des espèces exotiques sur la distribution des prédateurs natifs (Barber et al. 2008, Cameron & Bayne 2012), ou la conservation et la restauration des habitats et des services écosystémiques (Simberloff et al. 2013). Les chevauchements de niche et les réponses différentielles des espèces natives et exotiques aux mosaïques dôhabitats ont par contre été peu explorés jusquôà présent (Lugo et al. 2012, Strubbe et al. 2013) et sont des pistes de recherche particulièrement intéressantes pour le futur tant les espèces invasives peuvent être des actrices majeures du changement global (Didham et al. 2007).

1.3.4. De nouvelles méthodes pour de nouvelles données

Dans un environnement rendu de plus en plus incertain par les changements globaux, la question de la fiabilité et de la robustesse des données écologiques se pose avec une acuité accrue (Yoccoz et al. 2001). Plusieurs champs de recherches méthodologiques ont connu un développement important depuis une quinzaine dôannées en écologie des communautés, en particulier les questions dôéchantillonnage et de détectabilité des espèces (Buckland 2006, Alldredge et al. 2007), dôautomatisation de la collection de données (Dray et al. 2010, Rempel et al. 2013), de qualité des prédicteurs écologiques dans un contexte de gestion conservatoire (du Bus de Warnaffe & Dufrêne 2004), et dôutilisation de base de données de sciences citoyennes pour le monitoring de la biodiversité (Snäll et al. 2011, Bonter & Cooper 2012). Les communautés dôoiseaux et de papillons sont fréquemment échantillonnées par points dôécoute ou transects linéaires, dont la durée, la longueur ou la distance de détection ont été discutées (Blondel et al. 1981, Pollard & Yates 1993, Bibby et al. 2000, Buckland 2006, Bonthoux & Balent 2012, Pellet et al. 2012). Cependant, les biais dôestimation dôabondance ou de densité sont importants, en partie à cause de la mobilité des individus mais également à cause dôeffets dus à lôobservateur, lôespèce, les conditions météorologiques ou lôhabitat

(MacKenzie et al. 2002, Buckland 2006, Alldredge et al. 2007, Kéry 2010, Archaux et al. 2012). Des méthodes de correction basées sur la probabilité de détection, ódistance samplingô, double comptage ou observations répétées, ont donc été proposées et sont souvent intégrées aux modèles statistiques dôanalyse des données (Boulinier et al. 2001, Alldredge et al. 2007, Thomas et al. 2010, Pellet et al. 2012). Les méthodes permettant dôintégrer les probabilités de détection incluent par exemple lôutilisation de covariables en modèles linéaires généralisés, les modèles N-mixture ou les méthodes de Capture-Marquage-Recapture spatialisées (Archaux et al. 2012).

Dôune manière générale, les designs dôanalyse des données hiérarchisées sont adaptés à lôanalyse de la complexité des données en écologie des communautés et en biogéographie (Cushman & McGarigal 2002, du Bus de Warnaffe & Dufrêne 2004, Svenning et al. 2011, Pasher et al. 2013). Côest particulièrement le cas des inférences multi-modèles basées sur la sélection des meilleurs modèles prédictifs par lôAkaike Information Criterion (Burnham & Anderson 2002, Grueber et al. 2011). Des dispositifs dôanalyses emboîtées, incluant des mesures répétées dans le temps ou dans lôespace, sont notamment permises par lôutilisation de modèles mixtes et de lôinférence bayésienne (Bolker et al. 2009, Zuur et al. 2009, Kéry 2010). Des données autocorrélées dans lôespace ou dans le temps sont particulièrement fréquentes en biogéographie et en écologie (Legendre et al. 2005, Dormann et al. 2007), en particulier dans le cas des données radio-télémétriques (Calenge 2006, Dray et al. 2010). Si une majorité de ces données peut être analysée par des modèles linéaires mixtes, généralisés (GLMMs) ou additifs (GAMMs), la sélection de modèle en GLMM se situe encore à la frontière de lôart et de la science (Bolker et al. 2009, Zuur et al. 2009). Lôincertitude des données écologiques doit donc assez naturellement être accompagnée de méthodes permettant de tenir compte de biais potentiels dans la construction de modèles prédictifs (Yoccoz et al. 2001, Archaux et al. 2012), comme côest le cas des óspecies distribution modelsô (Brotons et al. 2012). Ainsi, lôutilisation en pleine expansion de larges jeux de données issus des sciences citoyennes (Snäll et al. 2011, Bonter & Cooper 2012, Jiguet et al. 2012) ou de dispositifs automatisés dôenregistrements acoustiques (Blumstein et al. 2011, Gasc et al. 2013, Rempel et al. 2013) ou télémétriques (Calenge 2006, Dray et al. 2010), devra être nécessairement entourée des précautions méthodologiques assurant la robustesse des analyses et des conclusions qui en seront tirées (Yoccoz et al. 2001).

1.4. Questions de recherche et structure du rapport

Le présent rapport est structuré sous la forme dôune sélection de huit publications parues dans des revues internationales dôécologie depuis 2007. Elles ont été rédigées par lôauteur (5 publications) ou en collaboration avec deux doctorants, Inge van Halder et Brice Giffard (3 publications) co-encadrés avec Hervé Jactel et Emmanuel Corcket. Ces publications sont organisées en deux grandes parties sôintéressant dôabord aux réponses multi-échelles des communautés de lépidoptères et dôoiseaux à la fragmentation et à lôhétérogénéité des paysages forestiers (4 publications), puis à la mise en évidence des interactions trophiques entre oiseaux et lépidoptères forestiers vues comme un facteur explicatif important de ces réponses multi-échelles (4 publications). Les questions et hypothèses de recherche sont détaillées spécifiquement dans chaque chapitre de la 2$^{\text{ème}}$ partie mais elles peuvent être synthétisées comme suit :

(1) quels sont les rôles respectifs de la composition et la fragmentation de lôhabitat forestier sur les communautés dôoiseaux et de lépidoptères dans des paysages hétérogènes ?

(2) les guildes trophiques et les traits dôhistoire de vie sont-ils de bons prédicteurs de la réponse de ces communautés à lôhétérogénéité multi-échelles de lôhabitat forestier ?

(3) quel est lôeffet de la densité dôun lépidoptère défoliateur forestier sur les réponses numériques et fonctionnelles dôoiseaux insectivores spécialistes et généralistes ?

(4) les interactions trophiques entre oiseaux insectivores et lépidoptères herbivores peuvent-elles affecter les réponses directes et indirectes des communautés dôoiseaux à la composition et à la fragmentation de lôhabitat forestier ?

Le plan de la 2^{e} partie du mémoire sôorganise donc comme suit, chaque paragraphe correspondant à une publication :

2ème partie : Diversité et fonction des communautés dôoiseaux et de lépidoptères dans les paysages forestiers fragmentés

2.1. Hétérogénéité des paysages forestiers et communautés dôoiseaux et de lépidoptères

2.1.1. Effets de la composition et de la structure du paysage sur la distribution spatiale des oiseaux et des carabiques

Barbaro L., Rossi J.P., Vetillard F., Nezan J., Jactel H. **2007** The spatial distribution of birds and carabid beetles in pine plantation forests: the role of landscape composition and structure. *Journal of Biogeography* 34: 652-664.

2.1.2. Rôle des intérieurs et des lisières dôhabitats pour les papillons des paysages forestiers fragmentés

van Halder I., **Barbaro L.,** Jactel H. **2011** Conserving butterflies in fragmented plantation forests: are edge and interior habitats equally important? *Journal of Insect Conservation* 15: 591-601.

2.2. Guildes et traits de vie : un lien entre diversité et fonction des communautés

2.2.1. Effet de la végétation environnante sur les guildes de lépidoptères herbivores

Giffard B., Jactel H., Corcket E., **Barbaro L. 2012** Influence of surrounding vegetation on insect herbivory: a matter of spatial scale and herbivore specialization. *Basic and Applied Ecology* 13: 458-465.

2.2.2. Relier les traits de vie des oiseaux, des carabiques et des papillons à la fragmentation des habitats

Barbaro L., van Halder I. **2009** Linking bird, carabid beetle and butterfly life-history traits to habitat fragmentation in mosaic landscapes. *Ecography* 32: 321-333.

2.3. Réponses numériques et fonctionnelles des oiseaux insectivores à un défoliateur forestier

2.3.1. Sélection multi-échelles de lôhabitat et écologie du foraging chez la huppe fasciée

Barbaro L., Couzi L., Bretagnolle V., Nezan J., Vetillard F. **2008** Multi-scale habitat selection and foraging ecology of the eurasian hoopoe (*Upupa epops*) in pine plantations. *Biodiversity and Conservation* 17: 1073-1087.

2.3.2. Réponses hivernales des oiseaux généralistes à un défoliateur forestier

Barbaro L., Dulaurent A.M., Payet K., Blache S., Vetillard F., Battisti A. **2013** Winter bird numerical responses to a key defoliator in mountain pine forests. *Forest Ecology and Management* 296: 90-97.

2.4. Effets directs et indirects de lôinsectivorie avienne en forêt

2.4.1. Effets de lisière et de surface sur les assemblages dôoiseaux et lôinsectivorie dans les forêts natives fragmentées

Barbaro L., Brockerhoff E., Giffard B., van Halder I. **2012** Edge and area effects on avian assemblages and insectivory in fragmented native forests. *Landscape Ecology*, 27: 1451-1463.

2.4.2. Effet indirect de la prédation par les oiseaux sur la résistance des plantules aux insectes herbivores

Giffard B., Corcket E., **Barbaro L.,** Jactel H. **2012** Bird predation enhances tree seedling resistance to insect herbivores in contrasting forest habitats. *Oecologia,* 168: 415-424.

2ème partie :

Diversité et fonction des communautés d'oiseaux et de lépidoptères dans les paysages forestiers fragmentés

2.1. Hétérogénéité des paysages forestiers et communautés d’oiseaux et de lépidoptères

2.1.1. Effets de la composition et de la structure du paysage sur la distribution spatiale des oiseaux et des carabiques en forêt de plantation

Résumé

Nous avons analysé ici les effets indépendants et conjoints de la localisation spatiale, de la composition et de la structure du paysage sur les patrons de distribution des assemblages d’oiseaux et de carabiques dans un paysage hétérogène en mosaïque, dominé par des plantations de pins. La zone d’étude est un paysage continu de 3000 ha composé de plantations de pin maritime *Pinus pinaster* de différents âges, de boisements feuillus et de milieux ouverts, situé dans la forêt des Landes de Gascogne dans le sud-ouest de la France. Nous avons échantillonné les oiseaux nicheurs par des points d’écoute de 20 minutes et les coléoptères carabiques par piège à fosse selon une grille systématique de 200 points tous les 400 m distribués sur tout le paysage. Trois jeux de variables explicatives ont été obtenus après cartographie des habitats sous SIG : (1) les variables spatiales (polynômes des coordonnées géographiques des points d’échantillonnage) ; (2) la composition du paysage (% de couvert des 6 habitats principaux) et (3) les métriques de structure du paysage, incluant des indices de fragmentation et d’hétérogénéité. Les effets indépendants et conjoints des trois jeux de prédicteurs sur l’ordination des assemblages d’espèces sont évalués par des ACC avec décomposition de la variance. Des corrélogrammes de Moran et des tests de Mantel sont utilisés pour analyser la structure spatiale des distributions d’espèces et leur relation avec les éléments du paysage. Le principal facteur expliquant la distribution des espèces à l’échelle de la maille de 400 x 400 m est la composition du paysage. Les effets indépendants des variables spatiales et de la structure du paysage sont encore significatifs pour les oiseaux une fois contrôlé l’effet de la composition, mais pas pour les carabiques. La distribution spatiale des deux taxa est influencée d’abord par la quantité de landes, jeunes plantations, parefeux et boisements feuillus. Les espèces liées aux feuillus montrent une réponse positive à la densité de lisières alors que les espèces de milieux ouverts répondent négativement à la fragmentation. L’hétérogénéité du paysage et la couverture forestière feuillue favorisent les oiseaux forestiers mais n’ont pas d’effet sur les carabiques. La fragmentation affecte négativement les oiseaux et les carabiques des milieux ouverts, la distribution des espèces spécialistes étant restreinte aux plus grandes landes et jeunes plantations. Plusieurs espèces d’oiseaux à enjeu de conservation sont associées à des mosaïques de forêts et de milieux herbacés, surtout prairies et parefeux enherbés. La conservation de la biodiversité dans les plantations de conifères dépend du maintien d’une proportion significative de milieux ouverts et d’îlots feuillus dans la mosaïque paysagère.

Abstract

Here, we aimed at evaluating the joint and independent effects of spatial location, landscape composition and landscape structure on the distribution patterns of bird and carabid beetle assemblages in a mosaic landscape dominated by pine plantation forests. The study was located in a continuous 3000-ha landscape mosaic with native maritime pine *Pinus pinaster* plantations of different ages, deciduous woodlands and open habitats, located in the Landes de Gascogne forest of south-western France. We sampled breeding birds by 20-min point counts and carabid beetles by pitfall trapping using a systematic grid-sampling of 200 points every 400 m over the whole landscape. Explanatory variables were composed of three data sets derived from G.I.S. habitat mapping: (i) spatial variables (polynomial terms of geographical coordinates of samples), (ii) landscape composition as the percentage cover of the six main habitats, and (iii) landscape structure metrics including fragmentation and spatial heterogeneity indices. We used Canonical Correspondence Analysis with variance partitioning to evaluate the joint and independent effects of the three sets of variables on the ordination of species assemblages. Moranôs I correlograms and Mantel tests were used to assess for spatial structure in species distribution and relationships with separate landscape attributes. Landscape composition was the main factor explaining the distribution patterns of birds and carabids at the meso-scale of 400 x 400 m. Independent effects of spatial variables and landscape structure were still significant for bird assemblages once landscape composition was controlled for, but not for carabid assemblages. Spatial distribution of birds and carabids were primarily influenced by the amount of heathlands, young pine plantations, herbaceous firebreaks and deciduous woodlands. Deciduous woodland species had positive responses to edge density, while open habitat species were positively associated with mean patch area. Forest birds were favoured by an increase in deciduous woodland cover and landscape heterogeneity, but there was no evidence for a similar effect on carabid beetles. Fragmentation of open habitats negatively affected both early-successional birds and carabids, specialist species being restricted to large heathlands and young plantations. Several birds of conservation concern were associated with mosaics of woodlands and grasslands, especially meadows and firebreaks. Conserving biodiversity in mosaic plantation landscapes could be achieved by the maintenance of a significant amount of early-successional habitats and deciduous woodland patches within a conifer plantation matrix.

Introduction

Depending on scale, the spatial patterns observed in biogeography can be caused by multiple factors. At the continental or regional scale, geomorphological and bioclimatic processes lead to the appearance of gradients and patchy structures, and landscape-scale heterogeneity is dependent on those non-random larger-scale processes (Allen & Starr, 1982). At the local-scale, micro-environmental and biotic interactions are the most important factors explaining species distribution patterns, especially within-community richness (Whittaker et al., 2001). At the landscape-scale, abiotic factors such as topography, geology or microclimate interact strongly with biotic and human processes such as land use and disturbance regimes, resulting in complex spatial patterns of species occurrence that may be difficult to relate to simple explanatory factors. However, the landscape level is the most relevant scale at which both conservation programmes and the sustainable management of human-piloted ecological systems is practiced (Wiens, 1995). In landscapes dominated by even-aged plantation forests submitted to frequent clear-cutting, biodiversity is expected to be a function of spatial heterogeneity created by the mosaic of stands of different age, structure and composition (Tews et al., 2004). In such heterogeneous mosaics, assessing the effects of matrix composition on biodiversity is best achieved when studying simultaneously several taxonomic groups that respond to different spatial scales, such as birds and insects (Mac Nally et al., 2004; Bossenbroek et al., 2005).

Understanding how landscape composition and structure influence the spatial patterns of species distributions requires the use of methods that take into account both spatial autocorrelation in the data sets and collinearity between explanatory variables (Heikkinen et al., 2004). Including the spatial structure in the modelling of species-environment relationships allows better predictions of species occurrence (Legendre & Legendre, 1998). It also allows one to distinguish when spatial structure is due mainly to biotic interactions, to an underlying unmeasured environmental factor or to a common spatial gradient shared by species data and environmental variables (Borcard et al., 1992). Previous studies have used Canonical Correspondence Analysis with variation partitioning to separate between confounding effects of space and environmental variation (Hobson et al., 2000; Heikkinen et al., 2004; Titeux et al., 2004; Legendre et al., 2005). Several authors have also separated between the effects of plot-, patch- and landscape-level variables using a multiple-scale hierarchical framework (Saab, 1999; Cushman & McGarigal, 2002; Herrando & Brotons, 2002; Miller et al., 2004; Bossenbroek et al., 2005).

The importance of distinguishing between the effects of landscape composition, as the relative amounts of each habitat type within the landscape mosaic, and landscape structure, as the physical layout of elements within the landscape, was underlined by Dunning et al. (1992). For bird communities, most studies have pointed out a greater effect of landscape composition than landscape structure or configuration, including patch shape, patch isolation and habitat fragmentation (Trzcinski et al., 1999; Drapeau et al., 2000; Cushman & McGarigal, 2002).

The type of landscape matrix surrounding a patch can mitigate the negative effect of habitat isolation for a given species, according to its degree of matrix habitat use (Sisk et al., 1997; Estades & Temple, 1999; Norton et al., 2000; Herrando & Brotons, 2002; Lindenmayer et al., 2002). In the case of farmland birds, the occurrence of rare, residual habitats can be the most important factor at the landscape-scale (Berg, 2002; Fuller et al., 2004). Two recent studies also suggest that matrix composition has a direct influence on post-disturbance colonization (Brotons et al., 2005) and responses to habitat fragmentation among different landscapes (Watson et al., 2005). For carabid beetles, habitat type is the most important factor explaining the distribution patterns of species at the regional and landscape scales (Dufrêne, 1992; Aviron et al., 2005; Eyre et al., 2005), but carabid assemblages are mainly affected by micro-habitat variation and biotic interactions at smaller scales (Niemelä et al., 1992; Antvogel & Bonn, 2001; Thomas et al., 2001; Brose, 2003). However, studies involving different arthropod taxa in agricultural landscapes suggest that species occurrence in habitat patches and movements between patches are influenced by surrounding matrix composition at the landscape-scale (Dauber et al., 2003; Duelli & Obrist, 2003; Weibull et al., 2003; Purtauf et al., 2005).

The aim of this study was to determine the joint and independent effects of spatial location, landscape composition and landscape structure on the distribution patterns of birds and carabid beetles in a 3000-ha landscape sampled with a grid of 400 x 400-m sized squares. We used an intermediate scale between macro-scale, where biogeographical factors are expected to be predominant, and micro-scale where local conditions may influence the spatial distribution of species (Whittaker et al., 2001). Firstly, we decomposed the joint and independent variation in the distribution of species assemblages explained by geographical location of samples, landscape composition and landscape structure using Canonical Correspondence Analysis with variation partitioning (Cushman & McGarigal, 2002; Heikkinen et al., 2004; Legendre et al., 2005). Secondly, we tested for the presence of spatial structure in individual species abundances and examined their correlations with particular attributes of landscape composition and structure using Moranôs I correlograms and Mantel tests (Leduc et al., 1992; Legendre & Legendre, 1998; Judas et al., 2002). We adressed the following questions: (i) is there a spatial structure in the distribution of species assemblages at the landscape-scale; (ii) what are the joint and independent effects of geographical location, landscape composition and landscape structure on species assemblages; and (iii) can individual species distributions be related to particular landscape composition and structure variables?

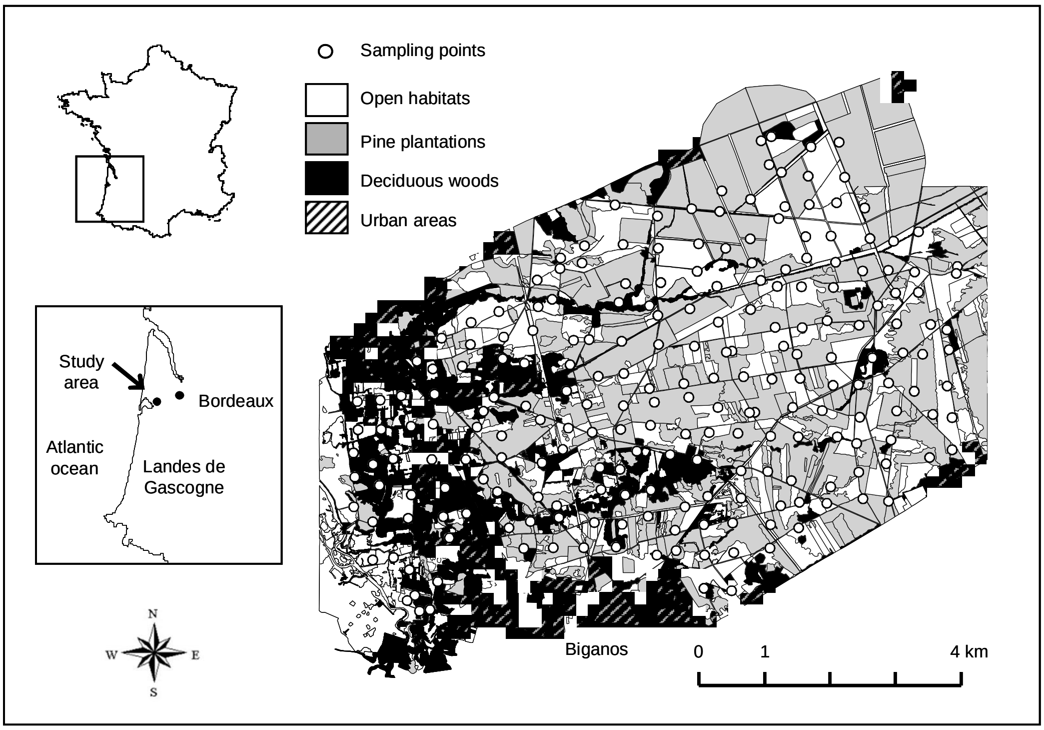


Fig. 1 Location map of the study area showing the grid of 200 sampling points.

Methods

Study area

The study area is located in south-western France in the Landes de Gascogne region, where an intensive plantation forest of native maritime pine *Pinus pinaster* covers ca 10,000 km^2. We selected a landscape of 3216 ha in size gathering the catchment areas of two small rivers (Tagon and Aiguemorte, 44°40ôN, 0°57ôE), adjacent to the Arcachon basin (Fig. 1). The climate is thermo-atlantic (mean annual temperature: 12°C; mean annual rainfall: 700 mm) and the elevation is low (ca 50 m a.s.l.). Soils are mostly podzols established on a sandy substrate (Maizeret, 2005). The eastern part of the area is dominated by a mosaic of maritime pine plantations of different ages, together with clearcuts, heathlands dominated by *Molinia caerulea, Pteridium aquilinum, Ulex europaeus, Erica cinerea, E. scoparia* and *Calluna vulgaris*, meadows and herbaceous linear firebreaks, deciduous forest patches dominated by *Quercus robur, Q. pyrenaica* and *Betula pendula* and linear riparian forest along streams with *Alnus glutinosa* and *Salix* spp. The western part includes large areas of meadows and oak woodlands that are expected to be source habitats for deciduous woodland species (Fig. 1).

Bird and carabid sampling

The overall landscape was divided into 200 squares of 16 ha in size (400 m x 400 m). We used a distance of 400 m between sampling points (Weibull et al., 2003), for three reasons: (i) it is a priori close to the grain size (mean patch area) of the studied landscape; (ii) it is above the auditory detection distance for most bird species sampled by point-counts; and (iii) it is also well above the distance of interaction between pitfall traps for the sampling of carabid beetles (Digweed et al., 1995). In each square, we established the sampling point for birds and carabid beetles as close as possible to the centre of the square (Fig. 1). Bird assemblages were sampled by the point-count method with two visits (Bibby et al., 2000) from early April to mid-May (first visit) and from mid-May to the end of June (second visit) in 2002-2003. Two observers performed the surveys and permutated first and second visits for a given point to avoid a possible observer effect. We recorded all birds heard and seen within the square during 20 min (Drapeau et al., 2000), using a semi-quantitative abundance index where a territorial male or pair was noted as 1 and a non-singing bird was noted as 0.5 (Norton et al., 2000). The final abundance index was the maximum score obtained for each species among the two visits. Point-counts were performed within 5 h after sunrise and rainy days were excluded. During the count, we mapped the virtual position of each individual bird around the observer to avoid double-counting. Carabid beetles were sampled with the pitfall trap method (Digweed et al., 1995). A systematic grid of 200 traps was established at the same locations as the bird point-counts from early spring to late autumn in 2002-2003. We used glass traps with a 9-cm diameter opening and a volume of 500-mL, levelled to the soil surface and covered with wood plates supported by four nails to protect traps from rain. We used a solution of quaternary ammonium diluted at 25% to fill the traps because it is a good preserving fluid even during the high summer evaporation period. Traps were collected every three weeks and carabid beetles were identified to the species level back in the laboratory. We pooled all individuals captured during the overall period in a given trap for further analyses.

Landscape and spatial variables

The study area was mapped using the GIS ArcView 3.2 (ESRI, Redlands, CA, USA) to obtain for each sampling point three sets of spatial, landscape composition and landscape structure variables. The first set of explanatory variables was composed of five spatial variables: geographical coordinates of the 200 sampling points (x, y) and their squares and cross product terms (x, y, x^2, y^2, xy) (Wartenberg, 1985). We did not include the cubic terms as proposed by Borcard et al. (1992) to keep a comparable number of factors for the three explanatory data sets. Habitat mapping was performed using colour aerial orthophotographs at the scale 1:25000 (Institut Géographique National, June 2000). Habitat type was assigned to each landscape patch according to the following classification, based on structural attributes identified by photo-interpretation and validated by field observation: herbaceous firebreak, heathland, young pine plantation (trees <7 m), mature pine plantation (trees >7 m), deciduous woodland and meadow. To calculate the percentage cover of each habitat and the landscape metrics, circular buffered areas of 400-m radius were established around each of the 200 sampling points (Dauber et al., 2003). We used a radius of 400 m (mean distance between sampling points) in order to minimize the spatial overlap between two adjacent buffered areas and consequently to avoid high redundancy of landscape attributes for two close samples. This distance also offered a compromise between the response scale of vertebrate taxa such as birds and invertebrate taxa such as carabid beetles (Barbaro et al., 2005). In preliminary analyses, we also tested the same variables calculated for 200-m radius buffers, but intra-set correlations between variables and species were always higher for the distance of 400 m. In the same buffered areas, we calculated a set of landscape metrics using a raster version of FRAGSTATS 3.3, with a cell size of 2.5 m (McGarigal et al., 2002). We selected the following landscape metrics according to previous studies (Heikkinen et al., 2004): edge density (i.e., total length of all edges between all habitat patches, in m.ha-1), mean patch area (in ha), landscape heterogeneity (measured by Shannon index) and mean shape index (mean of all patch shape indices measured as a ratio of perimeter on area of the patch). As we hypothesized an effect of increasing deciduous woodland cover from the east to the west of the study area, we also calculated the distance to the nearest deciduous wood from each sampling point.

Variance partitioning

For each taxon (birds and carabids), we first performed a direct ordination method, Canonical Correspondence Analysis (CCA), to evaluate the part of variation in species assemblages that can be explained by the total effect of the three sets of explanatory variables (Legendre & Legendre, 1998). Second, we used partial CCA with variation partitioning to decompose the variance explained by the independent and joint effects of spatial variables, habitat cover and landscape structure (Borcard et al., 1992; Anderson & Gribble, 1998; Heikkinen et al., 2004; Legendre et al., 2005). The significance of each separate analysis was assessed with Monte-Carlo permutation tests (2000 permutations) on the total variance explained by each set of explanatory variables, i.e., the percentage ratio of total inertia of each CCA on total inertia of unconstrained CA. To perform partial CCA, we used ADE-4 software by J. Thioulouse, D. Chessel and S. Dolédec, University Lyon 1, 2004.

In the case of three sets of explanatory variables, the total explained variance can be partitioned into seven fractions (see below): a, independent effect of habitat cover; b, independent effect of landscape structure; c, independent effect of spatial variables; d, joint effect of habitat and structure; e, joint effect of habitat and space; f, joint effect of structure and space; and g, joint effect of the three sets of variables (Heikkinen et al., 2004). For each taxon, we performed a set of CCA and partial CCA in three steps: (i) CCA of the separate effects of the three explanatory data sets: six variables of habitat cover, five variables of landscape structure and five spatial variables; (ii) partial CCA of the independent effect of habitat cover with landscape structure and spatial variables as covariables (fraction a), independent effect of landscape structure with habitat cover and spatial variables as covariables (fraction b) and independent effect of spatial variables with habitat cover and landscape structure as covariables (fraction c); (iii) partial CCA with elimination of the effect of habitat cover, i.e., the joint effect of landscape structure and spatial variables with habitat cover as covariable (fraction b + c + f), with elimination of the effect of landscape structure (fraction a + c + e), and with elimination of the effect of spatial variables (fraction a + b + d). We used the following equations for the calculations of fractions d, e, f, and g (Anderson & Gribble, 1998; Heikkinen et al., 2004):

$$d = (a + b + d) - (a + b)$$

$$e = (a + c + e) - (a + c)$$

$$f = (b + c + f) - (b + c)$$

$$g = (d + e + g) - (d + e) = (d + f + g) - (d + f) = (e + f + g) - (e + f)$$

Spatial statistics

The description of spatial structure (i.e., gradients, patchy structures or random distributions) and the degree of spatial autocorrelation in single species abundance and landscape variables were assessed by means of Moran's I correlograms (Legendre & Legendre, 1998). We calculate Moran's I value for 15 equidistant lags of 400 m (mean distance between two sampling points). A correlogram was considered significant when Moran's I was significant at the Bonferonni-corrected probability level $\alpha = 0.05/15 = 0.0033$ for at least one distance lag, according to a Monte-Carlo test with 1000 permutations. Mantel tests on distance matrices were used as non-parametric tests of association between single species abundance and separate landscape attributes (Legendre & Legendre, 1998). The method is based on distance matrices that contain all the pairwise distances between sampling locations. For species abundance data, Euclidean distances can be used to calculate distance matrices (Leduc et al., 1992). No transformation was applied to bird species abundance because we used a semi-quantitative index ranging from 0 to 5, but we log(x+1)-transformed the number of carabid beetles to normalize the data distribution (Judas et al., 2002). For landscape variables, we used square-root transformation for the distance to the nearest deciduous wood. The statistical significance for Mantel tests were assessed by Monte-Carlo tests with 1000 permutations, using the Bonferonni-corrected level of $\alpha = 0.05/10 = 0.005$.

Results

Ordination of species assemblages

We recorded a total number of 76 breeding bird species and 59 carabid beetle species in the 200 sampling points of the study area. After eliminating the rare species occurring in less than five samples for birds and three samples for carabids, species data sets were composed of 53 bird species and 36 carabid beetle species. The total variance explained by the CCA of the three sets of explanatory variables (16 factors) was 24.3% for breeding bird assemblages and 21.4% for carabid beetles, both significant at $P < 0.001$ (Monte-Carlo test with 2000 permutations). The first ordination axis for bird assemblages (Fig. 2) was a decreasing gradient from heterogeneous and fragmented landscape mosaics (Shannon index = -0.59; edge density = -0.58) to less fragmented mosaics dominated by heathlands (mean patch area = 0.62; heathlands = 0.65) along a south-north geographic gradient (latitude = 0.63). The second axis was a woodland composition gradient from landscapes dominated by mature pines (-0.86) to landscapes dominated by deciduous woods (0.63). Bird assemblages of heathland-dominated sites were composed of species requiring large areas of open grassy and shrubby habitats: skylark *Alauda arvensis*, red-backed shrike *Lanius collurio*, linnet *Carduelis cannabina*, cirl bunting *Emberiza cirlus*, grasshopper warbler *Locustella naevia* and Dartford warbler *Sylvia undata* (Fig. 2). Redstart *Phoenicurus phoenicurus*, spotted flycatcher *Muscicapa striata*, lesser spotted woodpecker *Dendrocopos minor* and Bonelliôs warbler *Phylloscopus bonelli* were associated with deciduous wood cover, while nightjar *Caprimulgus europaeus*, crested tit *Parus cristatus* and chiffchaff *Phylloscopus collybita* typically occurred in pine-dominated mosaics (Fig. 2).

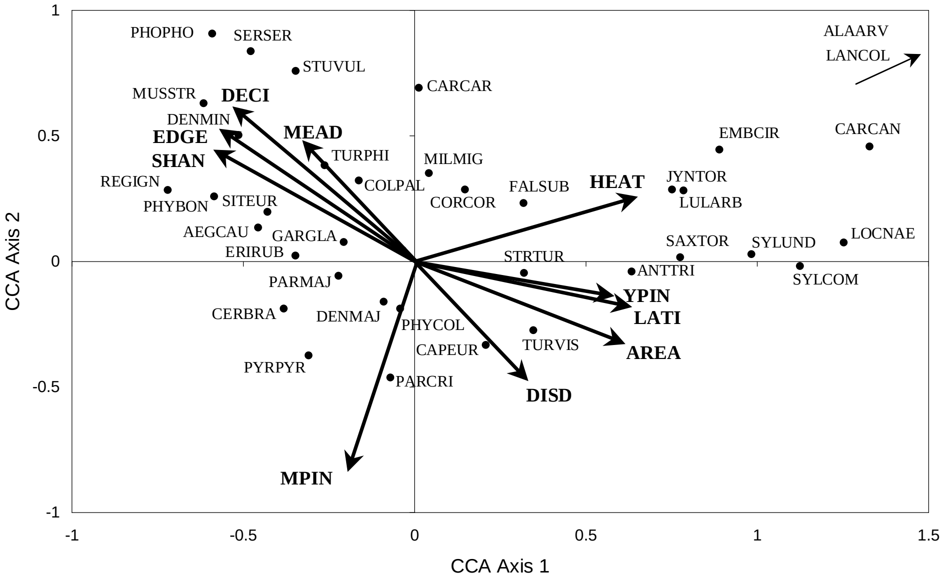


Fig. 2 CCA ordination biplot of bird assemblages and landscape attributes. Abbreviations of species use the first three letters of genus and species scientific names, as follows: CAPEUR *Caprimulgus europaeus*. Abbreviations of landscape attributes are AREA: mean patch area, DECI: deciduous wood cover, DISD: distance to the nearest deciduous wood, EDGE: edge density, FIRE: firebreak cover; HEAT: heathland cover, LATI: latitude, MEAD: meadow cover, MPIN: mature pine cover, SHAN: Shannon index, YPIN: young pine cover.

For carabid beetle assemblages (Fig. 3), the first ordination axis showed a landscape structure and composition gradient from less fragmented mosaics dominated by open habitats (firebreaks = -0.85) to more fragmented mosaics dominated by wooded habitats (edge density = 0.44; mature pines = 0.39), along the north-south geographic gradient (latitude = -0.76). The second axis was related to increasing landscape heterogeneity (Shannon index = 0.66) from homogeneous mosaics dominated by heathlands (-0.53) and distant from nearest deciduous wood (-0.47). A typical carabid assemblage with *Calathus fuscipes, C. cinctus, C. melanocephalus, Syntomus foveatus*, *Trechus quadristriatus* and *Carabus problematicus* occurred in mosaics dominated by large firebreaks, while *Platyderus ruficollis, Badister meridionalis*, *Leistus fulvibarbis*, *Nebria brevicollis*, *Notiophilus rufipes* and *Carabus purpurascens* were associated with mosaics of deciduous and pine woodlands (Fig. 3). The abundance of open-habitat species such as *Anisodactylus binotatus*, *Calathus erratus*, *Harpalus rufipalpis* and *Bembidion doris* was related to the cover of heathlands and young pine plantations.

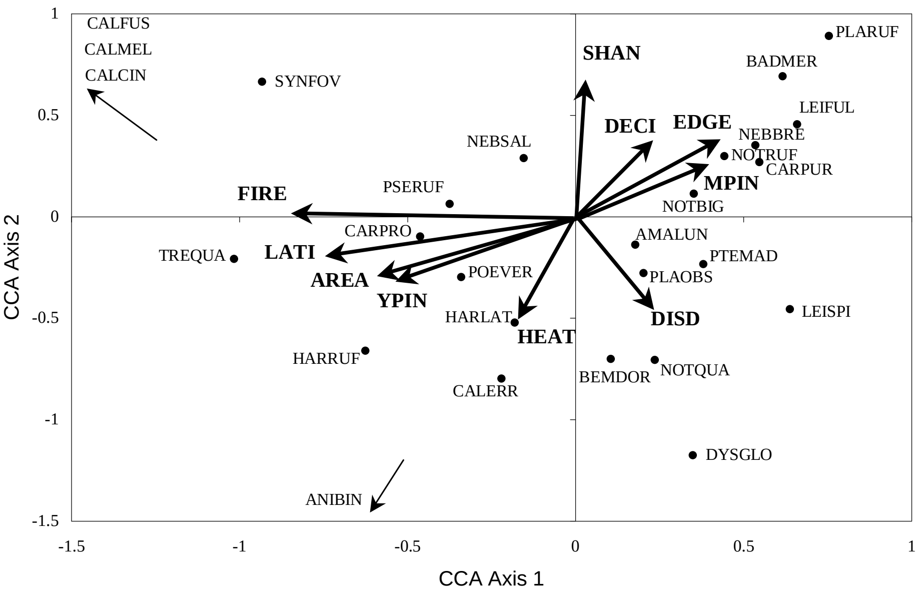


Fig. 3 CCA ordination biplot of carabid assemblages and landscape attributes. See Fig. 2 for abbreviations.

Variance partitioning for species assemblages

The decomposition of the variation explained by the three sets of explanatory variables showed that for both groups of taxa, the separate effects of landscape composition, landscape structure and spatial variables were significant at $P < 0.001$ (Monte-Carlo tests with 2000 permutations). For both groups of taxa, landscape composition explained the highest part of the variation: 16.0% for birds and 12.2% for carabids (Figs. 4 and 5). Considering the independent effects (i.e., after removing the joint effects of two other variable sets), landscape composition still explained more variation than landscape structure and spatial variables (10.1%, $P < 0.001$ for birds, 5.7 %, $P < 0.05$ for carabids). Independent effects of spatial variables (4.6%, $P < 0.001$) and landscape structure (3.3%, $P < 0.01$) were still significant for birds but not for carabids (Fig. 5). However, the joint effect of the three variable sets was higher than the independent effect of landscape structure for birds (Fig. 4). The joint effect of landscape composition and landscape structure, and the joint effect of spatial variables and landscape structure were very low for both taxa, whereas the joint effect of landscape composition and spatial variables represented a higher proportion of variation in the case of carabids (Fig. 5).

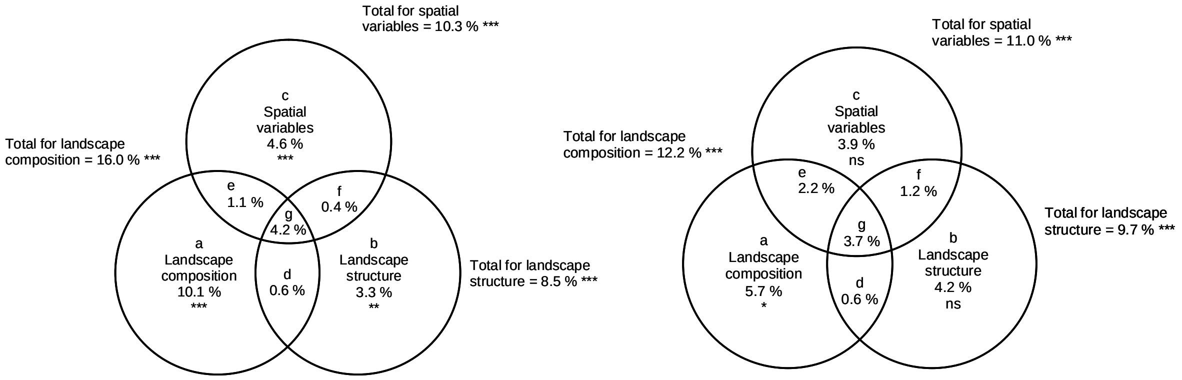


Fig. 4 et 5. Variance partitioning of total variance explained by a set of partial CCA for bird (left) and carabid (right) assemblages. Significance levels according to Monte-Carlo permutation tests with 2000 permutations: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns = non significant. The total variance explained by the three sets of explanatory variables is 24.3%*** for birds and 21.4%*** for carabids. Letters a, b, c indicate the independent effects of spatial variables, landscape composition and structure; d, e, f, g indicate the joint effects.

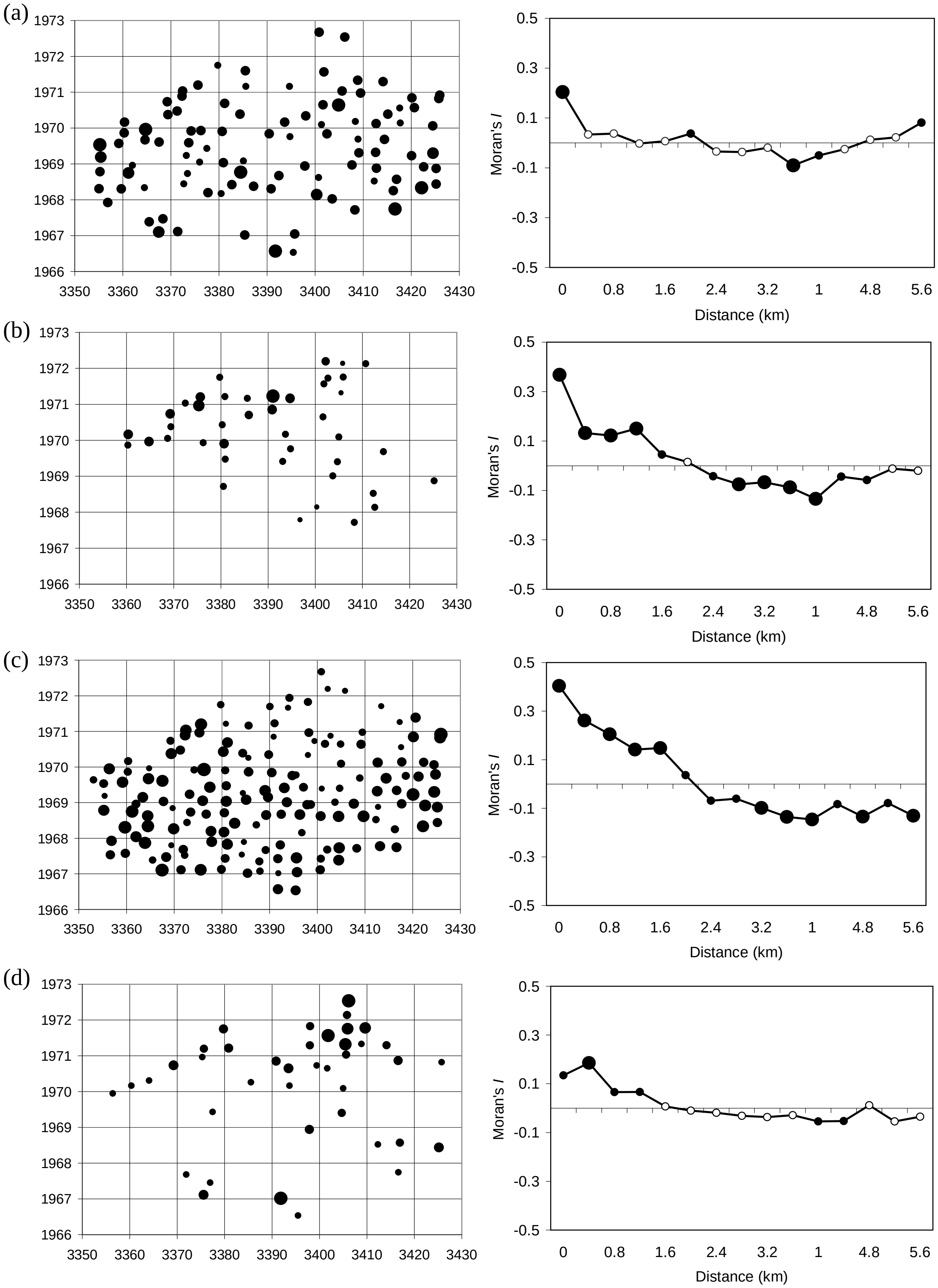


Fig. 6 Examples of abundance maps (geographical coordinates in Lambert II extended grid system) and Moranôs I correlograms for selected species of breeding birds: (a) Hoopoe *Upupa epops*, (b) Dartford warbler *Sylvia undata*; and carabid beetles: (c) *Carabus purpurascens*, and (d) *Harpalus rufipalpis*. On the maps, black dots are proportional to the abundance index ranging from 0.5 to 5 for birds and to the log-transformed number of caught individuals for carabids. The correlograms give Moranôs I coefficient for 15 equidistant lags of 400 m. Large black dots indicate a Bonferonni-corrected significance level of $P < 0.0033$, small black dots indicate a significance level of $P < 0.05$ and small white dots indicate unsignificant values, according to a Monte-Carlo test with 1000 permutations.

Species	Abbrev.	AREA	SHAN	EDGE	DISD	MEAD	FIRE	HEAT	YPIN	MPIN	DECI
Columba palumbus	COLPAL	0.013	0.008	0.100*	0.034	0.032	-0.003	-0.060	0.004	-0.040	0.117*
Streptopelia turtur	STRTUR	-0.036	-0.025	-0.050	0.024	-0.091	0.154*	-0.041	0.031	-0.008	-0.037
Upupa epops	UPUEPO	-0.039	-0.015	-0.030	-0.019	0.086*	-0.021	-0.026	-0.016	-0.002	0.001
Dendrocopos major	DENMAJ	0.011	0.015	0.083***	0.013	0.062	-0.020	-0.017	0.066	0.044	-0.019
Dendrocopos minor	DENMIN	-0.046	0.121**	0.096**	0.015	0.066	-0.006	-0.075	-0.063	0.017	0.166**
Alauda arvensis	ALAARV	0.113*	0.120**	0.007	-0.056	-0.078	0.195***	0.543***	0.185**	0.158***	-0.071
Anthus trivialis	ANTTRI	0.091**	0.051*	0.066***	0.006	-0.026	0.073*	0.229***	0.099***	0.019	0.039
Troglodytes troglodytes	TROTRO	0.056	0.043	0.053*	0.007	0.033	0.030	0.040	0.120***	0.091***	0.024
Erithacus rubecula	ERIRUB	0.048	0.054*	0.087***	0.015	0.062	-0.033	-0.028	-0.018	0.035	0.228***
Phoenicurus phoenicurus	PHOPHO	-0.046	-0.006	0.010	0.005	0.224*	-0.046	-0.067	-0.040	0.022	0.118*
Saxicola torquata	SAXTOR	0.025	0.036	0.001	-0.008	-0.076	-0.038	0.259***	0.106*	0.010	-0.036
Turdus merula	TURMER	0.073*	0.143***	0.208***	0.084*	0.161*	0.030	-0.041	0.008	0.060*	0.219***
Turdus philomelos	TURPHI	0.018	0.039	0.140***	0.042	0.043	-0.061	-0.070	-0.015	0.065*	0.304***
Turdus viscivorus	TURVIS	0.032	0.059	-0.013	-0.032	-0.090	0.153**	0.135*	-0.051	0.015	-0.075
Sylvia atricapilla	SYLATR	0.160***	0.154***	0.171***	0.087***	-0.018	0.028	0.091*	0.056	0.016	0.199***
Sylvia communis	SYLCOM	0.147***	0.089*	0.029	0.087*	-0.097	-0.014	0.211***	0.322***	0.043	-0.077
Sylvia undata	SYLUND	0.112*	-0.007	-0.007	-0.021	-0.095	-0.024	0.263***	0.076	-0.002	-0.095
Locustella naevia	LOCNAE	0.178***	0.095*	0.045	0.042	-0.087	0.016	0.257***	0.228***	0.037	-0.064
Hippolais polyglotta	HIPPOL	0.002	-0.012	-0.027	0.089**	-0.063	-0.043	-0.056	0.148***	-0.043	-0.051
Phylloscopus collybita	PHYCOL	0.025	0.016	0.029	-0.018	0.103*	0.007	0.103**	0.052	0.129***	0.063*
Muscicapa striata	MUSSTR	-0.004	0.023	0.093*	0.003	0.035	-0.030	0.001	-0.051	-0.042	0.235***
Parus caeruleus	PARCAE	0.054	0.101***	0.136***	0.112***	0.116*	-0.027	-0.049	-0.019	0.038	0.333***
Parus cristatus	PARCRI	0.002	0.049	0.053	-0.001	-0.027	-0.037	-0.041	-0.040	0.116***	-0.041
Sitta europaea	SITEUR	-0.042	0.044	0.042	0.042	0.112*	-0.057	-0.069	-0.059	-0.041	0.246***
Lanius collurio	LANCOL	0.234***	0.163***	0.052	0.028	0.010	0.251***	0.292***	0.207***	0.104*	-0.071
Corvus corone	CORCOR	0.004	0.020	0.015	0.001	0.100**	0.056*	0.021	0.038	0.048*	0.016
Garrulus glandarius	GARGLA	0.022	0.039	0.066***	0.020	0.045	-0.038	-0.041	-0.011	-0.010	0.086*
Sturnus vulgaris	STUVUL	-0.020	0.016	0.066*	-0.012	0.276***	0.089	-0.067	-0.028	0.066	0.110*
Carduelis cannabina	CARCAN	0.108*	0.069	0.008	-0.057	-0.086	0.076	0.191**	0.296***	0.172***	-0.072
Serinus serinus	SERSER	-0.034	-0.003	0.053	0.042	0.206*	-0.055	-0.045	-0.031	0.001	0.122*
Emberiza cirlus	EMBCIR	0.113*	0.027	-0.015	0.018	-0.031	0.230***	0.127*	0.116*	0.054	-0.088

Table 1 Mantel correlation coefficients between Euclidean distances of bird species abundance and landscape attributes. Significance level according to a Monte-Carlo test with 1000 permutations: *** P < 0.005 (Bonferonni-corrected); ** P < 0.01 and * P < 0.05. See Fig. 2 for the abbreviations of landscape attributes.

Species	Abbrev.	AREA	SHAN	EDGE	MEAD	FIREB	HEAT	YPINE	MPINE	DECID
Carabus purpurascens	CARPUR	0.064*	0.015	0.033*	0.042	0.106***	0.034	0.077**	0.027	-0.009
Carabus problematicus	CARPRO	0.117 *	0.025	-0.026	-0.106	0.231***	0.111*	0.032	0.028	-0.097
Carabus nemoralis	CARNEM	0.060	0.020	-0.045	-0.062	0.235***	0.236***	-0.037	-0.042	-0.089
Notiophilus rufipes	NOTRUF	0.004	0.014	0.096**	0.180**	-0.062	-0.069	-0.005	-0.014	0.094
Notiophilus biguttatus	NOTBIG	0.101*	0.073*	0.089**	0.092	-0.065	-0.080	-0.016	0.079*	0.025
Trechus quadristriatus	TREQUA	0.111*	0.077	-0.001	-0.034	0.301***	0.225**	0.011	0.043	-0.004
Pterostichus madidus	PTEMAD	0.016	0.073	0.108**	0.087	-0.039	0.106*	-0.033	-0.020	0.137**
Anisodactylus binotatus	ANIBIN	0.168*	0.178***	0.052	-0.070	0.066	0.303***	0.223***	0.142***	-0.048
Harpalus latus	HARLAT	0.155**	0.067	0.009	-0.050	0.059	-0.026	0.155***	0.060	-0.103
Harpalus rufipalpis	HARRUF	0.123*	0.092*	-0.008	-0.069	0.124*	0.291***	0.134***	0.116**	-0.085

Table 2 Mantel correlation coefficients between Euclidean distances of log-transformed abundance of carabid beetles and landscape attributes. Significance level according to a Monte-Carlo test with 1000 permutations: *** P < 0.005 (Bonferonni-corrected), ** P < 0.01 and * P < 0.05. See Fig. 2 for the abbreviations of landscape attributes. DISDEC had no significant values.

Spatial patterns in species abundances

All landscape attributes showed significant spatial autocorrelation for at least one distance lag in Moranŝ I correlograms. Shannon index and cover of deciduous woods gradually decreased from the south-west to the north-east of the study area, whereas mean patch area and cover of firebreaks and young pine plantations decreased from the north-east to the south-west. For birds, 31 species had significant correlograms at the Bonferonni-corrected level for at least one distance lag. Maps of species abundance and shape of associated correlograms pointed out three main types in spatial distribution: (i) species showing a patchy distribution across the whole landscape (e.g., hoopoe *Upupa epops*, Fig. 6a, melodious warbler *Hippolais polyglotta*), (ii) species showing a patchy distribution restricted to the south-western (e.g., wood pigeon *Columba palumbus*, Bonelliôs warbler) or the north-eastern parts of the landscape (e.g., skylark, grasshopper and Dartford warblers, Fig. 6b), and (iii) species showing gradient distributions from the south-west (e.g., blackbird *Turdus merula*, song thrush *Turdus philomelos*, blue tit *Parus caeruleus*) or the north-east (e.g., tree pipit *Anthus trivialis*, stonechat *Saxicola torquata*, whitethroat *Sylvia communis*). There was no significant autocorrelation in the abundance of several forest generalists because they were randomly distributed across the whole landscape (e.g., cuckoo *Cuculus canorus*, great spotted woodpecker *Dendrocopos major*, great tit *Parus major*, chaffinch *Fringilla coelebs*). For carabid beetles, eight species had significant Moransô I correlograms at the Bonferonni-corrected level for at least one distance lag. *Carabus purpurascens* (Fig. 6c), and *Notiophilus biguttatus* occurred in the whole landscape except the north-eastern part. *C. problematicus, C. nemoralis, Trechus quadristriatus, Anisodactylus binotatus, Harpalus latus* and *H. rufipalpis* (Fig. 6d) were rare or absent from the south-western part of the landscape and were more abundant in the northern part.

Species abundances and landscape attributes

The abundance of 31 bird species was significantly correlated with at least one landscape attribute at the uncorrected significance level, and 23 species at the Bonferonni-corrected significance level (Table 1). The abundance of 14 forest birds was correlated with deciduous wood cover, among which three were also correlated with distance to the nearest deciduous wood (blackbird, blackcap Sylvia atricapilla and blue tit). Most forest species were also correlated with edge density (wood pigeon, great and lesser spotted woodpeckers, wren *Troglodytes troglodytes*, robin *Erithacus rubecula*, blackbird, song thrush, blackcap, spotted flycatcher, blue tit and jay *Garrulus glandarius*). Four species using both deciduous woodland patches for nesting and open habitats for feeding (hoopoe, redstart, starling *Sturnus vulgaris* and serin *Serinus serinus*) were also associated with the cover of meadows, which is a rather rare habitat within the study area. Ten open habitat species had significant correlations with both heathlands and young pine plantations, except the Dartford warbler which was only associated with heathlands, and the melodious warbler with young pine plantations (Table 1). These open habitat specialists were also correlated with mean patch area, except for stonechat and melodious warbler. Firebreak cover was correlated with the abundance of six species nesting in woodlands or their edges, and feeding in grasslands: turtle dove *Streptopelia turtur*, tree pipit, mistle thrush, red-backed shrike, carrion crow *Corvus corone* and cirl bunting (Table 1). For carabid beetles, the abundance of 10 species was significantly correlated with at least one landscape attribute at the uncorrected significance level, and seven species at the Bonferonni-corrected significance level (Table 2). Three woodland carabids (*C. purpurascens, N. rufipes, N. biguttatus*) were significantly correlated with edge density but neither to deciduous wood cover nor to distance to nearest deciduous wood. *Pterostichus madidus* was the only forest species being significantly correlated with both deciduous wood cover and edge density. In addition, *N. rufipes* was correlated with the cover of meadows, and *N. biguttatus* to Shannon index and mature pine cover. Six carabids of open habitat (*C. problematicus, C. nemoralis, T. quadristriatus, A. binotatus, H. latus* and *H. rufipalpis*) were correlated with mean patch area and/or the cover of heathlands, firebreaks and young pine plantations (Table 2).

Discussion

The use of grid sampling on the same locations for two groups of taxa is an accurate method to test for spatial structure in species distribution patterns and to understand how these are shaped by landscape composition and structure. Moreover, the interest of comparing two groups of taxa is to examine whether similar trends exist among species with similar ecological preferences or life history traits, irrespective of their phylogeny (Mac Nally et al., 2004). The spatial distribution patterns of carabid beetles have been investigated at regional (Dufrêne, 1992; Eyre et al., 2005) or micro-habitat scales (Niemelä et al., 1992; Thomas et al., 2001), but less commonly at the landscape-scale (Aviron et al., 2005). Bird communities have been studied more extensively at the landscape-scale, but meso-scale studies on a large continuous area using a grid-based sampling are rare both for birds (Balent & Courtiade, 1992; Heikkinen et al., 2004; Titeux et al., 2004) and carabids (Judas et al., 2002; Holland et al., 2005). Our results suggest that spatial distribution patterns of bird and carabid species at a meso-scale of 400 x 400 m were mainly determined by landscape composition (habitat cover) rather than landscape structure or true spatial dependence. Canonical partitioning showed that 42% of the total explained variation for the ordination of bird assemblages was due to the independent effect of landscape composition, whereas the pure effects of spatial variables and landscape structure explained 19% and 14% of this total variation, respectively. For carabid beetles, 27% of the explained variation was due to the independent effect of landscape composition, which had the only pure significant effect among the three variable sets. Several authors have demonstrated that, for birds at the landscape-scale, a major part of spatial structure can be explained by environmental variation (Hobson et al., 2000; Lindenmayer et al., 2002; Titeux et al., 2004). Moreover, the effect of habitat cover is generally more important than the effect of landscape configuration or structure (Trzcinski et al., 1999; Drapeau et al., 2000; Cushman & McGarigal, 2002). At meso-scales, bird abundance is not related to landscape heterogeneity as such but depends more on the distribution patterns of important habitats, so that most of the spatial structure in bird abundance patterns can be explained by the clumping of preferred or avoided habitats (Virkkala et al., 2004). When there is a significant independent spatial effect, it can be caused by an unmeasured factor such as habitat quality, interspecific competition for food, or aggregated distributions of individual breeders (Wiens, 1995; Fuller et al., 2004). For carabid beetles, Judas et al. (2002) argued that microclimatic habitat associations scale up to meso-scale distributions within a landscape. Here, we found evidence that landscape composition had the only pure significant effect on the ordination of carabid beetles at the landscape-scale. However, as a large part of variation in carabid beetle assemblages remained unexplained, other factors involved in carabid speciesô distribution at finer scales may also have an important role at the meso-scale. These factors include microclimate, vegetation structure, prey density, predation, competition or localized oviposition sites (Niemelä et al., 1992; Antvogel & Bonn, 2001; Thomas et al., 2001; Magura, 2002; Brose, 2003).

Spatial heterogeneity and landscape matrix composition

Meso-scale spatial heterogeneity was an important factor for the ordination of bird and carabid beetle assemblages in this mosaic landscape dominated by pine plantations. Spatial heterogeneity or habitat diversity at the landscape level generally increases species richness of arthropods (Duelli & Obrist, 2003; Weibull et al., 2003) and birds (Balent & Courtiade, 1992; Titeux et al., 2004). However, species responses to spatial heterogeneity depend on the spatial scale at which heterogeneity is measured and on contrasting life history traits among species, such as home range sizes or food requirements (Wiens, 1995; Mac Nally et al., 2004; Tews et al., 2004; Aviron et al., 2005). Our results do not support the hypothesis that most species abundances are positively associated with spatial heterogeneity in the surrounding matrix. Thus, we argue that meso-scale spatial heterogeneity is not a direct factor to explain species distributions in complex landscapes but a surrogate for the occurrence of particular habitats. As pointed out by Heikkinen et al. (2004), this could be because habitat diversity indices and other landscape metrics do not take into account habitat quality. By contrast, landscape composition was the main factor for the ordination of both bird and carabid assemblages in the study area. One striking result was the importance of the amount of open habitats, especially heathlands, young pine plantations and firebreaks for both carabids and birds, although the whole landscape mosaic was largely dominated by forests. The other important habitat type was the cover of deciduous woods, especially for woodland birds. Landscape matrix composition is now considered to be a major factor to explain species occurrence within habitat patches (Wiens, 1995; Norton et al., 2000; Dauber et al., 2003; Watson et al., 2005), in contradiction with the island biogeography theory, where the area effect was considered to be predominant (Haila, 2002; Kupfer et al., 2006). However, this influence is often related to the occurrence of particular habitats, and especially semi-natural vegetation (Berg, 2002; Duelli & Obrist, 2003; Fuller et al., 2004; Purtauf et al., 2005). Habitat composition of the surrounding matrix may influence patch habitat quality (Sisk et al., 1997; Desender et al., 1999), especially the proximity to other habitats used as foraging areas (Estades & Temple, 1999; Saab, 1999). Our results suggest that some bird species used complex mosaics of habitats, because they generally bred in woodlands and foraged in adjacent grasslands, along road verges or firebreaks. Such species included turtle dove, hoopoe, mistle thrush, red-backed shrike, starling or cirl bunting, most of them having important conservation value (Virkkala et al., 2004). These species supported the habitat complementation hypothesis, which predict a need for non-substitutable resources found in two different adjacent habitats within a landscape mosaic (Dunning et al., 1992).

Fragmentation effects on woodland and open habitat species

The amount of native deciduous trees at both stand- and landscape-scale is a determining factor for the dynamics of species assemblages in conifer-dominated landscapes (Estades & Temple, 1999; Hobson et al., 2000; Norton et al., 2000; Lindenmayer et al., 2002). A geographical gradient from potential source forests can drive the spatial distribution of species within a landscape (Magura, 2002; Miller et al., 2004). We found such a spatial gradient with increasing abundance towards large deciduous woods of the western part of the landscape for many woodland birds, but such patterns were less obvious for woodland carabids, that are poor dispersers compared to birds. In addition, some bird species were restricted to oak and mixed oak-pine fragments within the study area (lesser spotted woodpecker, Bonelliôs warbler, spotted flycatcher and long-tailed tit *Aegithalos caudatus*). The abundance of some woodland birds significantly decreased with increasing distance from large deciduous forests (e.g., blackbird, blackcap and blue tit), indicating an overall negative effect of oak woodland fragmentation. The use of fragmentation variables calculated for specific habitats rather than for the whole landscape mosaic, irrespective of habitat, could have help detecting supplementary negative effects of forest fragmentation in the study area. However, fragmentation can also become a positive phenomenon, for example when food is taken outside the main breeding habitat (Dunning et al., 1992; Estades & Temple, 1999). For carabid beetles, edge effects between forests and clearcuts do not affect forest specialists (Heliölä et al., 2001) and increase species richness (Magura, 2002), but large-scale woodland fragmentation by agriculture negatively affects large forest species with low mobility (Desender et al., 1999; Aviron et al., 2005). Several authors have demonstrated that forest fragmentation can favour woodland birds because of positive edge effects (Sisk et al., 1997; Berg, 2002; Herrando & Brotons, 2002) or habitat compensation between patches (Norton et al., 2000; Lindenmayer et al., 2002). Some species may compensate for a loss of their preferred habitat by shifting to less preferred habitat types such as coniferous plantations, but these plantations may act as population sinks and ecological traps if they suffer lower reproductive success or higher mortality (Norton et al., 2000). However, regarding the relatively recent history of pine plantations in the study area, we assumed that time-lags and regional population dynamics acting at larger spatial and temporal scales may enhance or mitigate species responses to forest fragmentation.

Birds and carabid beetles specialists of open habitats were largely restricted to the largest patches of heathlands, young pine plantations and firebreaks of the north-eastern part of the landscape. As a result, species composition changed and species diversity increased when moderately large open habitats allowed early-successional specialists to penetrate into the wooded matrix of pine plantations. Such a colonization of open habitats within mosaic forests composed of different successional stages by early-successional species has been documented in boreal, temperate and Mediterranean forests for birds and carabid beetles (Gjerde & Saetersdal, 1997; Desender et al., 1999; Drapeau et al., 2000; Heliölä et al., 2001; Brotons et al., 2005). Cushman & McGarigal (2003) demonstrated that early-successional species were lost when mature forest covered more than 80% of the landscape, whereas mature forest species were still present in landscapes where mature forest was rare or absent. In the present study, most birds and carabids of open habitats had a patchy or aggregated distribution and high habitat specialization. Such species of conservation concern included woodlark *Lullula arborea*, tawny pipit *Anthus campestris*, Dartford warbler or red-backed shrike for birds; *Poecilus kugelanni, Calathus erratus, C. cinctus*, or *Harpalus neglectus* for carabids. We argue that open habitats are important to maintain at a moderate level within maritime pine plantation forests for the long-term conservation of early-successional species, which are probably relicts of the past open landscape (Barbaro et al., 2005). The maintenance of suitable open habitats within a forest matrix may enhance colonization by open habitat species after a strong disturbance such as clear-cutting (Brotons et al., 2005). As movement between habitat patches is the key process determining how the distribution of patches affects populations (Wiens, 1995), further research is needed on the mechanisms involved in the use of multiple habitats by species in mosaic landscapes, and on the importance of particular habitat combinations at the landscape-scale for the conservation of biodiversity.

References

Allen, T.F.H. & Starr, T.B. (1982) Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago.

Anderson, M.J. & Gribble, N.A. (1998) Partitioning the variation among spatial, temporal and environmental components in a multivariate data set. Australian Journal of Ecology, 23, 158-167.

Antvogel, H. & Bonn, A. (2001) Environmental parameters and microspatial distribution of insects: a case study of carabids in an alluvial forest. Ecography, 24, 470-482.

Aviron, S., Burel, F., Baudry, J. & Schermann, N. (2005) Carabid assemblages in agricultural landscapes: impacts of habitat features, landscape context at different spatial scales and farming intensity. Agriculture, Ecosystems and Environment, 108, 205-217.

Balent, G. & Courtiade, B. (1992) Modelling bird communities/landscape patterns relationships in a rural area of south-western France. Landscape Ecology, 6, 195-211.

Barbaro, L., Pontcharraud, L., Vetillard, F., Guyon, D. & Jactel, H. (2005) Comparative responses of bird, carabid, and spider assemblages to stand and landscape diversity in maritime pine plantation forests. Ecoscience, 12, 110-121.

Berg, A. (2002) Composition and diversity of bird communities in Swedish farmland-forest mosaic landscapes. Bird Study, 49, 153-165.

Bibby, C.J., Burgess, N.D., Hill, D.A. & Mustoe, S. (2000) Bird census techniques. Academic Press, London.

Borcard, D., Legendre, P. & Drapeau, P. (1992) Partialling out the spatial component of ecological variation. Ecology, 73, 1045-1055.

Bossenbroek, J.M., Wagner, H.H. & Wiens, J.A. (2005) Taxon-dependent scaling: beetles, birds and vegetation at four North American grassland sites. Landscape Ecology, 20, 675-688.

Brose, U. (2003) Bottom-up control of carabid beetle communities in early successional wetlands: mediated by vegetation structure or plant diversity? Oecologia, 135, 407-413.

Brotons, L., Pons, P. & Herrando, S. (2005) Colonization of dynamic Mediterranean landscapes: where do birds come from after fire? Journal of Biogeography, 32, 789-798.

Cushman, S.A. & McGarigal, K. (2002) Hierarchical, multi-scale decomposition of species-environment relationships. Landscape Ecology, 17, 637-646.

Cushman, S.A. & McGarigal, K. (2003) Landscape-level patterns of avian diversity in the Oregon coast range. Ecological Monographs, 73, 259-281.

Dauber, J., Hirsch, M., Simmering, D., Waldhardt, R., Otte, A. & Wolters, V. (2003) Landscape structure as an indicator of biodiversity: matrix effects on species richness. Agriculture, Ecosystems and Environment, 98, 321-329.

Desender, K., Ervynck, A. & Tack, G. (1999) Beetle diversity and historical ecology of woodlands in Flanders. Belgian Journal of Zoology, 129, 139-155.

Digweed, S.C., Currie, C.R., Carcamo, H.A. & Spence, J.R. (1995) Digging out the "digging-in effect" of pitfall traps: influences of depletion and disturbance on catches of ground beetles (Coleoptera: Carabidae). Pedobiologia, 39, 561-576.

Drapeau, P., Leduc, A., Giroux, J.F., Savard, J.P.L., Bergeron, Y. & Vickery, W.L. (2000) Landscape-scale disturbances and changes in bird communities of boreal mixed-wood forests. Ecological Monographs, 70, 423-444.

Duelli, P. & Obrist, M.K. (2003) Regional biodiversity in an agricultural landscape: the contribution of seminatural habitat islands. Basic and Applied Ecology, 4, 129-138.

Dufrêne, M. (1992) Biogéographie et écologie des communautés de Carabidae en Wallonie. PhD Thesis, Université Catholique de Louvain.

Dunning, J.B., Danielson, B.J. & Pulliam, H.R. (1992) Ecological processes that affect populations in complex landscapes. Oikos, 65, 169-175.

Estades, C.F. & Temple, S.A. (1999) Deciduous-forest bird communities in a fragmented landscape dominated by exotic pine plantations. Ecological Applications, 9, 573-585.

Eyre, M.D., Rushton, S.P., Luff, M.L. & Telfer, M.G. (2005) Investigating the relationships between the distribution of British ground beetle species (Coleoptera, Carabidae) and temperature, precipitation and altitude. Journal of Biogeography, 32, 973-983.

Fuller, R.J., Hinsley, S.A. & Swetnam, R.D. (2004) The relevance of non-farmland habitats, uncropped areas and habitat diversity to the conservation of farmland birds. Ibis, 146, 22-31.

Gjerde, I. & Saetersdal, M. (1997) Effects on avian diversity of introducing spruce Picea spp. plantations in the native pine Pinus sylvestris forests of western Norway. Biological Conservation, 79, 241-250.

Haila, Y. (2002) A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. Ecological Applications, 12, 321-334.

Heikkinen, R.K., Luoto, M., Virkkala, R. & Rainio, K. (2004) Effects of habitat cover, landscape structure and spatial variables on the abundance of birds in an agricultural-forest mosaic. Journal of Applied Ecology, 41, 824-835.

Heliölä, J., Koivula, M. & Niemelä, J. (2001) Distribution of carabid beetles (Coleoptera, Carabidae) across a boreal forest-clearcut ecotone. Conservation Biology, 15, 370-377.

Herrando, S. & Brotons, L. (2002) Forest bird diversity in Mediterranean areas affected by wildfires: a multi-scale approach. Ecography, 25, 161-172.

Hobson, K.A., Kirk, D.A. & Smith, A.R. (2000) A multivariate analysis of breeding bird species of western and central Canadian boreal forests: stand and spatial effects. Ecoscience, 7, 267-280.

Holland, J.M., Thomas, C.F.G., Birkett, T., Southway, S. & Hoaten, H. (2005) Farm-scale spatiotemporal dynamics of predatory beetles in arable crops. Journal of Applied Ecology, 42, 1140-1152.

Judas, M., Dornieden, K. & Strothmann, U. (2002) Distribution patterns of carabid beetle species at the landscape-level. Journal of Biogeography, 29, 491-508.

Kupfer, J.A., Malanson, G.P. & Franklin, S.B. (2006) Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. Global Ecology and Biogeography, 15, 8-20.

Leduc, A., Drapeau, P., Bergeron, Y. & Legendre, P. (1992) Study of spatial components of forest cover using partial Mantel tests and path-analysis. Journal of Vegetation Science, 3, 69-78.

Legendre, P. & Legendre, L. (1998) Numerical ecology. Elsevier, Amsterdam.

Legendre, P., Borcard, D. & Peres-Neto, P.R. (2005) Analyzing beta diversity: partitioning the spatial variation of community composition data. Ecological Monographs, 75, 435-450.

Lindenmayer, D.B., Cunningham, R.B., Donnelly, C.F., Nix, H. & Lindenmayer, B.D. (2002) Effects of forest fragmentation on bird assemblages in a novel landscape context. Ecological Monographs, 72, 1-18.

Magura, T. (2002) Carabids and forest edge: spatial pattern and edge effect. Forest Ecology and Management, 157, 23-37.

Maizeret, C. (2005) Les Landes de Gascogne. Delachaux et Niestlé, Paris.

McGarigal, K., Cushman, S.A., Neel, M.C. & Ene, E. (2002) FRAGSTATS: spatial pattern analysis program for categorical maps. Computer software program, University of Massachusetts, Amherst.

Mac Nally, R., Fleishman, E., Bulluck, L.P. & Betrus, C.J. (2004) Comparative influence of spatial scale on beta diversity within regional assemblages of birds and butterflies. Journal of Biogeography, 31, 917-929.

Miller, J.M., Dixon, M.D. & Turner, M.G. (2004) Response of avian communities in large-river floodplains to environmental variation at multiple scales. Ecological Applications, 14, 1394-1410.

Niemelä, J., Haila, E., Halme, E., Pajunen, T. & Puntilla, P. (1992) Small-scale heterogeneity in the spatial distribution of carabid beetles in the southern finnish taiga. Journal of Biogeography, 19, 173-181.

Norton, M.R., Hannon, S.J. & Schmiegelow, F.K.A. (2000) Fragments are not islands: patch vs landscape perspectives on songbird presence and abundance in a harvested boreal forest. Ecography, 23, 209-223.

Purtauf, T., Roschewitz, I., Dauber, J., Thies, C., Tscharntke, T. & Wolters, V. (2005) Landscape context of organic and conventional farms: influences on carabid beetle diversity. Agriculture, Ecosystems and Environment, 108, 165-174.

Saab, V. (1999) Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. Ecological Applications, 9, 135-151.

Sisk, T.D., Haddad, N.M. & Ehrlich, P.R. (1997) Bird assemblages in patchy woodlands: modeling the effects of edge and matrix habitats. Ecological Applications, 7, 1170-1180.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M. & Jeltsch, F. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography, 31, 79-92

Thomas, C.F.G., Parkinson, L., Griffiths, G.J.K., Garcia, A.F. & Marshall, E.J.P. (2001) Aggregation and temporal stability of carabid beetle distributions in field and hedgerow habitats. Journal of Applied Ecology, 38, 100-116.

Titeux, N., Dufrêne, M., Jacob, J.P., Paquay, M. & Defourny, P. (2004) Multivariate analysis of a fine-scale breeding bird atlas using a geographical information system and partial canonical correspondence analysis: environmental and spatial effects. Journal of Biogeography, 31, 1841-1856.

Trzcinski, M.K., Fahrig, L. & Merriam, G. (1999) Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. Ecological Applications, 9, 586-593.

Virkkala, R., Luoto, M. & Rainio, K. (2004) Effects of landscape composition on farmland and red-listed birds in boreal agricultural-forest mosaics. Ecography, 27, 273-284.

Wartenberg, D. (1985) Canonical trend surface analysis: a method for describing geographic patterns. Systematic Zoology, 34, 259-279.

Watson, J.E.M., Whittaker, R.J. & Freudenberger, D. (2005) Bird community responses to habitat fragmentation: how consistent are they across landscapes? Journal of Biogeography, 32, 1353-1370.

Weibull, A.C., Ostman, O. & Granqvist, A. (2003) Species richness in agroecosystems: the effect of landscape, habitat and farm management. Biodiversity and Conservation, 12, 1335-1355.

Whittaker, R.J., Willis, K.J. & Field, R. (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. Journal of Biogeography, 28, 453-470.

Wiens, J.A. (1995) Habitat fragmentation: island vs landscape perspectives on bird conservation. Ibis, 137, 97-104.

2.1.2. Rôle des intérieurs et des lisières d’habitats pour la conservation des papillons dans les paysages forestiers fragmentés

Résumé

Les effets de lisières dans les paysages forestiers tendent à augmenter avec la fragmentation par d’autres modes d’occupation du sol. Il est donc fondamental de comprendre comment les espèces répondent aux lisières pour en définir des modes de gestion adaptés. Nous avons comparé l’importance relative des habitats intérieurs et de lisières pour les papillons dans un paysage composé de plantations de pins équiennes en mosaïque avec des habitats semi-naturels. Les assemblages de papillons ont été échantillonnés dans les lisières et les intérieurs de 68 parcelles représentatives de 4 habitats : parefeux herbacés, coupes rases et jeunes plantations, plantations matures de pins et boisements feuillus. La richesse en papillons est plus grande en lisière qu’en intérieur, surtout pour les plantations de pins. La composition des assemblages diffère entre lisières et intérieurs sauf pour les parefeux. Parmi les 23 espèces dominantes, 7 espèces préfèrent les lisières, 5 les intérieurs et 11 n’ont pas de préférence significative. La présence d’une espèce donnée dans les lisières dépend de l’abondance des plantes-hôtes et nectarifères mais aussi de l’abondance de la même espèce dans l’habitat intérieur adjacent. La plupart des espèces utilisent des ressources supplémentaires ou complémentaires trouvées dans plusieurs habitats différents, par exemple des refuges micro-climatiques pour échapper aux fortes températures estivales. L’utilisation des habitats de lisières et d’intérieurs adjacents par les papillons dans de tels paysages en mosaïque souligne l’importance de l’hétérogénéité spatiale du paysage pour leur conservation.

Abstract

Edge effects are increasing in forest-dominated landscapes worldwide, due to increased fragmentation by other land uses. Understanding how species respond to edges is therefore critical to define adequate conservation measures. We compared the relative importance of interior and edge habitats for butterflies in a landscape composed of even-aged pine plantations interspersed with semi-natural habitats. Butterfly assemblages were surveyed simultaneously at the edge and the interior of 68 patches belonging to four main habitat types: herbaceous firebreaks, clearcuts and young pine stands, older pine stands, and deciduous woodlands. Butterfly species richness was higher at edges than in interior habitats, especially for pine stands. Assemblage composition differed significantly between edge and interior habitats, except for firebreaks. Of the 23 most abundant butterfly species, seven were significantly more abundant in one or all edge habitat types, five in interior habitats, and 11 species showed no edge-interior preference. Modelling the presence of individual species in edge habitats revealed the importance of habitat variables such as the abundance of nectar and host-plants, but also of the abundance of the same species in the adjacent interior habitat. Moreover, our results suggest that most species use several, different habitat types to find supplementary or complementary resources, including micro-climatic refuges to escape hot temperatures during summer. The use of adjacent edge and interior habitats by butterflies is probably a key process in such mosaic landscapes and underlines the importance of landscape heterogeneity for butterfly conservation.

Introduction

Fragmented landscapes are characterised by small habitat patches, with an exponentially increasing amount of habitat edges when patch size decreases (Fletcher 2005). The response of species to habitat edges and their subsequent dispersal behaviour is critical to our understanding of species dynamics in fragmented landscapes. Species either avoid edges, are more abundant near edges, or show no edge preference. Edge responses are species-specific and highly dependant on the type of edge encountered (Ries and Sisk 2004; Ewers and Didham 2006). The most important mechanisms that determine the individual species responses to habitat edges are the distribution of resources and the interactions between different species (Ries et al. 2004). Species that specialise on resources found only in interior habitat will generally avoid edges where habitat quality, predation risk or micro-climate are less favourable. These negative edge effects have been demonstrated for various taxa, including birds (Fletcher 2005), small mammals (Stevens and Husband 1998), herpetofauna (Lehtinen et al. 2003) and insects (Spector and Ayzama 2003), see also Ries et al. (2004) for a review. In fragmented landscapes these óinterior speciesô may be negatively affected by the higher edge to interior ratio and could, with ongoing fragmentation, become extinct as fragment size decreases. In contrast, positive edge effects on abundance of individual species have also been reported, for example for birds (Ries et al. 2004), spiders (Downie et al. 1996) and insects (Duelli et al. 2002; Ries and Sisk 2008). Species richness is often highest at habitat edges (Ewers and Didham 2006) and is thought to be caused by three mechanisms: (i) by spillover effects where individuals mix as they disperse between adjacent habitat patches, (ii) by the presence of resources at the edge that are rare or absent in adjacent patches, and (iii) by increased access to complementary resources that are located in two adjacent patches (Dunning et al. 1992; Ries and Sisk 2004). Species behaviour at edges is also an important factor that affects dispersal through the landscape. For example, edge avoidance behaviour may hinder dispersal between different patch types (Ries and Debinski 2001; Schtickzelle and Baguette 2003; Haynes and Cronin 2006), but could improve dispersal along corridors bordered by óhostileô edges (Sutcliffe and Thomas 1996; Haddad 1999).

In the present study we investigated the responses of butterflies to different edge types in a landscape dominated by pine plantation forests. The area of plantation forests is increasing worldwide and there is much debate about their role in biodiversity conservation compared to other land uses. Plantations can contribute to conservation by providing complementary and supplementary habitats and by increasing forest connectivity at the landscape scale (Brockerhoff et al. 2008). This study was conducted in Europeõs largest plantation forest, located in the south-west of France. Within this forest several internationally threatened butterfly species occur, as well in pine stands as in firebreaks with a heathland vegetation (van Halder et al. 2008). Previous studies in woodlands, along hedgerows or at field boundaries indicate that many butterfly species use the resources provided by diverse vegetation and sheltered sunny microclimatic conditions that are found at edges (Greatorex-Davies et al. 1993; Dover 1996; Dover and Sparks 2000). Butterfly diversity along woodland edges can be high, including typical forest species, edge species and grassland species (Robertson et al. 1995; Ferris and Carter 2000; Feber et al. 2001). However, studies that compare butterfly abundance between forest interiors and forest edges are rare (Ries and Sisk 2008), especially in plantation forests. Planted forests are often characterised by a high edge length (Niemela et al. 2007), but these edges are not always of high quality for biodiversity conservation. In planted forests most edges are abrupt and many edges are exposed edges along open habitats (e.g., edges of clearcuts or young stands). Within these landscapes dominated by plantation stands semi-natural habitat types, such as deciduous woodland fragments, play an important role in butterfly conservation (van Halder et al. 2008). Their edges may be of equal importance compared to plantation stand edges or may be characterized by a unique edge species assemblage.

We addressed the following questions to analyse the interior-edge patterns of butterfly diversity in pine plantation landscapes and to establish the role of edge habitats in conserving butterflies: (i) Are there differences in butterfly species richness, individual species abundance, and assemblage composition between the interior and edge of habitat patches? (ii) Do these differences depend on the type of habitat? (iii) What are the important environmental factors at the habitat and landscape scale that drive the presence of individual butterfly species in edge habitats?

Materials and methods

Study area

The study was conducted in the south-west of France in the Landes de Gascogne forest. This region is dominated by plantations of even-aged, native maritime pine *Pinus pinaster* stands that cover 1 million hectares and is the largest plantation forest in Europe. Soils are nutrient-poor, acidic podzols. Soil moisture greatly affects vegetation composition; *Molinia caerulea* dominates on wet sites, *Pteridium aquilinum* and *Ulex europaeus* in intermediate conditions, and *Calluna vulgaris* and *Erica cinerea* on dry sites. In this heavily modified landscape deciduous woodlands (along rivers, and as patches of a few hectares) and herbaceous firebreaks and powerlines (hereafter resumed as firebreaks) are the most important remnants of semi-natural vegetation. Deciduous woodlands are generally dominated by *Quercus robur* except on dry sites where *Quercus pyrenaica* occurs. Along rivers the vegetation is dominated by a mixture of *Alnus glutinosa* and *Q. robur*. Firebreaks have either a wet to dry heathland vegetation or a grassland vegetation. Management of firebreaks to suppress the growth of woody species is conducted every 4-8 years, however in some cases they are mown annually. The forested landscape is dissected by a dense network of sandy forest tracks that create many forest edges. Within this landscape two study sites were selected: Tagon (5,000 ha), situated 35 km southwest of Bordeaux and Solferino (10,500 ha), located 65 km to the south of Tagon.

Butterfly counts

Butterflies were surveyed in 68 patches of four habitat types: 26 open pine stands (clearcuts and young pines with a canopy height < 7 m), 18 closed canopy pine stands (canopy height > 7 m), 13 deciduous woodlands (isolated patches or riparian forests) and 11 firebreaks. The mean size of the surveyed open and closed pine stands was 8.8 and 10.7 ha respectively, whereas the deciduous woodland patches had a mean size of 3.4 ha. The surveyed firebreaks had a mean width of 40 m. Butterfly surveys were conducted both inside the habitat patch (interior habitat) and along its edge (edge habitat) using the line-transect method (Pollard and Yates 1993). Within the patch interior four sections of 50 m long and 5 m wide were laid out and butterflies were counted within this strip. In pine stands these sections were located at 50 m from the stand edge and were also at least 50 m away from the other edges (Fig. 1). In deciduous woodland patches sections were in general at 50 m from the edge, except in a few small woodland patches. In firebreaks the sections were laid out in the length of the firebreak, in the middle of its width. To survey the edge habitat four sections of 50 m were located at the edge of each surveyed interior habitat (Fig. 1). The edge habitat always consisted of a herbaceous strip with some shrub development along the stand edge, and was bordered by a sandy forest track of about three meters wide. The opposite habitat type on the other side of the forest track was always an open or closed pine stand. The two types of opposite habitat, open or closed pine stand, were evenly distributed for each inventoried habitat type. Each section was sampled four times (between May 14th and September 4th 2004) during appropriate weather conditions (temperature > 20°C, cloudless or just a few clouds and wind speed < 5 Beaufort). To avoid weather and seasonal effects on butterfly counts we surveyed each day different habitat types in a random order and alternated visits to the two study sites. The order of the plots was also randomized for each visiting period. Butterfly species were identified by sight or caught and released for species difficult to identify. For data analysis the total number of individuals per species was pooled over the four visits and the four sections of each habitat (i.e. edge or interior habitat). Butterfly species are named in the text according to Karsholt & Razowski (1996).

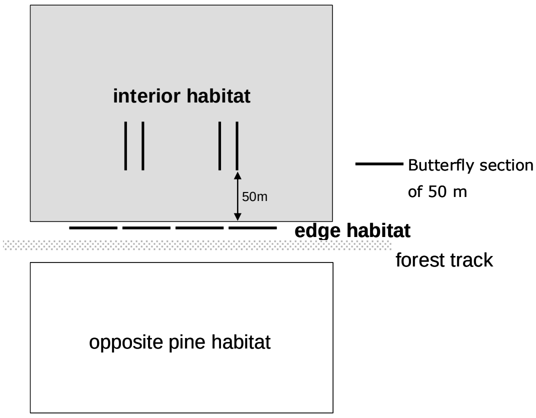


Fig. 1 Position of the four butterfly sections in the interior habitat and in the edge habitat in pine stands

Environmental variables

In order to interpret butterfly diversity, we measured several variables characterising the edge and interior habitat and the surrounding landscape. At the habitat edge and interior we measured important resources for butterflies, such as nectar-plants for adults, vegetation structure, and insolation. Flower abundance of plant species known to be used by butterflies was used as an estimate of nectar availability (Ebert and Rennwald 1991; van Halder personal observations). Since Ericaceae were the most important nectar source we separated nectar availability into two groups: Ericaceae and other nectar plants. At each sampling period the number of flowers was estimated per section using seven classes (Clausen et al. 2001; van Halder et al. 2008). For data analysis we summed, for each sampling period, the midvalues of each class over the four sections. Since each butterfly species only flies during a short period of the year we calculated for each species the flower abundance during its flying period by summing the flower abundances for the sampling periods where at least 90% of the individuals of that butterfly species were seen. Flower abundance was log-transformed to reduce the effect of outliers and because we hypothesized a non-linear relationship between butterfly and flower abundances. In autumn the presence of dicotyledonous host-plants of the observed butterfly species were recorded for each section of the edge habitat. Host plants used by butterflies were based on (Lafranchis 2000) and field observations. Grasses were not identified to species, but their percentage cover was estimated. To describe vegetation structure we estimated the percent vegetation cover in the edge and the interior habitat in two height tiers (herbaceous vegetation (< 0.7 m) and the shrub layer (0.7 -7 m)). The percentage cover of the main vegetation components of the herbaceous layer (grasses, dicots, *Ulex minor*, Ericaceae) was estimated to calculate a Shannon Diversity Index. Insolation was estimated in 8 classes (1 - sunny to 8 - very shady with no direct sun) and incorporated both the exposition of the edge (Clausen et al. 2001), tree height and canopy cover. At the landscape level, we mapped major land-use types in GIS (Arcview 3.3, ESRI) using aerial colour photos with a resolution of 50 cm, followed by field verification. The following 12 land-use types were distinguished: five stages of pine stands (from clearcuts to older pines), deciduous woodlands, firebreaks, hedgerows, meadows, crops, roads and constructed areas. Landscape metrics were calculated within circular buffers with a radius of 200 m, from the centre of the sampled edge, using Fragstats 3.3 in raster version. We used a relatively small buffer size to quantify the landscape composition and structure directly around the sampled edge. This buffer area is expected to contribute most to butterfly movements between the sampled edge and the surrounding landscape. Within each buffer the percentage cover of the four inventoried habitat types was calculated, as well as the Edge Density (i.e. length of all edge segments per hectare) and the Shannon Diversity Index (SHDI) (McGarigal et al. 2002). We selected these landscape metrics because they are ecological meaningful and are known to affect butterfly diversity (Weibull et al. 2000; Krauss et al. 2003; van Halder et al. 2008).

Data analysis

For environmental variables, differences between interior and edge habitats were analysed per habitat type with a paired t-test. For butterfly species richness, the effects of habitat type and of edge vs. interior were tested with a two-way ANOVA. For the edge samples separately the effect of the edge habitat type and the pine habitat type on the opposite side was tested with a two-way ANOVA. The effect of habitat type on species richness in interior samples was tested with a one-way ANOVA. Significant habitat effects were analysed by Tukeyȏs HSD tests. Differences in butterfly species richness between interior and edge habitats per habitat type were tested with paired t-tests. To meet the assumptions of normality and equal variance butterfly species richness data were Box-Cox transformed, and normality and equal variance were verified using the Shapiro-Wilk and Bartlett test respectively. Differences in assemblage composition were assessed by non-metric multi-dimensional scaling (NMDS) using a Bray-Curtis dissimilarity matrix (Clarke 1993). The Bray-Curtis distance metrics was chosen because it provides a meaningful measure of dissimilarity in community structure (McArdle and Anderson 2001). Pairwise differences in assemblage composition were tested with multi-response permutation procedure (MRPP) (Zimmerman et al. 1985). MRPP is a non-parametric method useful to test for differences (e.g., in assemblage composition) between predefined groups. MRPP tests were also based on the Bray-Curtis distance. The significance of the null hypothesis of no difference was assessed by a Monte Carlo permutation procedure with 1000 permutations. We tested for differences in assemblage composition between interior and edge habitat for all habitat types combined and for each habitat type. For edge habitats separately we tested for differences between edge types and we compared species assemblages between edges with open and closed pine stands as opposite habitat type. Butterfly abundance data were log transformed to reduce the effect of some very abundant species. Three open pine stands with no butterflies in the interior habitats where omitted from NMDS and MRPP analyses where interior data were used. Paired Wilcoxon signed rank-tests were used to compare differences in abundance of individual species between edge and interior habitats. Only species with more than 15 individuals were analysed. The effect of environmental variables on the presence of individual species in edge habitats was investigated with logistic regression models. The explanatory variables included both habitat and landscape variables, and the abundance of the same butterfly species in the adjacent, paired interior habitat. The latter variable would indicate a degree of butterfly exchange between the edge and interior of the same habitat patch. We used Akaikeȏs information criterion (AIC) as the selection criterion in a backward and forward selection procedure. All analyses were performed with the R software (R Development Core Team, 2007). We used the package car for ANOVA, MASS for NMDS, vegan for MRPP, stats for stepwise logistic regressions (glm) and exactRankTests for the paired Wilcoxon tests.

Results

Butterfly species richness

A total of 47 butterfly species and 2886 individuals were observed throughout the four sampling periods. In the interior habitats 40 species were observed (1094 individuals) and in the edge habitats 44 species (1792 individuals). Species that were absent in interior or in edge habitats were rare species with less than 13 individuals observed. Two-way ANOVA revealed that edge habitats were significantly richer in butterfly species (7.2 ± 0.4 species (mean ± SE)) than interior habitats (5.2 ± 0.4 species), (n = 136, F = 11.93, P < 0.001, Fig. 2). It also revealed a significant effect of habitat type (n = 136, F = 9.80, P < 0.001) and no interaction (n = 136, F = 2.22, P = 0.09). Tukeyôs HSD tests showed that firebreaks were significantly richer in butterfly species than the other three habitat types (all P Ò 0.01). For edge samples taken separately, the two-way ANOVA showed no effect of habitat type (n = 68, F = 2.15, P = .10) and no effect of the opposite habitat type (n = 68, F = 0.45, P = 0.51). For interior samples the one-way ANOVA indicated a significant overall effect of habitat type on butterfly species richness (n = 68, F = 9.36, P < 0.001), with a higher species richness in firebreaks than in the other three habitat types (Tukeyôs HSD tests, all P < 0.01). The comparison of edge and interior habitats per habitat type showed that edges of open and closed pine stands had significantly more butterfly species than the paired habitat interiors (t = 4.84, d.f. = 25 for open pine stands, t = 5.01, d.f. = 17 for closed pine stands, both P < 0.001). There was no difference in species richness between edge and interior habitats for firebreaks and deciduous woodlands (Fig. 2).

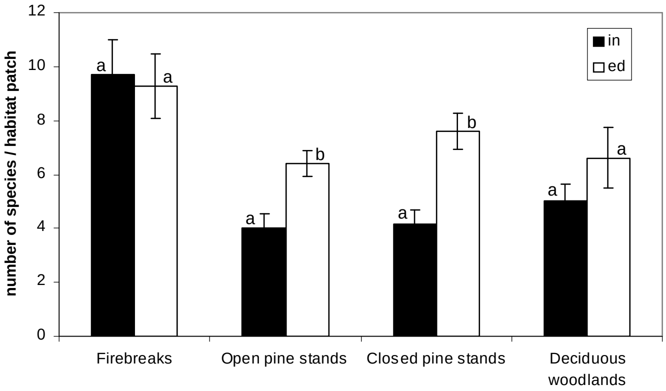


Fig. 2 Mean species richness (± SE) of butterflies in edge and interior habitats per habitat patch type. Different letters per habitat patch type indicate significant differences between interior and edge habitats for that particular patch type (P < 0.05, pairwise t-test per patch type).

Butterfly assemblages

The MRRP indicated a significant (A = 0.018, P < 0.001) difference in butterfly assemblages between interior and edge habitats. Similarly MRPP tests per habitat type also showed significant differences between interior and edge habitats for deciduous woodlands (A = 0.028, P = 0.018), open pine stands (A = 0.027, P < 0.001) and closed pine stands (A = 0.035, P = 0.002), Fig. 3), but not for the comparison between interiors and edges of firebreaks (A = -0.005, P = 0.61). Butterfly assemblages of firebreak interiors were however different from the other edge types (all P < 0.005). Similarly, pairwise comparisons of the different edges types showed significant differences in almost all cases (A Ó 0.02, P Ò 0.01), except for the comparison between edges of closed and open pine stands (A = -0.003 , P = 0.67). MRRP tests showed an overall effect of the opposite habitat type (A = 0.011, P = 0.003) when all edges were combined, but separate tests per edge type showed no effect of the opposite edge type (P > 0.10 in all cases).

Individual butterfly species

Paired Wilcoxon tests of edge-interior habitat preferences of the 23 most abundant species showed that seven species were significantly more abundant in one or more edge habitat types, five species were significantly more abundant in one or more interior habitats, and eleven species showed no preference (Table 1). The analyses per habitat type showed that óedge speciesô occurred mostly in open pine stands and that only one species was more abundant at firebreak edges than in their interiors. óInterior speciesô were not associated with a particular habitat type (Table 1). For 18 out of 23 species a significant logistic regression model could be constructed but the percentage explained deviance differed between species. Both habitat and landscape variables were significant components of the models. The most important habitat variables were the abundance of nectar flowers and host plants, whereas the percentage cover of firebreaks and closed pine stands were most important landscape variables. The abundance of a butterfly species in the adjacent interior habitat was an important determinant of edge abundance for almost half of the species tested.

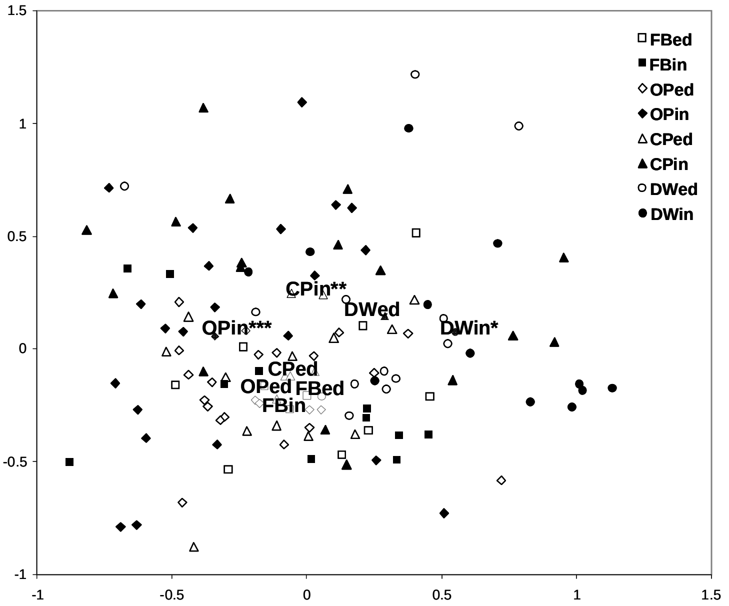


Fig. 3 NMDS ordination plot based on Bray-Curtis distances. Each point represents an edge habitat (open symbols) or interior habitat (closed symbols). The position of the names of the habitat types indicates the centre of all plots of the corresponding type. Pairwise differences between edge and interior habitats per habitat type were tested with MRPP (* P < 0.05; ** P < 0.01; *** P < 0.001, ns not significant). FBed ï firebreak edges, FBin ï firebreak interiors, OPed - open pine stand edges, OPin ï open pine stand interiors, CPed ï closed pine stand edges, CPin ï closed pine stand interiors, DWed - deciduous woodland edges, DWin ï deciduous woodland interiors. Two-dimension stress = 0.27.

Species	**Total abun**	**All habitats**			**Firebreaks**			**Open pine stands**			**Closed pine stands**			**Deciduous woodlands**		
		int	edge	*P*	int	edge	*P*	int	edge	*P*	int	edge	*P*	int	edge	*P*
More abundant in edge habitats																
Pyronia tithonus	694	2.1	8.1	*** (ed)	4.7	10.9	** (ed)	0.9	6.4	*** (ed)	2.3	12.1	*** (ed)	1.8	3.8	
Coenonympha pamphilus	425	1.4	4.9	*** (ed)	3.3	3.6		1.7	6.7	*** (ed)	0.8	5.6	** (ed)	0.1	1.3	* (ed)
Lycaena phlaeas	253	1.5	2.2	* (ed)	3.3	3.3		0.4	1.4	* (ed)	2.4	2.0		1.0	3.2	* (ed)
Maniola jurtina	201	1.3	1.6		3.9	5.4		0.2	0.8	* (ed)	0.7	0.6		2.3	1.6	
Hipparchia statilinus	106	0.5	1.1	* (ed)	1.4	0.7		0.2	1.5	** (ed)	0.7	1.3		0.0	0.3	
Aricia agestis	46	0.3	0.3		0.4	0.1		0.0	0.3	* (ed)	0.4	0.3		0.9	0.6	
Thymelicus sylvestris	28	0.1	0.3	* (ed)	0.5	0.8		0.0	0.1		0.0	0.4		0.0	0.2	
More abundant in interior habitats																
Coenonympha oedippus	135	1.6	0.4	*** (in)	2.1	1.0		2.1	0.3	** (in)	1.7	0.3	* (in)	0.2	0.2	
Cupido argiades	103	1.0	0.5		4.8	1.0	* (in)	0.6	0.7		0.1	0.1		0.0	0.2	
Euphydryas aurinia	84	0.8	0.4		3.8	1.0	* (in)	0.2	0.3		0.1	0.2		0.4	0.4	
Pararge aegeria	63	0.7	0.2	* (in)	0.0	0.0		0.0	0.1		0.1	0.0		3.6	1.0	* (in)
Heteropterus morpheus	29	0.3	0.1	* (in)	0.8	0.5		0.2	0.0		0.3	0.2		0.0	0.0	
No significant differences																
Minois dryas	175	1.2	1.4		1.6	0.8		1.7	1.9		0.9	1.9		0.1	0.2	
Gonepteryx rhamni	107	0.7	0.9		0.7	0.6		0.5	0.8		0.6	1.1		1.0	1.0	
Polyommatus icarus	65	0.4	0.6		2.0	2.3		0.0	0.5		0.1	0.2		0.0	0.1	
Thymelicus lineola	50	0.4	0.4		2.3	1.7		0.0	0.0		0.0	0.0		0.1	0.4	
Ochlodes venata	47	0.2	0.5		0.1	0.1		0.2	0.2		0.3	1.1		0.3	0.5	
Coenonympha arcania	44	0.3	0.4		0.0	0.0		0.2	0.3		0.4	0.9		0.7	0.0	
Hipparchia semele	30	0.2	0.3		0.0	0.0		0.1	0.2		0.3	0.7		0.3	0.2	
Limenitis reducta	26	0.1	0.2		0.5	0.5		0.0	0.1		0.0	0.2		0.4	0.4	
Colias croceus	26	0.1	0.3		0.7	0.3		0.0	0.3		0.0	0.4		0.0	0.0	
Melitaea cinxia	17	0.1	0.1		0.8	0.6		0.0	0.0		0.0	0.0		0.0	0.1	
Brintesia circe	15	0.1	0.1		0.2	0.7		0.0	0.0		0.0	0.1		0.2	0.1	

Table 1 Total abundance (Total abun) of butterfly species in interior and edge habitats (only species with Ó 15 individuals are mentioned). Per species the mean abundance in all interior and edge habitats is given, as well as per patch type. int= interior. P = the P-value of a pairwise Wilcoxon test between interior and edge habitats: * P < 0.05; ** P < 0.01; *** P < 0.001. Species are ordered in three groups according to their preference for edge habitats, interior habitats or no preference, respectively. (ed) = significant preference for edge; (in) = significant preference for interior.

Discussion

Overall, edge habitats had a higher species richness and distinctly different butterfly assemblages compared to adjacent interior habitats. These differences were most pronounced at the edge of pine stands, but were not apparent at firebreaks. The differences in butterfly richness and species composition between edge and interior habitats can be related to the observed differences in vegetation composition and nectar abundance (Dover 1996; Kuussaari et al. 2007), as well as in insolation for closed stands. Our results are consistent with other studies that show the importance of forest edges for butterflies (Ferris and Carter 2000; Kuussaari et al. 2007; Ohwaki et al. 2007).

Edge species

Although many species are often more abundant at edges, identifying real edge species, i.e. species that need resources only found at edges, is difficult and such obligate edge species are rare. Duelli et al. (1990) showed that of the 113 tested species of carabids, staphylinids and spiders in an agricultural landscape only two were obligate edge species. Similarly Paquet et al. (2006) found no bird species strictly indicative of edge habitats in a woodland-farmland landscape. Most bird species considered to prefer forest edges in agricultural landscapes are in fact early-successional species that could not find shrubland conditions apart from the edges of forest fragments (Imbeau et al. 2003). Although obligate edge species are rare, some butterfly examples do exist. In Sweden, Bergman (1999) showed that *Lopinga achine* is restricted to a narrow zone along forest edges that harboured more host plants, and corresponded to a zone of higher egg survival compared to adjacent open habitat or shaded woodland. In Finland *Euphydryas maturna* is restricted to south facing forest edges where it finds a warm microclimate, suitable host plants, and in adjacent clearcuts nectar sources and perching sites for males (Wahlberg 2001). Most species that were more abundant at edges in our study are classified as grassland or heathland species (Ebert and Rennwald 1991; Lafranchis 2000; Asher et al. 2001), which is reflected in the herbaceous vegetation that dominated the sampled edges. For several species in this group, such as *Pyronia tithonus*, *Coenonympha pamphilus* and *Thymelus sylvestris*, the studied edges can be considered as a habitat since all essential resources are present at edges. The results of the logistic regressions confirmed that for these species habitat characteristics were important, notably nectar and host plants. These edge preferring species were rare in adjacent pine stands and their presence in interior habitat is probably a spill-over effect. Other butterfly species, such as *Neozephyrus quercus*, *Satyrium ilicis*, *Limenitis reducta*, *Celastrina argiolus*, *Iphiclides podalirius*, that are often observed along woodland edges or hedgerows in Europe (Ebert and Rennwald 1991; Dover and Sparks 2000) were rare in our survey. We think that their rareness may be attributed to the sharp edge boundaries at our study sites that lack a developed tree and shrub zone.

Role of edges vs interiors for butterflies

Plantation forests are generally considered to have little or no value as habitat for butterflies apart from stand edges (Ferris and Carter 2000; Asher et al. 2001). Plantation forests have broad similarities with agricultural landscapes where linear elements such as hedgerows and grass verges are known to be important for butterflies (Feber et al. 1996; Clausen et al. 2001) and where crops represent non-habitat. In contrast to previous work we showed that interior portions of plantation forest stands harbour some butterfly species and that they are a habitat for one of Europeǒs most threatened species, *Coenonympha oedippus* (van Swaay and Warren 1999). The presence of species at edges but also inside some or all habitat types, the overlap in species composition between edge and interior habitats and the frequent selection in GLMs of the species abundance in the habitat interior next to the edge raises questions regarding the relative importance of these different elements in providing resources to butterflies. The most important resources for butterflies are host plants, nectar plants, vegetation structure and micro-climate (related to thermoregulation and survival of different stages) (Dennis et al. 2003; Tudor et al. 2004; Hardy et al. 2007). In landscapes composed of a mosaic of different habitat types the presence of particular butterfly species may depend on the presence of a certain resource in several, nearby habitat patches (landscape supplementation) or on the presence of different resources in different habitat patches (landscape complementation) (Dunning et al. 1992). In our study many species were observed as well at edges as in interior habitats of one or several habitat types. At firebreaks these species may find the same resources in edge and interior habitats (supplementation), but this seems less plausible for contrasted edges such as of older pine stands and deciduous woodlands. In such cases the use of different resources in adjacent habitats seems more probable. The use of different vegetation types for ovipositing, nectar feeding or resting has been demonstrated for several butterfly species, e.g. for *Leptidea sinapis* (Wiklund 1977) and *Maniola jurtina* (Ouin et al. 2004). In our study nectar abundance was greater at edges than in interior habitats, and this may explain the presence of for example *Gonepteryx rhamni* in edge habitats even though its host plant *Frangula alnus* occurs in the interior of pine stands. Selection for specific microclimatological conditions might also explain the presence of species at edges and inside habitats. Depending on the weather conditions butterflies will select specific vegetation structures to provide shelter (Dennis and Sparks 2006), a warmer microclimate (Shreeve 1984), or will use the shade of trees to prevent overheating in summer (Vanreusel et al. 2007). In this study several species were observed inside shady, closed stands where no apparent nectar or host plants were present. For example, the presence of *Aricia agestis* and *Hipparchia semele* in these forested stands seemed related to daily movements to escape unfavourable conditions in open habitats during hot weather. *M. jurtina*, a species that is normally characterized as a grassland butterfly (Dennis 2004), was also frequently observed in the interior of shady deciduous woodlands (Table 2). This butterfly species showed a clear seasonal pattern. More than 80% of *M. jurtina* individuals were observed in firebreaks and at edges during visit one (mid May - mid June) and four (August), whereas during visit three (second half of July) 76% of the individuals were found in deciduous woodland interiors (percentages corrected for sampling effort). This pattern of multi-habitat use corresponds with an estivation in shady habitats in the middle of the flight season to avoid hot temperatures, as was observed in Italy and southern Germany (Ebert and Rennwald 1991).

Edges vs firebreaks as butterfly habitats

Our results showed that butterfly species richness and assemblage composition were similar between firebreak interiors and their edges, but that the species composition of firebreak interiors and edges differed from that of other edge types. This suggests that firebreaks have a distinct role in butterfly conservation compared to stand edge habitats. Similarly, Ockinger and Smith (2007) demonstrated that field margins with a perennial grassland vegetation close to semi-natural grasslands had higher butterfly species richness than field margins farther away and that these grasslands acted as source populations for surrounding field margins. In our study area firebreaks are very likely to play a similar role as source habitat and may have a positive effect on butterfly diversity in nearby stand edges. For most butterfly species the resources used in firebreaks and at stand edges are probably quite similar and supplementation of resources could explain the simultaneous presence of species in these elements. Moreover species can use firebreaks or their edges as a refuge when one of them is disturbed by management. Firebreaks are less drained and less frequently managed than edge habitats which may explain the higher abundance of some species (*Euphydryas aurinia, Coenonympha oedippus, Heteropterus morpheus and Cupido argiades*) associated with humid, *Molinia caerulea* dominated, heathland vegetations in firebreak interiors compared to edge habitats (Table 2).

Conclusions and implications for conservation

Our study highlights the importance of edge habitat for the conservation of butterfly diversity in fragmented plantation forest landscapes. Stand edges and small open areas in forests are essential for woodland butterflies, as well as for other arthropods such as carabids or spiders (Barbaro et al. 2005; Lin et al. 2007). Compared to other open habitats such as clearcuts and young pine stands, edges were richer in butterfly species and supported a different assemblage. Maintaining and creating edges in forested landscapes will have a small impact on forestry economics, while favouring many butterfly species. However conservation management of edges does not mean that stand interiors can be neglected. *C. oedippus*, which is critically endangered in Europe, was more abundant inside habitat patches than at their edges and several other species used stand interiors as part of their habitat. The use of several patch types by a species may be a frequent phenomenon in fragmented forests and other mosaic landscapes, and it can be a necessary mechanism for species survival in these landscapes. Maintenance of a diversity of habitat types through small-scale landscape heterogeneity seems therefore an important strategy for butterfly conservation.

References

Asher J, Warren M, Fox R, Harding P, Jeffcoate G, Jeffcoate S (2001) The millennium atlas of butterflies in Britain and Ireland. Oxford University Press, Oxford

Barbaro L, Pontcharraud L, Vetillard F, Guyon D, Jactel H (2005) Comparative responses of bird, carabid, and spider assemblages to stand and landscape diversity in maritime pine plantation forests. Ecoscience 12:110-121

Barbaro L, van Halder I (2009) Linking bird, carabid beetle and butterfly life-history traits to habitat fragmentation in mosaic landscapes. Ecography 32:321-333

Bergman KO (1999) Habitat utilization by Lopinga achine (Nymphalidae : Satyrinae) larvae and ovipositing females: implications for conservation. Biol Conserv 88:69-74

Bink FA (1992) Ecologische atlas van de dagvlinders van Noordwest-Europa. Schuyt & Co, Haarlem

Brockerhoff EG, Jactel H, Parrotta JA, Quine CP, Sayer J (2008) Plantation forests and biodiversity: oxymoron or opportunity? Biodiv Conserv 17:925-951

Clarke KR (1993) Nonparametric multivariate analyses of changes in community structure. Aust J Ecol 18:117-143

Clausen HD, Holbeck HB, Reddersen J (2001) Factors influencing abundance of butterflies and burnet moths in the uncultivated habitats of an organic farm in Denmark. Biol Conserv 98:167-178

Dennis RLH (2004) Butterfly habitats, broad-scale biotope affiliations, and structural exploitation of vegetation at finer scales: the matrix revisited. Ecol Entomol 29:744-752

Dennis RLH, Sparks TH (2006) When is a habitat not a habitat? Dramatic resource use changes under differing weather conditions for the butterfly Plebejus argus. Biol Conserv 129:291-301

Dennis RLH, Shreeve TG, Van Dyck H (2003) Towards a functional resource-based concept for habitat: a butterfly biology viewpoint. Oikos 102:417-426

Dover JW (1996) Factors affecting the distribution of satyrid butterflies on arable farmland. J Appl Ecol 33:723-734

Dover J, Sparks T (2000) A review of the ecology of butterflies in British hedgerows. J Environ Manage 60:51-63

Downie IS, Coulson JC, Butterfield JEL (1996) Distribution and dynamics of surface-dwelling spiders across a pasture-plantation ecotone. Ecography 19:29-40

Duelli P, Studer M, Marchand I, Jakob S (1990) Population movements of arthropods between natural and cultivated areas. Biol Conserv 54:193-207

Duelli P, Obrist MK, Fluckiger PF (2002) Forest edges are biodiversity hotspots - also for Neuroptera. Acta Zool Hung 48:75-87

Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological processes that affect populations in complex landscapes. Oikos 65:169-175

Ebert G, Rennwald E (1991) Die Schmetterlinge Baden-Württembergs. Band 1 & 2 Tagfalter. Verlag Eugen Ulmer, Stuttgart

Ewers RM, Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biol Rev 81:117-142

Feber RE, Smith H, Macdonald DW (1996) The effects on butterfly abundance of the management of uncropped edges of arable fields. J Appl Ecol 33:1191-1205

Feber RE, Brereton TM, Warren MS, Oates M (2001) The impacts of deer on woodland butterflies: the good, the bad and the complex. Forestry 74:271-276

Ferris R, Carter C (2000) Managing rides, roadsides and edge habitats in lowland forests. Forestry Commission Bulletin 123

Fletcher RJ (2005) Multiple edge effects and their implications in fragmented landscapes. J Anim Ecol 74:342-352

Greatorex-Davies JN, Sparks TH, Hall ML, Marrs RH (1993) The influence of shade on butterflies in rides of coniferised lowland woods in southern England and implications for conservation management. Biol Conserv 63:31-41

Haddad NM (1999) Corridor use predicted from behaviors at habitat boundaries. Am Nat 153:215-227

Hardy PB, Sparks TH, Isaac NJB, Dennis RLH (2007) Specialism for larval and adult consumer resources among British butterflies: Implications for conservation. Biol Conserv 138:440-452

Haynes KJ, Cronin JT (2006) Interpatch movement and edge effects: the role of behavioral responses to the landscape matrix. Oikos 113:43-54

Imbeau L, Drapeau P, Mokkonen M (2003) Are forest birds categorised as "edge species" strictly associated with edges? Ecography 26:514-520

Karsholt O, Razowski J (1996) The Lepidoptera of Europe. A distributional checklist. Apollo Books, Stenstrup

Krauss J, Steffan-Dewenter I, Tscharntke T (2003) How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? J Biogeogr 30:889-900

Kuussaari M, Heliola J, Luoto M, Poyry J (2007) Determinants of local species richness of diurnal Lepidoptera in boreal agricultural landscapes. Agr Ecosyst Environ 122:366-376

Lafranchis T (2000) Les papillons de jour en France, Belgique et Luxembourg et leurs chenilles. Biotope, Mèze (France)

Lehtinen RM, Ramanamanjato JB, Raveloarison JG (2003) Edge effects and extinction proneness in a herpetofauna from Madagascar. Biodivers Conserv 12:1357-1370

Lin YC, James R, Dolman PM (2007) Conservation of heathland ground beetles (Coleoptera, Carabidae): the value of lowland coniferous plantations. Biodivers Conserv 16:1337-1358

McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: A comment on distance-based redundancy analysis. Ecology 82:290-297

McGarigal K, Cushman SA, Neel MC, Ene E (2002) FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following web site: www.umass.edu/landeco/research/fragstats/fragstats.html

Niemela J, Koivula M, Kotze DJ (2007) The effects of forestry on carabid beetles (Coleoptera: Carabidae) in boreal forests. J Insect Conserv 11:5-18

Ockinger E, Smith HG (2007) Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. J Appl Ecol 44:50-59

Ohwaki A, Nakamura K, Tanabe SI (2007) Butterfly assemblages in a traditional agricultural landscape: importance of secondary forests for conserving diversity, life history specialists and endemics. Biodiv Conserv 16:1521-1539

Ouin A, Aviron S, Dover J, Burel F (2004) Complementation/supplementation of resources for butterflies in agricultural landscapes. Agr Ecosyst Environ 103:473-479

Paquet JY, Vandevyvre X, Delahaye L, Rondeux J (2006) Bird assemblages in a mixed woodland-farmland landscape: The conservation value of silviculture-dependant open areas in plantation forest. For Ecol Manag 227:59-70

Pollard E, Yates TJ (1993) Monitoring butterflies for Ecology and Conservation. Chapman & Hall, London

Ries L, Debinski DM (2001) Butterfly responses to habitat edges in the highly fragmented prairies of Central Iowa. J Anim Ecol 70:840-852

Ries L, Sisk TD (2004) A predictive model of edge effects. Ecology 85:2917-2926

Ries L, Sisk TD (2008) Butterfly edge effects are predicted by a simple model in a complex landscape. Oecologia 156:75-86

Ries L, Fletcher RJ, Battin J, Sisk TD (2004) Ecological responses to habitat edges: Mechanisms, models, and variability explained. Ann Rev Ecol Evol Syst 35:491-522

Robertson PA, Clarke SA, Warren MS (1995) Woodland management and butterfly diversity. In: AS Pullin (ed) Ecology and conservation of butterflies, Chapman & Hall, London, pp. 113-122

Schtickzelle N, Baguette M (2003) Behavioural responses to habitat patch boundaries restrict dispersal and generate emigration-patch area relationships in fragmented landscapes. J Anim Ecol 72:533-545

Shreeve TG (1984) Habitat selection, mate location, and microclimatic constraints on the activity of the speckled wood butterfly (Pararge aegeria). Oikos 42:371-377

Spector S, Ayzama S (2003) Rapid turnover and edge effects in dung beetle assemblages (Scarabaeidae) at a Bolivian Neotropical forest-savanna ecotone. Biotropica 35:394-404

Stevens SM, Husband TP (1998) The influence of edge on small mammals: evidence from Brazilian Atlantic forest fragments. Biol Conserv 85:1-8

Sutcliffe OL, Thomas CD (1996) Open corridors appear to facilitate dispersal by ringlet butterflies (Aphantopus hyperantus) between woodland clearings. Conserv Biol 10:1359-1365

Tscharntke T, Stefan-Dewenter I, Krueus A, Thies C (2002) Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. Ecol Appl 12:354-363.

Tudor O, Dennis RLH, Greatorex-Davies JN, Sparks TH (2004) Flower preferences of woodland butterflies in the UK: nectaring specialists are species of conservation concern. Biol Conserv 119:397-403 van Halder I, Barbaro L, Corcket E, Jactel H (2008) Importance of semi-natural habitats for the conservation of butterfly communities in landscapes dominated by pine plantations. Biodiv Conserv 17:1149-1169

van Swaay CAM, Warren MS (1999) Red Data book of European butterflies (Rhopalocera). Council of Europe Publishing, Strasbourg

Vanreusel W, Maes D, Van Dyck H (2007) Transferability of species distribution models: a functional habitat approach for two regionally threatened butterflies. Conserv Biol 21:201-212

Wahlberg N (2001) On the status of the scarce fritillary Euphydryas maturna (Lepidoptera : Nymphalidae) in Finland. Entomologica Fennica 12:244-250

Weibull AC, Bengtsson J, Nohlgren E (2000) Diversity of butterflies in the agricultural landscape: the role of farming system and landscape heterogeneity. Ecography 23:743-750

Wiklund C (1977) Oviposition, feeding and spatial separation of breeding and foraging habitats in a population of Leptidea sinapis (Lepidoptera). Oikos 28:56-68

Zimmerman GM, Goetz H, Mielke PWJ (1985) Use of an improved statistical method for group comparisons to study effects of prairie fire. Ecology 66:606-611

Photo 1. Quelques espèces de papillons caractéristiques de la forêt de plantation des Landes de Gascogne. De gauche à droite et de haut en bas : damier de la succise *Euphydryas aurinia*, agreste *Hipparchia semele*, sylvain azuré *Limenitis reducta*, miroir *Heteropterus morpheus*, thécla de lôyeuse *Satyrium ilicis*, et oedippe *Coenonympha oedippus* (Inge van Halder).

2.2. Guildes et traits de vie: un lien entre diversité et fonction des communautés

2.2.1. Effet de la végétation environnante sur les guildes de lépidoptères herbivores

Résumé

Les interactions entre une plante et ses insectes herbivores peuvent être modifiées par la végétation environnante en gênant (résistance par association) ou en favorisant (susceptibilité par association) la localisation et la colonisation de la plante-hôte. Nous avons comparé les effets de la concentration de la plante-hôte sur lôintensité dôherbivorie par des lépidoptères et hyménoptères spécialistes (larves mineuses) et des lépidoptères généralistes (chenilles tordeuses) en augmentant expérimentalement la densité de plantules de chêne pédonculé *Quercus robur*. Nous avons aussi testé les effets de la composition et de la structure de la végétation environnante aux échelles de la placette et de la parcelle forestière. Les dégâts des lépidoptères généralistes phyllophages dépendent de la structure des communautés végétales à lôéchelle de la parcelle et augmentent avec le recouvrement des arbres forestiers. Au contraire, les dégâts des insectes herbivores spécialistes (mineuses) sont affectés par la végétation locale entourant les plantules et diminuent avec le recouvrement arbustif et la diversité de stratification. Lôaugmentation de lôabondance des mineuses avec la densité de plantules de chêne est un résultat en faveur de lôhypothèse de concentration de la plante-hôte. Cependant, lôabondance des mineuses spécialistes est corrélée négativement à celle des lépidoptères défoliateurs généralistes, suggérant des interactions de compétition entre insectes herbivores spécialistes et généralistes.

Abstract

The diversity of surrounding vegetation is thought to modify the interactions between a focal plant and its herbivores, disrupting (associational resistance) or enhancing (associational susceptibility) host plant location and colonisation. We compared the effects of host plant concentration on herbivory by generalist and specialist insects feeding on oak seedlings by increasing local concentration of seedlings. We also assessed the effects of the composition and structure of surrounding vegetation, both at stand and local levels. The damage caused by generalist leaf-feeding insects depended on the structure of plant communities at stand level, and increased with tree cover. By contrast, infestation by specialist leaf miners was affected by local understorey vegetation surrounding oak seedlings, and decreased with increasing shrub cover and stratification diversity. Leaf mine abundance was higher at higher oak seedling density, giving support to the host concentration hypothesis. However, the abundance of these specialist herbivores was also negatively correlated with damage caused by the generalist external leaf-feeders, suggesting competitive interactions.

Introduction

Interactions between plants and herbivores have long been viewed as binary relationships between resistance traits and herbivore communities, but the importance of the surrounding vegetation is increasingly recognised (Barbosa, Hines, Kaplan, Martinson, Szczepaniec et al. 2009). The diversity of the surrounding vegetation has been reported to reduce herbivore damage to a focal plant, by providing associational resistance (Root 1973) in many ecosystems, such as crops (Tonhasca & Byrne 1994), forests (Jactel & Brockerhoff 2007; Vehviläinen, Koricheva, & Ruohomäki 2007) and grasslands (Unsicker, Baer, Kahmen, Wagner, Buchmann et al. 2006). However, some studies have failed to confirm this relationship (Vehviläinen, Koricheva, Ruohomäki, Johansson, & Valkonen 2006; Scherber, Mwangi, Temperton, Roscher, Schumacher et al. 2006), or even reported the opposite response: associational susceptibility with higher herbivory in more diverse plant communities (Vehviläinen et al. 2007; Schuldt, Baruffol, Bohnke, Bruelheide, Härdtle et al. 2010). Resource concentration may account for a significant proportion of the decrease in damage due to specialist herbivores within diverse plant communities (Root 1973). The relative abundance and nature of the neighbouring plants determine the probability of a plant being colonised by herbivores (Barbosa et al. 2009). In more diverse plant communities, host plants are proportionally less frequent and non-host neighbouring plants can provide chemical or physical barriers to host plant location (Hambäck & Beckerman 2003, Randlkofer, Obermaier, Hilker, & Meiners 2010, Jactel, Birgersson, Andersson, & Schlyter 2011). For example, unpalatable or spiny shrubs may provide a physical barrier protecting tree seedlings against mammalian grazers (Baraza, Zamora, & Hódar 2006).

These plantï herbivore interactions may also vary with the spatial scale at which they occur (Banks 1998; Gunton & Kunin 2007). The effect of plant neighbours on herbivory depends on the distance between a focal plant and its neighbours (Barbosa et al. 2009). Many studies have reported a significant influence of plant diversity on herbivores in small plots, whereas experiments over large spatial scales have tended to show no such benefits of plant diversity (Bommarco & Banks 2003). Finally, the magnitude and direction of the relationship between plant diversity and insect herbivory seems to vary with the mobility of herbivores and their diet breadth (Banks 1998). Associational susceptibility would be expected to be most prevalent with polyphagous herbivores, because they are able to feed on multiple host plant species (Unsicker, Oswald, Koehler, & Weisser 2008), whereas specialist herbivores are limited by the numbers of suitable hosts (Bertheau, Brockerhoff, Roux-Morabito, Lieutier, & Jactel 2010). Plant neighbours may disrupt host finding by specialist insects, whereas generalist insects may simply shift from one host plant to another. The objective of this study was therefore to investigate the effect of host concentration on insect herbivory on pedunculate oak *Quercus robur* seedlings, by manipulating the local concentration of focal host plants. We also investigated the influence of the composition (species diversity) and structure (cover and stratification) of the surrounding vegetation of oak seedlings at local and stand levels. We hypothesized that specialist and generalist herbivores associated with oak seedlings would not be influenced in the same direction and magnitude by surrounding vegetation. We compared the effect of neighbouring plants on specialist leaf miners and on generalist external feeders.

Methods

Study system

This study was conducted in the Landes de Gascogne forest, in south-western France, a region covered by one million hectares of native maritime pine plantations (*Pinus pinaster*). Pedunculate oak (*Quercus robur*) regenerates naturally within pine stands and becomes co-dominant in older plantations. Other broadleaf species present are: chestnut (*Castanea sativa*), European holly (*Ilex aquifolium*), red and Holm oaks (*Q. rubra* and *Q. ilex*), and silver birch (*Betula pendula*). The predominant understorey species are common bracken (*Pteridium aquilinum*), moor grass (*Molinia caerulea*), dwarf and common gorse (*Ulex europaeus, U. minor*), heather species (*Erica scoparia, E. cinerea, Calluna vulgaris*), glossy buckthorn (*Frangula alnus*), blackberry (*Rubus* spp.) and European honeysuckle (*Lonicera periclymenum*).

Experimental design

We investigated the effects of host plant concentration and surrounding vegetation on insect herbivory in eight mixed stands of *Q. robur* and *P. pinaster* (40 ï 45 years of age). We established two experimental plots within each stand (Fig. 1). In the low-host concentration treatment ("low HC plot"), three oak seedlings were planted about 60 cm apart in a 2.25 m² (1.5 x 1.5 m) plot. In the high-host concentration treatment ("high HC plot"), we planted six additional seedlings around the three target seedlings, reducing the distance between seedlings to about 30 cm in a 2.25 m² plot (Fig. 1). In total, 96 one-year-old *Q. robur* seedlings were randomly transplanted in February 2009: 48 target seedlings (3 replicate seedlings × 2 plots × 8 stands) and 48 additional seedlings (6 replicates × 1 high HC plot × 8 stands). The oak seedlings had been grown in nursery for one year and were about 45 ± 2 cm high (mean ± SE) and had 47 ± 3 leaves.

Insect herbivory on focal species

Most of the insect damage occurring on *Q. robur* leaves is caused by generalist external leaf-feeders (chewer and skeletoniser guilds), principally lepidopteran larvae and grasshoppers, which are able to feed on several plant species. A few lepidopteran species are specialist feeders, but these species had very low abundance in the area studied and caused little damage (Giffard, Corcket, Barbaro, & Jactel 2012 and unpublished data). All external insect damage was pooled and considered to correspond to damage caused by external leaf-feeders. Leaf miners are specialist herbivores and the species feeding on *Q. robur* are mostly small moths (Lepidoptera). We therefore used the abundance of leaf mines (presence of mines in leaves) as a proxy for herbivory. Herbivory by external leaf-feeders and the abundance of leaf mines were assessed by visual inspection of all leaves in each of the 48 target oak seedlings. The leaf area removed (LAR) by generalist insects was estimated with transparent 0.25-cm² grid and divided by the total leaf area (estimated with a 1 cm² grid) to calculate a percentage LAR. Insect herbivory was assessed twice during a single growing season, in June and September 2009, as well as the number of the main insect herbivore species. Within a given plot, LAR and leaf mine abundance were averaged over the three seedling replicates.

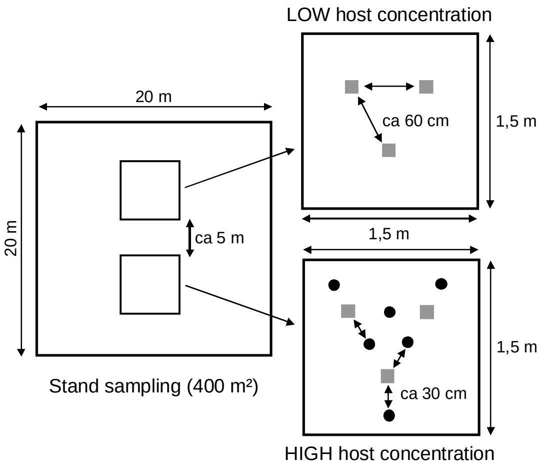


Fig. 1 Experimental design for assessing the effect of host plant concentration and surrounding vegetation on insect herbivory on oak seedlings. Stand vegetation was sampled over an area of 400 m² around the two experimental plots. The "low host concentration" plot consisted of 3 focal oak seedlings (grey squares, topï right) and the "high host concentration" plots consisted of 3 focal oak seedlings (grey squares) and 6 additional oak seedlings (solid circles, bottomï right). The vegetation of the plot was sampled over an area of 2.25 m²

Stand and plot vegetation sampling

The vegetation present in the eight stands and the 16 plots was sampled in August 2009. We recorded all vascular plants and their cover in an area of 400 m² around the two experimental plots in each forest stand (Fig. 1). Species covers were assessed using the Braun-Blanquet semi-quantitative scale (Sutherland 1996). The vegetation layers considered were the tree layer (trees higher than 7 m), the shrub layer (woody species 2-7 m high), and the herbaceous layer (all plants less than 2 m high). Plant cover was assessed visually for each vegetation layer, regardless of species composition. We also estimated mean *Q. robur* cover in the herbaceous layer (recruitment) and in both the tree and shrub layers (saplings and mature trees). At the plot level, we recorded all plant species in the herbaceous layer (< 2 m high) and estimated shrub and herbaceous cover (Fig. 1). We also estimated the *Q. robur* cover in the herbaceous layer. We then calculated plant species richness and Shannon's index of diversity, in each layer at both stand and plot levels. We also calculated an index of stratification diversity at both stand and plot levels (Prodon & Lebreton 1981). At the plot level, stratification diversity increased with decreasing herbaceous cover and increasing shrub cover.

Statistical analyses

Because vegetation variables were correlated, we first performed principal component analyses (PCA), at stand and plot levels separately, to select a minimum set of meaningful variables capturing most of the variation in the complete data set. Then we selected the original variable best correlated to each of the first two axes even though other non-selected variables might have been also relevant to insect herbivory. Oak cover and tree cover were retained for the stand level (17 and 23% contribution to axis 1 and 2, respectively) and stratification diversity and herbaceous diversity for the plot level (31 and 34% contribution to axis 1 and 2, respectively). Next, linear mixed model analyses (LMM) were performed on LAR by external leaf-feeders, after logit transformation for proportion data (Warton & Hui 2011). Generalised linear mixed model analyses (GLMM) were performed on the abundance of leaf mines, with Poisson distribution fitting and the use of a log link function and Laplace approximation for count data (Zuur et al. 2009).

In all models, we considered "stand" as random effect to account for the spatial non-independence of the two plots within a given forest stand (high and low HC plots), and ñplotò as random effect to account for the two repeated measurements conducted in a each plot. We investigated the fixed effects of host concentration, season, selected vegetation variables (oak and tree covers at stand level, and stratification and herbaceous diversities at plot level) and their interactions in two complete models, for LAR by external leaf-feeders and leaf mine abundance separately. For the two complete models, likelihood-ratio tests were then performed in each model to assess the significant effects of predictive variables and their interactions on insect herbivory. Non-significant variables were successively removed until the minimal model best explaining the data was obtained (Zuur et al. 2009). When significant three-way interactions were found (season x host concentration x vegetation variable), we made two separated models (for each season) in order to highlight the effects of the experimental treatments. We carried out analyses with maximum likelihood methods, to compare models with different fixed effect structures. We checked the normality and homoscedasticity of the residuals of all minimal models. Finally, we performed GLMM to investigate the effect of LAR by external leaf-feeders on the abundance of leaf mines. For both GLMMs and LMMS, the likelihood ratio R^2 was estimated if a continuous variable was found to have a significant effect (Kramer 2005) and we used a more conservative p-value of 1% as the significance threshold for z-values for GLMMs (Zuur et al. 2009).

Analyses were performed with the ade4 package for multivariate analyses (Dray & Dufour 2007), the nlme package for LMM analyses (Pinheiro, Bates, Debroy, Sarkar et al. 2011) and lme4 for GLMM analyses (Bates, Maechler, & Bolker 2011) with R software (R Development Core Team 2010). Intercepts and slopes and their standard errors were estimated with the AICcmodavg package (Mazerolle 2011) and then exponentially transformed to represent raw data on figures.

Results

Effect of season

The abundance of leaf mines ($n = 32$, $G^2 = 13.4$, $df = 1$, $P < 0.001$) and LAR by generalist insects, i.e., external leaf-feeders ($F_{1,15} = 81.83$, $P < 0.001$) increased significantly from June to September (Fig. 2). Treatment effects, i.e. host concentration and continuous vegetation variables, were consistent regardless of season for LAR by external leaf-feeders, indicated by non-significant interaction terms (no significant three-way interactions). By contrast, analyses of leaf mine abundance showed significant interactive effects of vegetation variables with season and host concentration treatments (significant three-way interactions) and we then tested vegetation effects and their interactions with host concentration separately for each date. In June, there was no significant relationship between LAR by generalist insects and leaf mine abundance whereas the leaf mine abundance decreased with increasing LAR by generalist insects in September, regardless of host plant concentration ($n = 16$, $G^2 = 24.45$, $df = 1$, $P < 0.001$) (Fig. 3a).

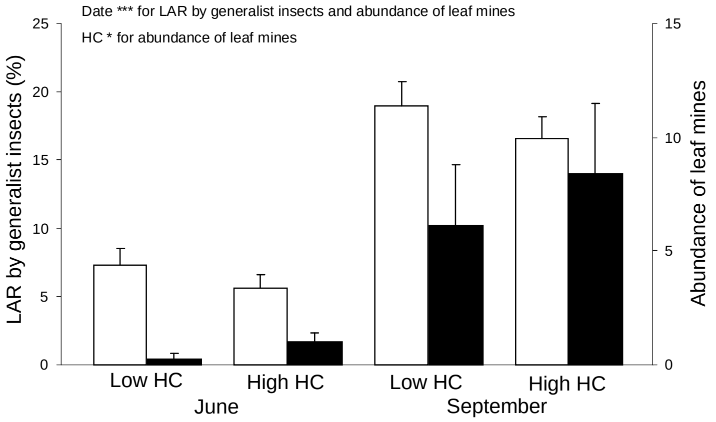


Fig. 2 Mean (+ SE) percent leaf area removed (% LAR) by generalist insects (white bars) and abundance of leaf mines (black bars) on oak seedlings planted in low Host Concentration (HC) and high HC plots, in June and September.

Effect of host plant concentration

The addition of conspecific seedlings had different effects on damage, according to host plant specialisation of insect herbivores (Fig. 2). Regardless of the season, the abundance of leaf mines on oak seedlings was significantly higher in high-HC plots ($n = 32$, $G^2 = 4.60$, $df = 1$, $P = 0.03$), but the HC effect was weak on each date ($n =16$, $G^2 = 3.42$, $df = 1$, $P = 0.06$ and $n =16$, $G^2 = 2.80$, $df = 1$, $P = 0.09$, for June and September, respectively). Conversely, damage by generalist insects tended to be lower in high HC plots, if non-significantly ($F_{1,7} = 1.91$, $P = 0.20$).

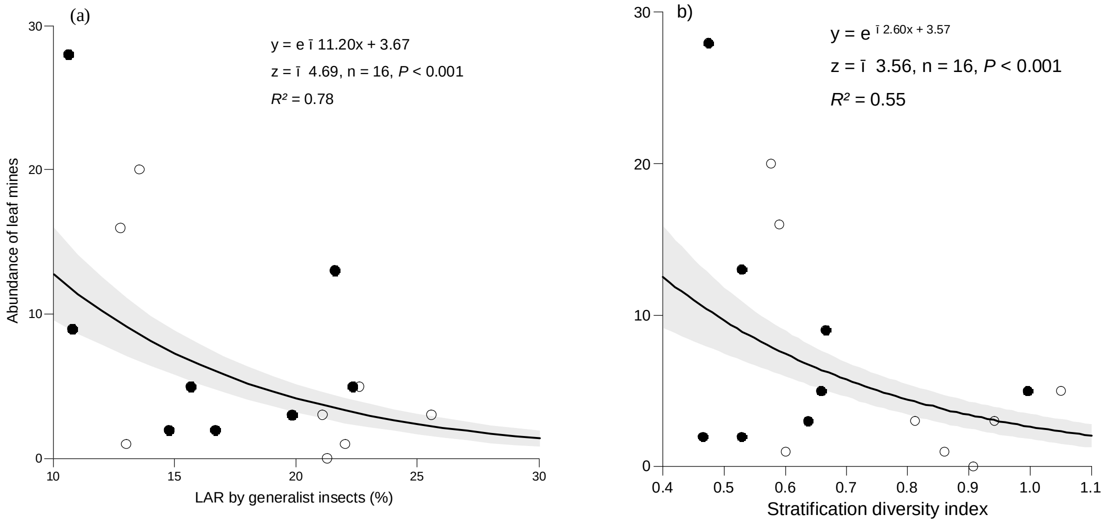


Fig. 3 Relationship between leaf mine abundance and (a) percent leaf area removed by generalist insects (% LAR), for oak seedlings in September; and (b) stratification diversity index, at the plot level, in September. Open and closed circles represent low and high host plant concentration plots, respectively.

Effects of plot diversity on insect herbivory

LAR by generalist insects was not significantly affected by vegetation variables estimated at the local level (all P > 0.10). The structure of the surrounding vegetation significantly influenced herbivory by specialist insects in September (n = 16, $G^2 = 11.31$, df = 1, $P < 0.001$) but not in June (n = 16, $G^2 = 0.05$, df = 1, P = 0.82). The abundance of leaf mines significantly decreased with increasing stratification diversity (Fig. 3b).

Effects of stand diversity on insect herbivory

Effects of stand vegetation variables were not consistent among host plant concentration treatments for LAR by generalist leaf-feeders. We found a significant interaction term between host concentration and tree cover ($F_{1,5}$ = 6.8, P = 0.05), so we performed separate analyses for each level of HC (high and low HC plots). The structure and composition of the tree layer significantly influenced LAR by generalist leaf-feeders on oak seedlings only in plots with low HC (Fig. 4). LAR significantly increased with increasing tree cover ($F_{1,6}$ = 7.70, P = 0.03), whereas no significant effect was found in plots with high HC ($F_{1,6}$ = 0.10, P = 0.77). The abundance of leaf mines was not significantly affected by vegetation variables estimated at the stand level in both June and September (all P > 0.10). We did not find any significant effect of oak cover on LAR by generalist leaf-feeders or leaf mine abundance.

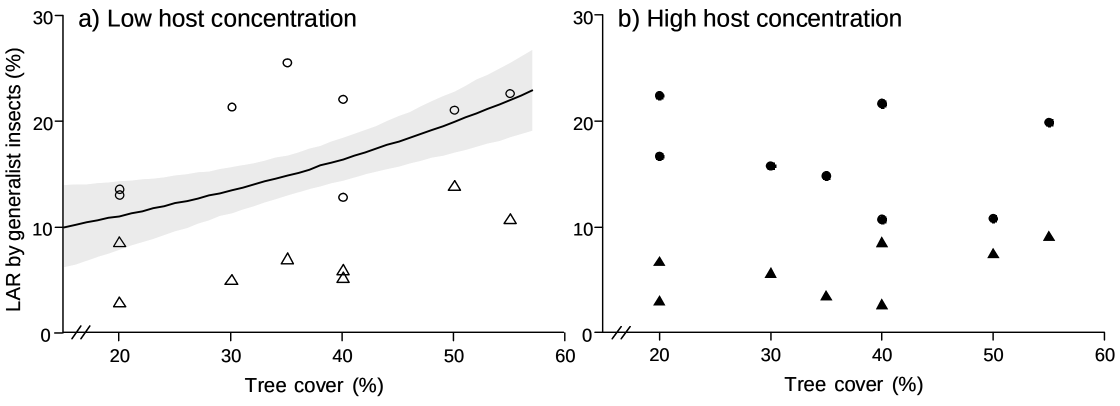


Fig. 4 Effects of tree cover at the stand level on percent leaf area removed (% LAR) by generalist insects from oak seedlings in plots with a) low and b) high host plant concentration. Triangles and circles indicate the results for June and September, respectively.

Discussion

These results provide new experimental evidence that neighbouring plants can affect insect herbivory on a focal plant. However, we observed considerable variation in the direction and magnitude of the influence of surrounding vegetation. The diet breadth of insect herbivores and the spatial scale over which neighbouring plants are considered emerged as two key factors explaining damage response to plant diversity or structure. We found that damage caused by generalist leaf-feeding insect herbivores increased with increasing vegetation diversity (associational susceptibility), whereas the abundance of specialist insects decreased (associational resistance). Herbivory by generalist insects was best explained by tree cover and by structural complexity of surrounding vegetation for specialist insects. However, we found strong covariation between structural (cover or stratification diversity) and compositional (richness and diversity) vegetation variables. For example tree cover positively covaried with shrub and herbaceous diversities and stratification diversity was correlated to shrub oak cover. It was therefore difficult to identify which of these variables were the most relevant for explaining insect herbivory patterns.

The effect of the surrounding vegetation on herbivory was stronger over short distances for specialist insects (at the plot level) and stronger over larger distances for generalist insects (at the stand level). According to the resource concentration hypothesis, the likelihood of specialised herbivores locating their host plants is lower in more diverse plant communities (Root 1973). Here we found new evidence to support this hypothesis since leaf miner abundance decreased with increasing stratification diversity of vegetation around oak seedlings, and also when oak seedlings were less concentrated. Host plants are proportionally less frequent and are chemically or visually hidden from insects by non-host neighbours in plant communities more diverse in terms of structure or composition (Hambäck et al. 2003). By contrast, generalist herbivorous insects attacking oak seedlings, mostly composed of external leaf-feeders (Appendix A Table 1), may benefit from richer plant communities, which provide access to multiple host species, enabling insects to increase the size of their populations and/or their fitness (Unsicker et al. 2008), as they can easily shift from one host species to another (Jactel et al. 2007; Bertheau et al. 2010). Many examples of these opposite patterns of response have been reported, with greater damage due to polyphagous herbivores (Massey, Massey, Press, & Hartley 2006; Scherber et al. 2006; Pigot & Leather 2008; Schuldt et al. 2010), or lower levels of damage due to oligophagous herbivores (Otway, Hector, & Lawton 2005; Giffard et al. 2012) in more diverse plant communities.

High concentration of host plants facilitated host location, whereas the presence of non-host plants may deter insect herbivores, particularly if those plants are unpalatable (Otway et al. 2005; Massey et al. 2006). However, some studies have suggested that individual host plants may be less likely to be colonised in larger populations, due to a dilution effect (Otway et al. 2005; Bañuelos & Kollmann 2011). In our experiment, planting conspecific neighbours artificially increased host plant concentration and resulted in higher levels of leaf miner damage on focal oak seedlings. However, we did not observe an increase in abundance of leaf mines when oak density increased at the stand level. This would have been observed if the abundance of leaf miners had been high enough to exploit most of the food resources provided by canopy oak trees and then requiring a spill over onto other potential hosts such as oak seedlings. At the plot level, we found that the abundance of specialist insects was affected by the stratification diversity, which was also correlated to shrub oak cover. We can thus hypothesize a local effect of host plant concentration, as focal oak seedlings diluted amongst a natural regeneration of oaks were less likely to be colonized by leaf miners. Another mechanism underlying associational resistance to specialist herbivores involves the disruption of host plant location, with neighbouring plants hindering the detection of visual or olfactory cues by female moths before oviposition (Ross, Berisford, & Godbee 1990; Jactel et al. 2011). Vegetation diversity results in a complexity of plant chemical and structural cues, which may disturb arthropod orientation and mobility (Randlkofer et al. 2010). Such disruption is more likely to occur in close proximity of focal plants than at a larger scale, potentially accounting for the effect of vegetation complexity on the abundance of leaf miners on oak seedlings being limited at the plot level. Furthermore, the surrounding vegetation can conceal the host plant even if it is not particularly diverse (Hambäck et al. 2003).

By contrast, generalist herbivores display a remarkable ability to shift between diverse host plants (Bertheau et al. 2010) and may not be influenced by local sparseness of a particular plant species. This may account for the lack of a significant effect of host plant concentration on damage to oak seedlings caused by generalist herbivores. On the other hand, tree seedlings may suffer higher levels of damage than other plants, due to the vertical transfer of generalist insect herbivores from canopy trees (White & Whitham 2000; Pigot et al. 2008). This is consistent with our observation that damage to oak seedlings due to external feeders increased with increasing tree cover. However, tree, shrub and herbaceous covers positively covaried with tree, shrub and herbaceous diversities at stand level. Not only the amount but also the diversity of feeding resources may have then benefited generalist herbivores before they spill over onto oak seedlings but our experimental design did not allow disentangling the two mechanisms. The vegetation around tree seedlings may modify light and microclimate conditions, and this may also account for the effect of neighbouring plants on herbivory in focal plants (Barbosa et al. 2009). Leaves exposed to the sun generally have higher concentrations of defence compounds and lower nitrogen and water contents than shaded leaves (Dudt & Shure 1994), which may render them less attractive to insect herbivores. Our results about herbivory by generalist insects support this hypothesis, since we found that their damage decreased with decreasing tree cover i.e. with increasing light availability. However, we found the opposite to be true, with higher abundance of leaf mines in seedlings surrounded by low shrub cover and, hence, more exposed to light. Barber and Marquis (2011) also reported higher levels of herbivory on saplings previously exposed to high light intensity and argued that the search for oviposition sites may have led females to choose saplings with more foliage.

Insect herbivory may also be affected by top-down regulation. The natural enemies hypothesis predicts higher predator species richness and abundance in more diverse plant communities, resulting in lower levels of herbivory (Root 1973; Langellotto & Denno 2004). At the plot level, we observed a negative correlation between stratification diversity and abundance of leaf mines, which might have been due to higher levels of regulation by natural enemies. However, we found the opposite pattern at the stand scale, with higher levels of damage by generalist insects in stands with higher tree cover. Foraging by insectivorous birds or predatory arthropods may also be hindered by greater structural complexity (Sanders, Nickel, Grützner, & Platner 2008), resulting in larger populations of their prey, which then cause more extensive damage to plants (Giffard et al. 2012). Finally, we found that damage due to specialist insects was inversely correlated with damage due to generalist insects at the end of the growing season. This is consistent with previous findings of negative interactions between herbivore guilds (Kaplan & Denno 2007), particularly between exophytic and endophytic insects. In addition, generalist insect damage early in the season may have indirectly induced stronger chemical defences in oak leaves, thus decreasing their quality as oviposition sites for leaf miners.

References

Banks, J.E. (1998). The scale of landscape fragmentation affects herbivore response to vegetation heterogeneity. Oecologia, 117, 239-246.

Bañuelos, M.J., & Kollmann, J. (2011). Effects of host-plant population size and plant sex on a specialist leaf-miner. Acta Oecologica, 37, 58-64.

Baraza, E., Zamora, R., & Hódar, J.A. (2006). Conditional outcomes in plant-herbivore interactions: neighbours matter. Oikos, 113, 148-156.

Barber, N.A., & Marquis, R.J. (2011). Light environment and the impacts of foliage quality on herbivorous insect attack and bird predation. Oecologia, 166, 401-409.

Barbosa, P., Hines, J., Kaplan, I., Martinson, H., Szczepaniec, A., & Szendrei, Z. (2009). Associational Resistance and Associational Susceptibility: Having Right or Wrong Neighbors. Annual Review of Ecology Evolution and Systematics, 40, 1-20.

Bates, D., Maechler, M., & Bolker, B. (2011). lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-39.

Bertheau, C., Brockerhoff, E.G., Roux-Morabito, G., Lieutier, F., & Jactel, H. (2010). Novel insect-tree associations resulting from accidental and intentional biological 'invasions': a meta-analysis of effects on insect fitness. Ecology Letters, 13, 506-515.

Bommarco, R., & Banks, J.E. (2003). Scale as modifier in vegetation diversity experiments: effects on herbivores and predators. Oikos, 102, 440-448.

Dray, S., & Dufour, A.B. (2007). : The ade4 package: implementing the duality diagram for ecologists. Journal of Statistical Software, 22, 1-20.

Dudt, J.F., & Shure, D.J. (1994). The influence of light and nutrients on foliar phenolics and insect herbivory. Ecology, 75, 86-98.

Giffard, B., Corcket, E., Barbaro, L., & Jactel, H. (2012). Bird predation enhances tree seedling resistance to insect herbivores in contrasting forest habitats. Oecologia, 168, 415-424.

Gunton, R.M., & Kunin, W.E. (2007). Density effects at multiple scales in an experimental plant population. Journal of Ecology, 95, 435-445.

Hambäck, P.A., & Beckerman, A.P. (2003). Herbivory and plant resource competition: a review of two interacting interactions. Oikos, 101, 26-37.

Jactel, H., Birgersson, G., Andersson, S., & Schlyter, F. (2011). Non-host volatiles mediate associational resistance to the pine processionary moth. Oecologia, 166, 703-711.

Jactel, H., & Brockerhoff, E.G. (2007). Tree diversity reduces herbivory by forest insects. Ecology Letters, 10, 835-848.

Kaplan, I., & Denno, R.F. (2007). Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory. Ecology Letters, 10, 977-994.

Kramer, M. (2005). R2 statistics for mixed models. Proceedings 17th Conference on Applied Statistics in Agriculture. Kansas State University.

Langellotto, G.A., & Denno, R.F. (2004). Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. Oecologia, 139, 1-10.

Massey, F.P., Massey, K., Press, M.C., & Hartley, S.E. (2006). Neighbourhood composition determines growth, architecture and herbivory in tropical rain forest tree seedlings. Journal of Ecology, 94, 646-655.

Mazerolle, M.J. (2011). AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 1.15.

Otway, S.J., Hector, A., & Lawton, J.H. (2005). Resource dilution effects on specialist insect herbivores in a grassland biodiversity experiment. Journal of Animal Ecology, 74, 234-240.

Pigot, A.L., & Leather, S.R. (2008). Invertebrate predators drive distance-dependent patterns of seedling mortality in a temperate tree Acer pseudoplatanus. Oikos, 117, 521-530.

Pinheiro, J., Bates, D., Debroy, S., & Sarkar, D. (2011). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-100.

Prodon, R., & Lebreton, J.D. (1981). Breeding avifauna of a Mediterranean succession ï the holm oak and cork oak series in the eastern Pyrenees. 1. Analysis and modelling of the structure gradient. Oikos, 37, 21-38.

R Development Core Team (2011). R: A language and environment for statistical computing. V, Austria, ISBN: 3-900051-07-0.

Randlkofer, B., Obermaier, E., Hilker, M., & Meiners, T. (2010). Vegetation complexity ï The influence of plant species diversity and plant structures on plant chemical complexity and arthropods. Basic and Applied Ecology, 11, 383-395.

Root, R.B. (1973). Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (Brassica oleracea). Ecological Monographs, 43, 95-124.

Ross, D.W., Berisford, C.W., & Godbee, J.F. (1990). Pine tip moth, Rhycionia spp., response to herbaceous vegetation control in an intensively site-prepared loblolly-pine plantation. Forest Science, 36, 1105-1118.

Sanders, D., Nickel, H., Grützner, T., & Platner, C. (2008). Habitat structure mediates top-down effects of spiders and ants on herbivores. Basic and Applied Ecology, 9, 152-160.

Scherber, C., Mwangi, P.N., Temperton, V.M., Roscher, C., Schumacher, J., Schmid, B., & Weisser, W.W. (2006). Effects of plant diversity on invertebrate herbivory in experimental grassland. Oecologia, 147, 489-500.

Schuldt, A., Baruffol, M., Bohnke, M., Bruelheide, H., Härdtle, W., Lang, A.C., Nadrowski, K., von Oheimb, G., Voigt, W., Zhou, H.Z., & Assmann, T. (2010). Tree diversity promotes insect herbivory in subtropical forests of south-east China. Journal of Ecology, 98, 917-926.

Sutherland, W.J. (1996). Ecological Census Techniques: A Handbook. Cambridge: Cambridge University Press.

Tonhasca, A.J., & Byrne, D.N. (1994). The effects of crop diversification on herbivorous insects: a meta-analysis approach. Ecological Entomology, 19, 239-244.

Unsicker, S.B., Baer, N., Kahmen, A., Wagner, M., Buchmann, N., & Weisser, W.W. (2006). Invertebrate herbivory along a gradient of plant species diversity in extensively managed grasslands. Oecologia, 150, 233-246.

Unsicker, S.B., Oswald, A., Koehler, G., & Weisser, W.W. (2008). Complementarity effects through dietary mixing enhance the performance of a generalist insect herbivore. Oecologia, 156, 313-324.

Vehviläinen, H., Koricheva, J., Ruohomäki, K., Johansson, T., & Valkonen, S. (2006). Effects of tree stand species composition on insect herbivory of silver beach in boreal forests. Basic and Applied Ecology, 7, 1-11.

Vehviläinen, H., Koricheva, J., & Ruohomäki, K. (2007). Tree species diversity influences herbivore abundance and damage: meta-analysis of long-term forest experiments. Oecologia, 152, 287-298.

Warton, D.I., & Hui, F.K.C. (2011). The arcsine is asinine: the analysis of proportions in ecology. Ecology, 92, 3-10.

White, J.A., & Whitham, T.G. (2000). Associational susceptibility of cottonwood to a box elder herbivore. Ecology, 81, 1795-1803.

Zuur, A.F., Ieno I.E., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009). Mixed effects models and extensions in ecology with R. Berlin: Springer.

Photo 2. Cages dôexclusion des oiseaux (à gauche) et des arthropodes prédateurs (à droite) utilisées dans le dispositif expérimental (Brice Giffard).

2.2.2. Relier les traits de vie des oiseaux, des carabiques et des papillons à la fragmentation des habitats

Résumé

Nous nous intéressons ici à l'influence de la configuration du paysage sur la distribution des traits de vie au sein des communautés d'oiseaux, de carabiques et de papillons des paysages forestiers en mosaïque du sud-ouest de la France. Nous avons renseigné pour chaque espèce des trois taxa échantillonnés 12 traits biologiques et écologiques caractérisant la rareté, l'origine biogéographique, la taille, la guilde trophique, la capacité de dispersion, le potentiel reproductif et la phénologie. Nous avons utilisé une méthode d'ordination à trois tableaux, l'analyse RLQ, pour relier directement les traits des oiseaux, carabiques et papillons au même jeu de métriques paysagères calculées dans des buffers de 400 m autour des points d'échantillonnage. Les analyses RLQ montrent des corrélations significatives entre traits de vie et configuration du paysage pour les trois taxa. Les espèces à enjeu de conservation des trois taxa se caratérisent par une combinaison de traits qui les rend particulièrement sensibles à la fragmentation des milieux ouverts à l'échelle du paysage. Ces traits sont une faible productivité, une taille intermédiaire, une aire biogéographique restreinte, une phénologie tardive et une alimentation à terre pour les oiseaux ; une taille intermédiaire, une activité adulte printanière, une distribution nordique, et une période de reproduction estivale pour les carabiques ; et une aire restreinte, un hivernage sous forme d'œufs ou de chenilles, une faible mobilité, une spécialisation alimentaire et une courte période de vol pour les papillons. La prise en compte des traits apporte une perspective fonctionnelle à la définition de mesures de conservation adéquates des espèces menacées d'oiseaux, de carabiques et de papillons dans les paysages forestiers en mosaïque.

Abstract

The goal of the present study is to assess how landscape configuration influenced the distribution of life traits across bird, carabid beetle and butterfly communities of mosaic forest landscapes in south-western France. A set of 12 traits was selected for each species, characterizing rarity, biogeographical distribution, body size, trophic guild, dispersal power, reproductive potential and phenology. We used a three-table ordination method, RLQ analysis, to link directly bird, beetle and butterfly traits to the same set of landscape metrics calculated in 400 m-radius buffers around sample points. RLQ analyses showed significant associations between life-history traits and landscape configuration for all three taxonomical groups. Threatened species from all groups were characterized by a combination of life traits that makes them especially sensitive to the fragmentation of herbaceous and shrub-dominated habitats at the landscape scale. These key life traits were low productivity, intermediate body mass, restricted geographic range, late phenology and ground gleaning for threatened birds, intermediate body size, spring adult activity, northern distribution and summer breeding period for threatened carabids, and restricted range, overwintering as eggs or larvae, low mobility, monophagy and short flight periods for threatened butterflies. Focusing on species life traits can provide a functional perspective, which helps to determine adequate measures for the conservation of threatened species and communities of several taxonomical groups in mosaic landscapes.

Introduction

A major consequence of global change on biodiversity is the biotic homogenization of species communities through the gradual replacement of native taxa by non-indigenous species (McKinney and Lockwood 1999). Species communities are thus increasingly composed of generalists, whereas specialists show a general decline (Warren et al. 2001, Julliard et al. 2003, Kotze and OôHara 2003). At the functional level, declining species are expected to share particular life-history traits, such as large size, low fecundity, rarity, slow dispersal or high specialization, irrespective of taxonomy (McKinney and Lockwood 1999, Cofre et al. 2007). These functional types of species will be affected more than others by habitat loss and fragmentation (Davies et al. 2000, Ewers and Didham 2006). The knowledge of which traits make a species sensitive to habitat fragmentation may consequently be a useful tool for the identification of target groups of species in applied conservation biology (Summerville et al. 2006, Samways and Lu 2007). The following traits have proved to be relevant predictors of species sensitivity to fragmentation: population size and fluctuation, competition and disturbance sensitivity, micro-habitat specialization, matrix use, rarity and biogeographic position (Henle et al. 2004). Other traits such as dispersal ability, body size or trophic position may also predict species response to fragmentation, depending on scale and interactions with other traits (Davies et al. 2000, Baguette and Van Dyck 2007). Focusing on the distribution of life-history traits across environmental gradients instead of species themselves allows generalizing the results for both theoretical and applied purposes (McGill et al. 2006). Moreover, some authors have stated that ecosystem functioning depends more strongly on functional diversity, i.e. the value and range of species traits, than species richness per se (Diaz and Cabido 2001). Conserving functional diversity at the landscape level may consequently help to maintain large-scale and long-term ecosystem processes by functional compensations between species (Loreau et al. 2003, Tscharntke et al. 2008). As a result, the relevance of life-history trait-based methods to analyze species responses to disturbance is increasingly acknowledged (Söderström et al. 2001, Cole et al. 2002, Summerville et al. 2006). There is actually a need for multiscale and multitaxa approaches taking into account the distinct responses of different species guilds to landscape structure and composition (Grand et al. 2004, Cushman et al. 2008). However, to date few studies have attempted to directly link landscape attributes to the distribution of a set of species life traits (Ribera et al. 2001, Hausner et al. 2003). Here, we examined how landscape structure and composition could be related to the distribution of bird, carabid beetle and butterfly traits in mosaic landscapes dominated by maritime pine *Pinus pinaster* plantation forests in south-western France.

The maritime pine plantations of south-western France represent a good example of production landscapes harbouring an important animal biodiversity. Previous studies have demonstrated the importance of maintaining semi-natural habitat patches embedded within the pine plantation matrix (firebreaks, heathlands, meadows and deciduous woodlands) for the long-term conservation of threatened species (Barbaro et al. 2007, van Halder et al. 2008). Such ôsletsô probably act as key habitats (e.g., for feeding, wintering, or breeding requirements) in the life cycle of a large range of sensitive species that may be lost in case of increasing landscape homogenization (Tscharntke et al. 2002, Duelli and Obrist 2003, Purtauf et al. 2005). In plantation forests, management actions should be compatible with the conservation of keystone and threatened species, as well as functional diversity, through the maintenance of a structurally complex landscape matrix including patches and corridors of native vegetation (Fischer et al. 2006). However, little information exists about the management of landscape mosaics for the conservation of several species having contrasting responses to the same landscape configurations (Holzkämper et al. 2006). In the present work, we aimed at linking directly the distribution of life-history traits in bird, carabid beetle and butterfly communities to the same set of explanatory variables characterizing landscape structure and composition. Our goal was to define functional groups of species sharing similar life traits and similar responses to environmental variables, regardless of their taxonomic status. We performed a set of RLQ analyses, a three-table ordination method that allows a direct ordination of species life traits according to various environmental variables through the link provided by the site x species table (Doledec et al. 1996, Ribera et al. 2001, Hausner et al. 2003, Cleary et al. 2007, Mellado et al. 2008). We used a multitaxa data set collected in the same study area in order to define conservation priorities from a functional, rather than only taxonomical, point of view. Our main objective was to identify, across a wide range of organisms, which combination of life-history traits make species sensitive to habitat loss and fragmentation in mosaic landscapes.

Methods

Study area

The study was located in plantation forests that cover around 1 million ha in the Landes de Gascogne region, south-western France. The landscape is dominated by even-aged stands of native maritime pine with a rotation cycle of 40-50 years. Such a forest management creates mosaic landscapes composed of even-aged pine stands interspersed with recent clearcuts covered by grassland or heathland vegetation, and fragments of semi-natural habitats. The most important semi-natural elements of the landscape are herbaceous or shrubby firebreaks and remnants of deciduous woodlands dominated by *Quercus robur, Q. pyrenaica* and *Betula pendula* occurring along rivers or as patches of a few hectares. Three areas were selected for species surveys and GIS-mapping of land cover types: Tagon (5000 ha, 44°40ôN, 0°57ôW), Cestas (8000 ha, 44°44ôN, 0°46ôW) and Solferino (10500 ha, 44°08ôN, 0°55ôW). The nine main land cover types represented in the regional landscape included four stages of the rotation cycle in maritime pine plantations (herbaceous clearcut, shrubby clearcut, young pine (<7 m) and mature pine stands (>7 m), four semi-natural habitats (hay meadow, herbaceous firebreak, deciduous woodland and deciduous hedgerow), and crops (maize field).

Species surveys

Species surveys were performed using a stratified sampling design according to the main land cover types cited above, except crops that were not sampled (see Barbaro et al. 2007 and van Halder et al. 2008 for a detailed description of the sampling design). We surveyed bird communities at 287 sampling plots using point-counts with unlimited distance (Bibby et al. 2000). Two censuses per year were performed, the first during the early breeding season (early April to mid-May) and the second during the late breeding season (mid-May to late June) in 2002-2003. There was a systematic permutation of first and second census between the two observers involved, in order to eliminate a potential observer effect. Points were established at least 400 m apart to avoid double counting, and each visit lasted 20 min, within 5 h after sunrise and avoiding adverse weather conditions such as strong wind and heavy rain (Bibby et al. 2000). We recorded all birds heard and seen except waterbirds, raptors and aerial feeders (swallows and swifts). We used a semi-quantitative abundance index ranging from 0.5 for a non-singing bird to a maximum score of 5, each territorial male or pair being noted as 1. The maximum score obtained between the two visits was the species abundance index used in further analyses (Hausner et al. 2003).

We sampled carabid beetles at 244 sampling plots using pitfall traps, a standardized sampling method allowing the comparison of ground-dwelling beetle assemblages at different sites when it is not necessary to know the actual species abundances (Rainio and Niemelä 2003). We used removable glass traps (opening diameter = 9 cm, volume = 500 ml) levelled to the soil surface and covered with wood plates supported by four nails to protect traps from rain (Purtauf et al. 2005). Each trap was filled with a solution of quaternary ammonium diluted at 25 % and collected every three weeks. Trapping went continuously from April to October in 2002-2003. The number of individuals caught in a given trap during the entire trapping period was pooled for data analyses (Cole et al. 2002). Butterflies were surveyed in 81 plots using line-transects (Pollard and Yates 1993). Within each plot and along its edge, a 400 m-long and 5 m-wide linear transect was laid out and all butterflies were counted within this strip. Each plot was visited four times (between mid-May and early September of 2004) during appropriate weather conditions (t°C >20, cloudless or just a few clouds and wind speed <5 Beaufort). Butterfly species were identified by sight or caught and released after determination for species difficult to identify. We pooled the total number of individuals per species over the two transects for each plot (interior and edge) and the four visits for data analyses. Interior and edge counts were summed because we aimed at linking species assemblages and life traits to landscape metrics rather than local habitat variables, and sampling only stand interiors would have underestimated the abundance of several species more abundant at stand edges than in the interiors (Ohwaki et al. 2007).

Life-history traits

We selected a set of 12 life-history traits that were expected to be good predictors of species response to fragmentation for the three taxonomical groups (Henle et al. 2004). We used only traits for which detailed and complete information has been published for all species recorded. Although it was not possible to use the same traits and categories for the three species groups, we aimed at characterizing the main life attributes regarding (i) rarity and biogeographical distribution, (ii) trophic guild, (iii) breeding parameters, (iv) body size or mass, (v) mobility, and (vi) phenology (Tables 1-3). For the three taxa, we retained four attributes related to rarity, biogeography and conservation status (Kotze and OôHara 2003): (i) overall population trend at the national level, (ii) national and (iii) regional rarities, defined as the percentage of national or regional range where the species is present, and (iv) biogeographic position of the European range (northern, widespread or southern). Species conservation status was evaluated with the most updated data available for birds (Julliard and Jiguet 2005) and butterflies (Lafranchis 2000) at the national and regional levels. For carabid beetles, we estimated conservation status (trend and rarity) at the European level using red-list data because complete information was not available at the French national level (Turin 2000), and the regional rarity was defined according to Tessier (2000). Data on other life-history attributes were taken from Cramp et al. (1994) for birds, Turin (2000) and Ribera et al.

(2001) for carabids, Bink (1992) and Lafranchis (2000) for butterflies. We used categories defined in Laiolo et al. (2004) for bird foraging techniques, and Tscharntke et al. (2002) for butterfly polyphagy levels. Additional data on butterfly life traits that are relevant at the regional level (regional rarity, local flying period, local polyphagy and host plant categories) were recorded by van Halder and Jourdain (unpubl. data). Finally, the number of categories per trait was also partly determined by the number of species that shared the same category, in order to keep a balanced number of species per category (cf Annexes 1 et 2) .

Landscape metrics

The three study regions were GIS-mapped (ArcView, ESRI, USA) according to land-use types using aerial colour photographs (summer 2000 and 2002) with a resolution of 50 cm as background layer, followed by field validation. We distinguished 10 land cover types on these maps: the eight surveyed habitats plus croplands and urban areas. The latter type was not used in further analyses because urbanization pressure is still low in these forest-dominated landscapes and the percentage cover of urban areas is negligible. Landscape metrics were calculated within 400 m-radius circular buffers (50.3 ha), from the center of the sampled plots, using Fragstats 3.3 in raster version and a cell size of 2.5 m (McGarigal et al. 2002). As we aimed at relating species life traits to the same landscape metrics for the three sampled groups, we used a distance of 400 m because it is ecologically meaningful for these three taxa (Weibull et al. 2003). A distance of 400 m is actually above the mean foraging or dispersal distances for most bird and carabid species involved in the present study (Riecken and Raths 1996, Paradis et al. 1998, Barbaro et al. 2008). Within each buffer, we calculated the following metrics characterizing both composition and configuration of the landscape: the percentage cover of the nine main land cover types, edge density (in m.ha^{-1}), mean patch area (in ha) and the Shannon index of habitat diversity (McGarigal et al. 2002). The selection procedure used for landscape metrics is fully described in previous works (Barbaro et al. 2007, van Halder et al. 2008).

	Birds		Carabid beetles		Butterflies	
RLQ axes	F1	F2	F1	F2	F1	F2
Eigenvalue	0.043	0.010	0.206	0.091	0.057	0.040
Covariance	0.207	0.102	0.454	0.302	0.239	0.199
Correlation	0.226	0.152	0.371	0.403	0.266	0.289
R/RLQ	86.3	89.9	89.8	88.5	92.3	86.6
L/RLQ	45.4	40.1	42.1	47.3	43.7	56.0
Q/RLQ	73.5	79.1	60.7	79.2	57.1	67.6

Table 1. Results of RLQ analyses and comparison with the separate analyses. R/RLQ represents the percentage of the variance of the separate analysis of R (landscape variables table) accounted for by each of the first two ordination axes of the RLQ analyses. L/RLQ is the same for the separate analysis of L (species composition table) and Q/RLQ is the same for the separate analysis of Q (species traits table). It is calculated as the ratio of the axis eigenvalue of RLQ analysis on the corresponding axis eigenvalue of separate analysis.

Data analysis

The methodological question of directly linking life traits of species to environmental variables through the ordination of the species abundance matrix was resolved by Doledec et al. (1996). They named RLQ analysis a generalization of co-inertia analysis (Dray et al. 2003) for analysing the joint structure of three-table data sets where R is the matrix of p environmental variables recorded at m sites, L is the matrix of k species abundances noted at m sites, and Q the matrix of n life traits characterizing the k species (Ribera et al. 2001). In such a design, R, L, and Q tables are linked both by their m rows (sites) and k columns (species), and the ordination of the L-species table represents the link between the R-environment table and the Q-trait table (Doledec et al. 1996). The first step of RLQ analysis is the separate analyses of R, L and Q-tables. The L-species abundance tables of bird, beetle and butterfly species were first analysed by Correspondence Analyses (CA), after eliminating the rare species recorded with less than 10 individuals for birds and less than 5 individuals for beetles and butterflies (Ribera et al. 2001, Cleary et al. 2007). We consequently analysed final data tables of 287 sites x 52 species for birds, 244 sites x 45 species for carabids and 81 sites x 42 species for butterflies. The R-environment tables were analysed by normed Principal Correspondence Analyses (PCA) with CA site scores used as row weighting to allow the coupling of R and L (Hausner et al. 2003). The Q-trait tables were analysed by Multiple Correspondence Analyses (MCA) using CA species scores for column weighting. When the L-table is analysed by way of a CA, RLQ analysis aims at selecting ordination axes that maximize the covariance between linear combinations of the columns of R- and Q-tables (Doledec et al. 1996). RLQ analysis is a doubly constrained ordination where the stand scores in the R-table constrain the stand scores in the L-table, and the species scores in the Q-table constrain the species scores in the L-table (Hausner et al. 2003). The overall significance of the relationships between landscape variables of the R-tables and species traits of the Q-tables was assessed by a Monte-Carlo test with 1000 permutations on total inertia of the RLQ analyses (Doledec et al. 1996). We compared the total inertia of the three RLQ analyses with the inertia of unconstrained separate analyses of R, L and Q to evaluate the percentage of the variation in separate analyses taken into account by the RLQ analysis on the main ordination axes (Hausner et al. 2003). RLQ analyses were performed using the ćade4ô package in R software (Dray and Dufour 2007).

Results

Birds

There was a significant overall association between bird species traits and landscape variables (permutation test, P < 0.001). The first two axes of RLQ analysis accounted for most of the variance of the corresponding axes in the separate analyses of landscape metrics, species traits and species composition tables (Table 1). The landscape variables that correlated best with the first axis were mean patch area on the negative side and edge density and deciduous wood cover on the positive side (Table 2 and Fig. 1a). It matched a landscape fragmentation gradient from mosaics dominated by large open habitats (young pines, crops and clearcuts) to more diverse mosaics with semi-natural habitat fragments including deciduous woods, hedgerows and meadows. The species traits showing the highest correlation ratios with the first axis were foraging technique, national and regional rarities, nest location and migration status (Table 6). Rare and threatened species (RR_3, NR_3, T_londec) of mid size and low productivity (BM_3, CS_1) having either northern or southern distributions (B_north, B_south) and being mostly ground gleaners and tropical migrants (F_grglean, M_tromig) were associated with the less fragmented open habitats of the younger stages of the silvicultural cycle (Fig. 1b). They included *Anthus campestris* or *Lanius collurio* as typical species (Fig. 1c). Fragmented landscape mosaics with deciduous woods and meadows were associated with ground probers, bark foragers, cavity nesters and early breeders of high productivity, including both large species such as *Turdus merula* and smaller species such as *Parus major* (Fig. 1c). These species are not threatened (T_increa, NR_1, RR_1) and resident or temperate migrants (M_resid, M_temmig). The second axis was related to a gradient of landscape composition from mosaics including non-forest habitats (crops and meadows) to mosaics dominated by continuous mature plantations (Fig. 1a). The species traits correlated with this axis were foraging technique, clutch size and body mass (Table 3). Small canopy gleaners with high productivity and small home ranges (BM_1, F_caglea, CS_3, H_small) tended to occur in landscapes dominated by continuous pine plantations, whereas large ground foragers or seed eaters with low productivity (CS_1, BM_3, D_graniv, F_grprob) were preferably found in landscapes where plantations are mixed with other non-forest habitats (Fig. 1b). Typical species included *Phylloscopus collybita* or *Parus cristatus* on one side, and *Lullula arborea* or *Streptopelia turtur* on the other side (Fig. 1c).

Landscape variables	Abbrev.	F1-Bird	F2-Bird	F1-Beet	F2-Beet	F1-Butt	F2-Butt
Edge density (m.ha-1)	EDGE	**0.41**	0.01	**0.45**	-0.13	**0.46**	-0.07
Mean patch area (ha)	AREA	**-0.43**	0.15	**-0.43**	0.18	**-0.35**	0.11
Shannon diversity index	SHDI	0.30	0.05	0.29	-0.15	**0.43**	0.01
Firebreak cover (%)	FIRE	-0.12	0.01	-0.30	0.29	0.19	-0.02
Meadow cover (%)	MEAD	0.28	**0.38**	0.25	**0.46**	0.06	-0.20
Crop cover (%)	CROP	-0.14	0.33	0.04	-0.01	-0.16	**-0.54**
Clearcut cover (%)	CLEA	-0.24	0.26	-0.09	-0.11	-0.01	0.09
Shrubland cover (%)	SHRU	0.11	-0.25	-0.08	-0.04	**0.48**	**0.42**
Young pine cover (%)	YPIN	**-0.37**	0.20	**-0.40**	0.22	0.04	0.27
Mature pine cover (%)	MPIN	-0.07	**-0.69**	-0.08	**-0.61**	-0.33	0.13
Deciduous wood cover (%)	DECI	**0.42**	0.09	**0.35**	0.21	0.27	**-0.59**
Hedgerow cover (%)	HEDG	0.23	0.26	0.26	**0.39**	0.04	-0.18

Table 2. Correlations between landscape variables and RLQ axes for birds, carabid beetles and butterflies. Highest correlation values are indicated in bold.

Carabid beetles

The RLQ analysis showed a significant association between life traits of carabid beetles and landscape variables (permutation test, P < 0.001). The first two axes accounted for a large part of the variance in the separate analyses of environment, traits and species tables (Table 2). The first axis had the highest correlations with edge density on the positive side, and mean patch area and young pine cover on the negative side (Table 2 and Fig. 2a). As with the bird trait analysis, it was related to a gradient of landscape fragmentation. The highest correlation ratios were obtained for regional rarity, biogeography and activity period (Table 3 and Fig. 2b). Regionally common species (RR_1, RR_2) of southern distribution (B_south) and active in summer and autumn (P_sumaut) were associated to fragmented landscapes with deciduous woods (e.g., *Carabus purpurascens* or

Pterostichus madidus). On the contrary, regionally rare and declining species (T_declin, RR_3, RR_4) of northern distribution (B_north), often active in late spring (P_latspr), were more abundant in less fragmented landscapes with young pine plantations and firebreaks (e.g., *Harpalus rufipalpis* or *Poecilus versicolor*, Fig. 2c). The second axis of the RLQ analysis was correlated with mature pine cover on the negative side, meadow cover and hedgerow cover on the positive side. This axis was hence similar to the landscape composition gradient obtained for the analysis of bird traits (Fig. 2a). The best correlation ratios for beetle traits on this axis were obtained for body size, diet and breeding season (Table 3). Large predatory and brachypterous autumn breeders (BS_5, D_predat, W_brachy, S_autumn) tended to prefer landscape mosaics dominated by continuous mature pine plantations, whereas small phytophagous and dimorphic spring breeders (BS_4, D_phyto, W_dimor, S_spring) occurred preferably in heterogeneous landscape mosaics including semi-natural herbaceous habitats, such as firebreaks and meadows (Figs. 2b and c).

Bird life traits	F1	F2	Beetle life traits	F1	F2	Butterfly life traits	F1	F2
National trend	0.10	0.04	European trend	0.13	0.14	National trend	**0.27**	**0.18**
National rarity	**0.12**	0.03	European rarity	0.01	0.01	National rarity	0.13	0.16
Regional rarity	**0.12**	0.02	Regional rarity	**0.30**	0.12	Regional rarity	**0.20**	0.07
Biogeography	0.09	0.06	Biogeography	**0.19**	0.14	Biogeography	0.06	**0.24**
Foraging	**0.20**	**0.23**	Daily activity	0.08	0.03	Polyphagy level	0.04	0.09
Diet	0.04	0.05	Diet	0.03	**0.22**	Host plant type	0.07	0.09
Nest location	**0.12**	0.06	Overwintering	0.01	0.05	Overwintering	0.02	**0.33**
Home range	0.01	0.04	Body color	0.01	0.01	Population density	0.15	0.04
Clutch size	0.09	**0.19**	Breeding season	0.08	**0.16**	Number of eggs	**0.17**	0.04
Body mass	0.06	**0.12**	Body size	0.09	**0.24**	Wing length	0.06	0.11
Migration	**0.12**	0.04	Wing development	0.06	0.13	Mobility	0.00	**0.29**
Laying date	0.06	0.11	Activity period	**0.21**	0.11	Flying period	**0.19**	0.09

Table 3. Correlation ratios between life traits and RLQ axes for birds, carabid beetles and butterflies. Highest correlation ratios are indicated in bold.

Butterflies

There was a significant overall association between butterfly life traits and landscape variables (permutation test, $P < 0.001$). The first two axes of the RLQ analysis accounted for a large part of the variance in the separate analyses of tables (Table 1). The first axis was correlated with shrubland cover, edge density and Shannon diversity index on the positive side, mean patch area and mature pine cover on the negative side (Table 2 and Fig. 3a). The main gradient of landscape structure is therefore slightly different for butterflies than for birds and beetles, opposing landscape mosaics dominated by large and homogeneous mature pine plantations with diverse and fragmented mosaics including open habitats (shrublands and firebreaks). On this axis, national trend, regional rarity, flying period and number of eggs had the highest correlation ratios (Table 3 and Fig. 3b). Nationally declining species with one spring generation or two generations and high egg productivity (T_dec2, F_2gener, NR_2, NE_4, F_1spring) tended to occur in fragmented landscape mosaics with high diversity, whereas regionally rare to common species with three flight generations and mid to low productivity (RR_3, NE_2, F_3gener, RR_1) preferred plantation-dominated mosaics with low habitat diversity and low fragmentation. The first species group included *Euphydryas aurinia* or *Melitaea cinxia*, and the second group included *Coenonympha pamphilus* or *Lasiommata megera* (Fig. 3c). The second axis matched a landscape composition gradient since it was negatively correlated with deciduous woodland cover and crop cover, and positively with shrubland cover (Table 2 and Fig. 3a). The species traits with highest correlation ratios were overwintering, mobility, biogeography and national trend (Table 3). Large, widespread, polyphagous and mobile species overwintering as chrysalis or imago, and using shrub or tree as host plant (O_chrysa, H_shrub, P_polyph, WL_4, B_widesp, M_mobile, M_ratsed) were associated with landscape mosaics where pine plantations are fragmented by other land uses such as cropland or deciduous woodland (Fig. 3b). This species group typically included *Vanessa cardui* or *Gonepteryx rhamni* (Fig. 3c). On the contrary, nationally rare and large-scale declining species with northern or southern distribution, being sedentary, rather small, overwintering as eggs or young caterpillar and flying in one summer generation (T_dec3, B_north, NR_3, O_eggs, M_sedent, WL_2, B_south, F_1summ) were preferably found in landscape mosaics including open habitats created by the silvicultural cycle, i.e., secondary shrublands and young pine plantations (Fig. 3b). Species associated with this group were *Coenonympha oedippus* or *Heteropterus morpheus* (Fig. 3c).

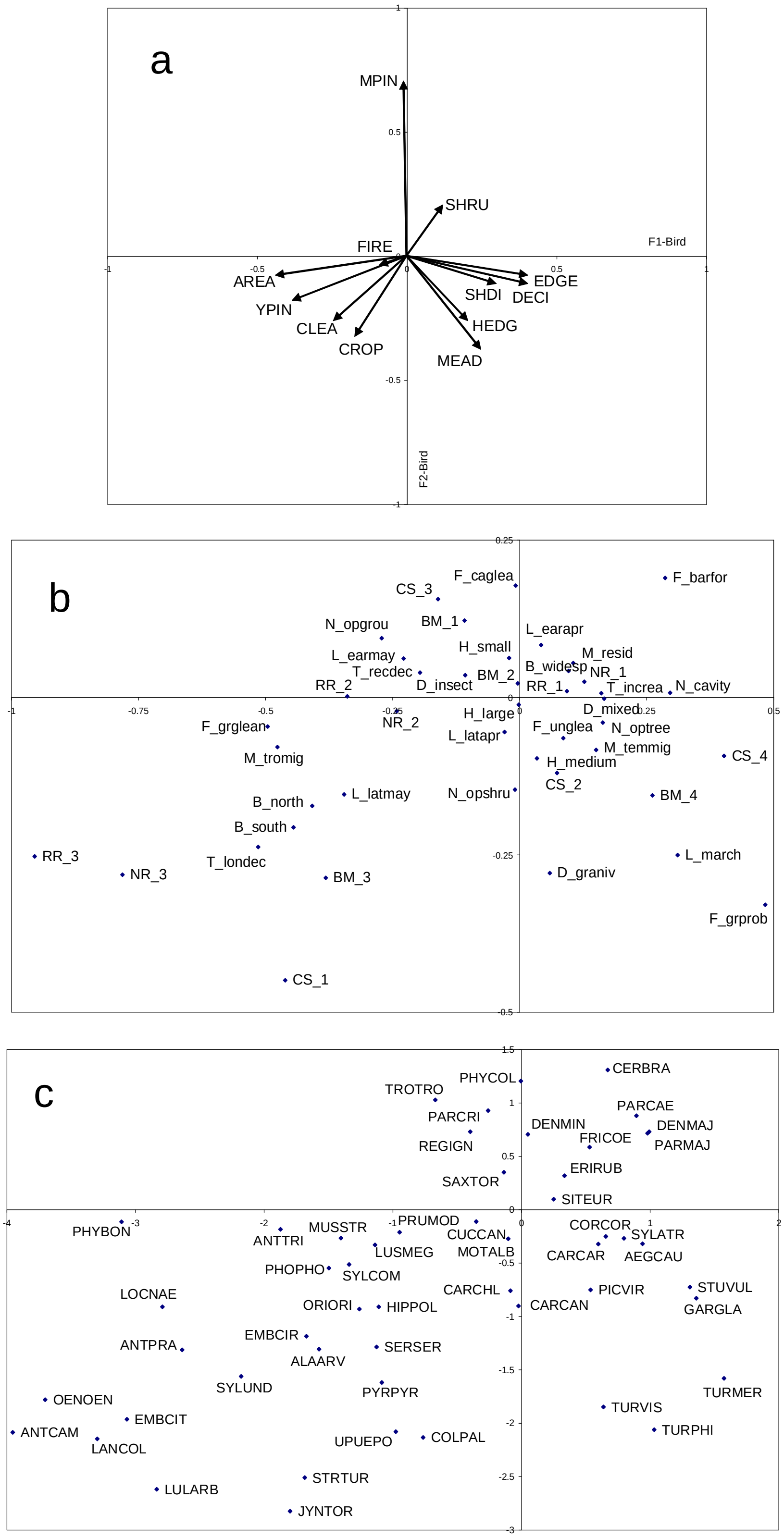


Fig. 1 Graphical display of RLQ scores of (a) landscape variables, (b) life traits categories and (c) bird species. See Annexe 1 for the codes of life traits and Table 2 for landscape variables. Abbreviations of bird species names use the first three letters of genus and species scientific names, e.g. PHYBON = *Phylloscopus bonelli.*

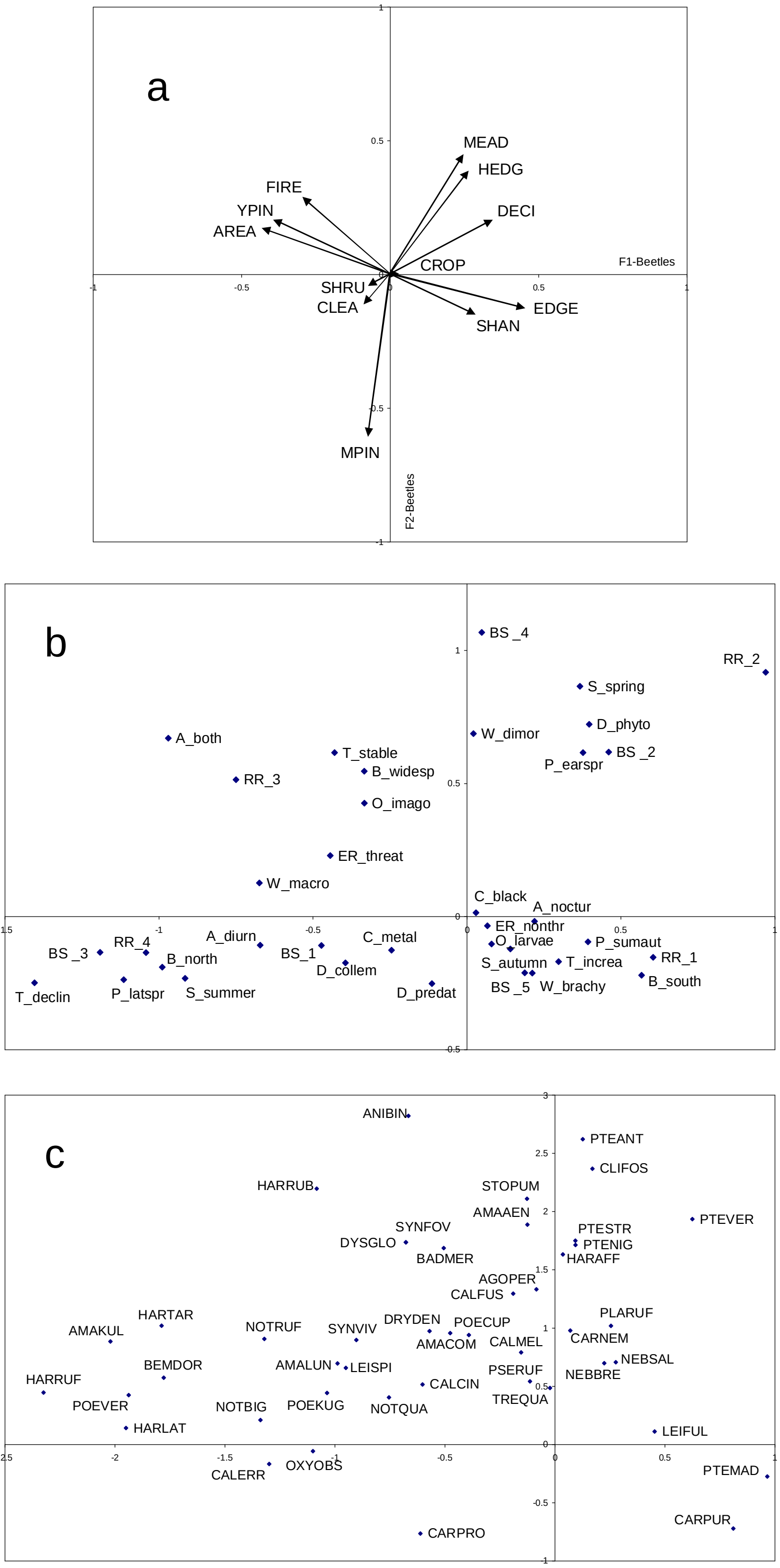


Fig. 2 Graphical display of RLQ scores of (a) landscape variables, (b) life traits categories and (c) carabid beetle species. Abbreviations of beetle species names use the first three letters of genus and species scientific names, e.g., HARRUF = *Harpalus rufipalpis*.

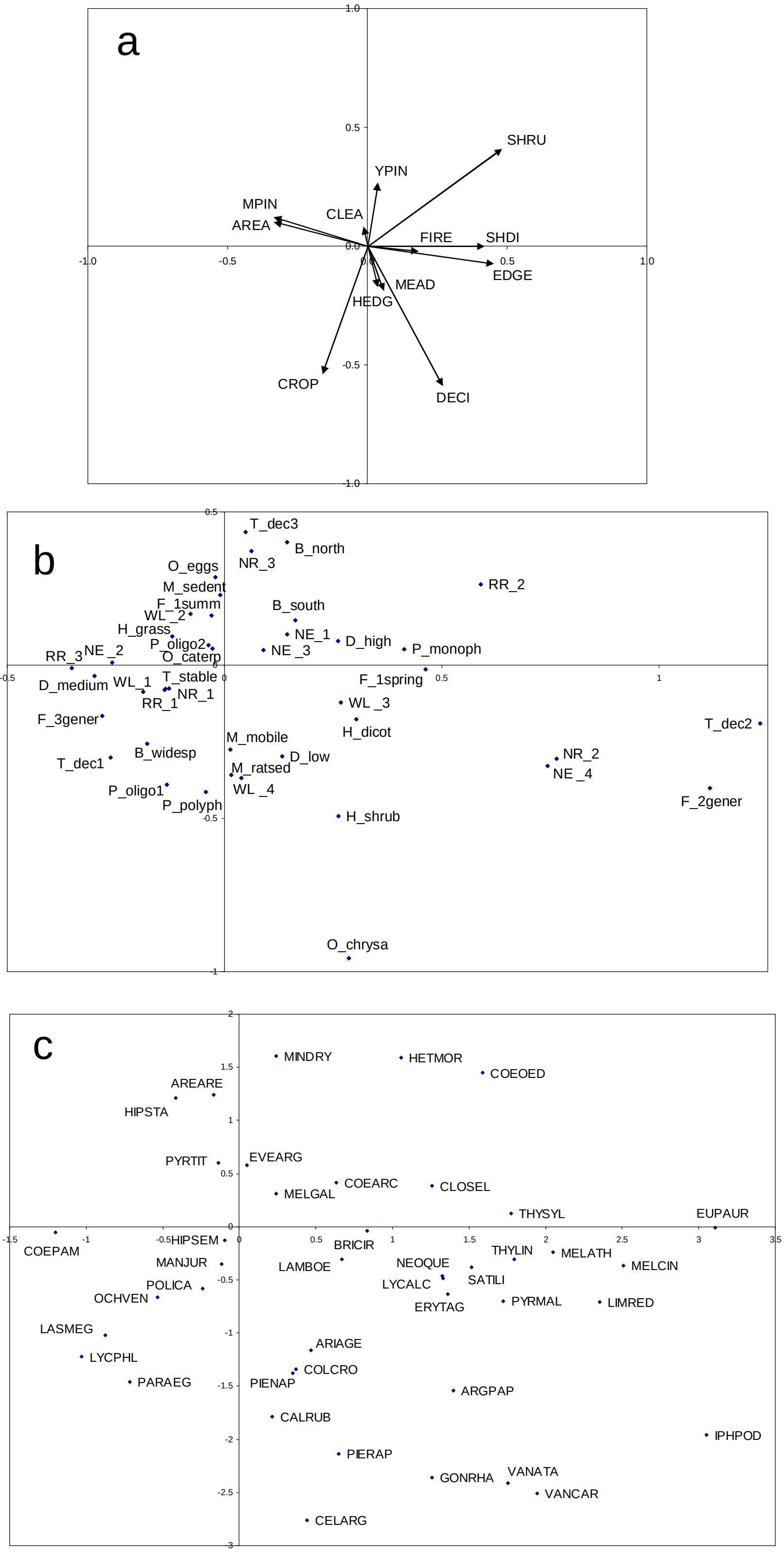


Fig. 3 Graphical display of RLQ scores of (a) landscape variables, (b) life traits categories and (c) butterfly species. See Annexe 2 for the codes of life traits. Abbreviations of butterfly species names use the first three letters of genus and species scientific names, e.g., MINDRY = *Minois dryas*.

Discussion

The three taxonomical groups showed a consistent pattern in the distribution of life-history traits on the main gradients of landscape structure and composition. RLQ analyses allowed to identify a combination of species traits sensitive to environmental changes that may represent useful indicators of large-scale impacts of human activities, such as forestry and agriculture, on the conservation of biodiversity (Ribera et al. 2001, Hausner et al. 2003, Cleary et al. 2007, Mellado et al. 2008). Habitat fragmentation and composition in the mosaic landscapes of the study area were directly related to species attributes characterizing rarity and biogeography, trophic guild, body size, mobility, reproductive potential and phenology. Moreover, the life attributes related to species conservation status were correlated with the gradients of landscape configuration for the three taxonomical groups studied. Birds of conservation concern showed a consistent and negative response to the landscape-scale fragmentation of open habitats and were largely restricted to landscape mosaics with the highest cover of young pine plantations and clearcuts. They tended to avoid both landscapes dominated by continuous mature pine plantations and fragmented landscapes with high habitat diversity including deciduous woodlands and meadows. They were characterized by low productivity, rather large body mass (25-50g), restricted biogeographic range (either northern or southern), late phenology, and their foraging technique was mainly ground gleaning. Threatened carabid beetles were likewise restricted to the less fragmented landscape mosaics, preferring those with high cover of young pine plantations and herbaceous firebreaks. As noticed for threatened birds, they avoided continuous mature plantations as well as heterogeneous mosaics with deciduous woods and meadows. These species tended to share intermediate body size, spring adult activity, northern biogeographic distribution and summer breeding period. The butterflies of highest conservation concern seemed to be less sensitive to landscape fragmentation but they depended more on the occurrence of particular habitats, favouring shrublands, young pine plantations and firebreaks against mature pine plantations, crops and deciduous woods. Associated life traits were restricted range, overwintering as eggs or young larvae, low mobility, monophagy and short flight period.

Rarity and biogeography

Species life attributes related to the degree of rarity in a given area, or to the restriction of biogeographical range, have proven to be good predictors of species sensitivity to environmental changes, such as habitat fragmentation (Kotze and Oô Hara 2003, Cofre et al. 2007). Species with a restricted distribution range often show strong negative responses to forest fragmentation (Cleary et al. 2007, Ohwaki et al. 2007). However, rare species should be used with care because the rarity of a given taxon is not a good indicator for the occurrence of other rare taxa (Grand et al. 2004). Populations close to the margins of the species range are also more likely to experience long-term declines than those close to the range core (Warren et al. 2001). We found that birds, butterflies and carabid beetles with northern distribution in Europe, and therefore close to their southern range limit in south-western France, favoured landscapes with less fragmented open habitats, i.e., large grasslands and heathlands. These northern species are probably more prone to decline than others in the context of current global change (Julliard et al. 2003, Hampe and Petit 2005). Moreover, the past landscape in the study region was mostly composed of large patches of grasslands and heathlands before the general afforestation process in the middle of the 19th century (Barbaro et al. 2007). The current landscape can therefore be viewed as the result of long-term and large-scale fragmentation of the past open habitats, and homogenization of previously patchy and heterogeneous vegetation, by modern intensive forestry. As elsewhere in Europe where semi-natural grasslands and heathlands have seriously decreased during the last decades, the species with unfavourable conservation status occurring in the study area were mostly grass-shrubland specialists (Söderström et al. 2001, Warren et al. 2001, Duelli and Obrist 2003).

Trophic guild

The use of trophic guilds in understanding species responses to disturbance or habitat fragmentation is widely used by ecologists (Tscharntke et al. 2002, Purtauf et al. 2005, Cleary et al. 2007), although the results obtained are not always consistent with theoretical predictions (Henle et al. 2004). In the present work, bird foraging technique was clearly dependent on landscape configuration. Large ground insectivore gleaners responded negatively to open-habitat fragmentation, whereas ground probers and seed eaters favoured high landscape diversity, including meadows and deciduous woodlands. Granivore abundance is known to increase significantly following human disturbance, whereas large ground insectivores are often negatively affected by grazing or logging (Söderström et al. 2001, Cleary et al. 2007, Tscharntke et al. 2008). For carabid beetles, habitat fragmentation tends to affect predators more strongly than phytophagous species (Davies et al. 2000), which benefit from surrounding landscape diversity, especially semi-natural grasslands (Ribera et al. 2001, Weibull et al. 2003, Purtauf et al. 2005). We found a similar pattern, with seed-eating carabids being associated with meadows and deciduous woods in the surrounding matrix. For butterflies, high landscape diversity and presence of shrublands and firebreaks favoured monophagous species, whereas polyphagous species were associated with the presence of crops and deciduous woodlands in the surrounding landscape. This is consistent with other studies showing the higher sensitivity of monophagous butterflies to habitat loss (Tscharntke et al. 2002, Ohwaki et al. 2007).

Body size and mobility

Body size and dispersal ability may also be good predictors of species sensitivity to landscape fragmentation, although generally interacting with other correlated traits (Henle et al. 2004, Baguette and Van Dyck 2007). Large carabid beetles are known to be more fragmentation-sensitive than smaller species because of their lower dispersal ability (Kotze and OöHara 2003, Rainio and Niemelä 2003). Large birds are also negatively affected by forest fragmentation (Cleary et al. 2007), although a recent review on tropical agroecosystems failed to detect higher sensitivity to landscape composition in large birds (Tscharntke et al. 2008). Here, we did not detect a negative effect of overall landscape fragmentation on large birds, carabids and butterflies, but instead a positive effect of landscape diversity, the largest species preferring the most diverse landscape mosaics including deciduous woodlands and meadows. However, this is probably due to the naturally patchy and heterogeneous vegetation in the study area compared to most of the studies dealing with habitat fragmentation. Long-distance migrating birds and macropterous carabids tended to be more fragmentation-sensitive than their less mobile counterparts (resident and short-distance migrant birds and brachypterous carabids), whereas mobile butterflies were more dependent on landscape composition, especially on the presence of crops and deciduous woodlands. For butterflies and carabids, high mobility is considered to be an adaptation to disturbed habitats and is generally expected to prevent species from decline (Ribera et al. 2001, Warren et al. 2001). However, strong flight can also be a key trait for rare butterflies, as a compensation for extreme habitat specialization and scarcity of the host-plant (Samways and Lu 2007). For birds, long-distance migrants have declined more than short-distance migrants since 1970, indicating higher sensitivity to habitat loss (Sanderson et al. 2006). Greater dispersal ability can lead to greater vulnerability to fragmentation among species, especially in case of greater mortality during dispersal, as demonstrated, e.g., for amphibians (Cushman 2006). Dispersal is however not a species-specific fixed trait but varies with landscape configuration, because mobility can increase in populations inhabiting more fragmented landscapes (Baguette and Van Dyck 2007).

Reproductive potential and phenology

Breeding parameters such as a low reproductive potential may also indicate a higher sensitivity to habitat fragmentation (Henle et al. 2004), and is generally correlated with a large body mass and a low dispersal ability (Kotze and OöHara 2003, Baguette and Van Dyck 2007). Here we found evidence that birds with both a low productivity and a late phenology were associated with a low fragmentation of open habitats at the landscape scale. For carabid beetles and butterflies, breeding phenology and overwintering mode appeared to be key indicator traits for species responses to landscape configuration. Summer-breeding carabids were associated with low fragmented open habitats, whereas spring breeders were favoured by the presence of meadows and hedgerows. Spring breeders are known to benefit from increasing grassland cover in the surrounding landscape (Weibull et al. 2003), since they usually hibernate as adults, migrate into the fields from surrounding overwintering sites and establish the öearly seasonô carabid community (Purtauf et al. 2005). For butterflies, we found that a restricted flight period and overwintering as eggs or young larvae were good indicator traits for species response to the landscape composition gradient, which is consistent with other studies (Summerville et al. 2006, Ohwaki et al. 2007).

Life-history traits as a tool for conservation

Using life-history traits in the analysis of species responses to fragmentation helps to predict potential changes in ecosystem functioning following changes in the composition of species communities (Diaz and Cabido 2001, Cole et al. 2002). It also allows to define functional response groups on the basis of shared life traits among species (Ribera et al. 2001, Hausner et al. 2003), and increases our ability to predict why certain species are more prone to decline than others (Henle et al. 2004). As a functional relationship exists between particular habitats and the requirements of species with particular life histories (Duelli and Obrist 2003), life trait-based approaches therefore provide deeper insights into the processes linking species to their habitat (McGill et al. 2006, Summerville et al. 2006). Moreover, many ecosystem functions, including seed dispersal, pollination or biological control, will be affected by changes in bird and insect functional groups following modifications in landscape composition (Tscharntke et al. 2008). In the study area, some particular landscape configurations need more urgently to be preserved than others because they harbour species sharing a combination of life traits associated with unfavourable conservation status. Maintaining large fragments of grasslands and heathlands is the most adequate conservation issue for threatened species in such mosaic landscapes dominated by silviculture-dependent habitats, whereas the conservation of areas with high landscape diversity will help to maintain high levels of species richness for several taxa. The specific landscape history of the study area (i.e., the large-scale afforestation of naturally fragmented and heterogeneous habitat mosaics by modern forestry) can also explain why positive responses to fragmentation were observed for most forest species (Barbaro et al. 2007). This is also partly due to confounding factors interacting with the fragmentation process per se, especially the ability of surrounding matrix habitats to supply additional resources to forest species by complementation or supplementation, and to regulate dispersal and dispersal-related mortality (Ewers and Didham 2006, Barbaro et al. 2008). Contradictory effects of landscape fragmentation are therefore explained by the different ways in which specialized and generalist species perceive landscape heterogeneity as a continuum of habitat or as isolated patches (Tscharntke et al. 2002). As a result, key indicator traits of species sensitivity to habitat loss and fragmentation might become useful tools for conservation management of mosaic landscapes in the future.

References

Baguette, M. and Van Dyck, H. 2007. Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. ï Landscape Ecol. 22: 1117-1129.

Barbaro, L. et al. 2007. The spatial distribution of birds and carabid beetles in pine plantation forests: the role of landscape composition and structure. ï J. Biogeogr. 34: 652-664.

Barbaro, L. et al. 2008. Multi-scale habitat selection and foraging ecology of the eurasian hoopoe (Upupa epops) in pine plantations. - Biodivers. Conserv. 17: 1073-1087.

Bibby, C. J. et al. 2000. Bird census techniques. - Academic Press.

Bink, F. A. 1992. Ecologische atlas van de dagvlinders van Noordwest-Europa. - Schuyt & Co.

Cleary, D. F. R. et al. 2007. Bird species and traits associated with logged and unlogged forest in Borneo. - Ecol. Appl. 17: 1184-1197.

Cofre, H. L. et al. 2007. Rarity in Chilean forest birds: which ecological and life-history traits matter? ï Divers. Distrib. 13: 203-212.

Cole, L. J. et al. 2002. Relationships between agricultural management and ecological groups of ground beetles (Coleoptera: Carabidae) on Scottish farmland. - Agr. Ecosyst. Environ. 93: 323-336.

Cramp, S. et al. 1994. Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic. Vol. I-IX. - Oxford Univ. Press.

Cushman, S. A. 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. - Biol. Conserv. 128: 231-240.

Cushman, S. A. et al. 2008. Do forest community types provide a sufficient basis to evaluate biological diversity? ï Front. Ecol. Environ. 6: 13-17.

Davies, K. F. et al. 2000. Which traits of species predict population declines in experimental forest fragments? - Ecology 81: 1450-1461.

Diaz, S. and Cabido, M. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. - Trends Ecol. Evol. 16: 646-655.

Doledec, S. et al. 1996. Matching species traits to environmental variables: a new three-table ordination method. ï Environ. Ecol. Stat. 3: 143-166.

Dray, S. et al. 2003. Co-inertia analysis and the linking of ecological data tables. - Ecology 84: 3078-3089.

Dray, S. and Dufour, A. B. 2007. The ade4 package: implementing the duality diagram for ecologists. ï J. Stat. Software 22: 1-20.

Duelli, P. and Obrist, M. K. 2003. Regional biodiversity in an agricultural landscape: the contribution of seminatural habitat islands. - Basic Appl. Ecol. 4: 129-138.

Ewers, R. M. and Didham, R. K. 2006. Confounding factors in the detection of species responses to habitat fragmentation. - Biol. Rev. 81: 117-142.

Fischer, J. et al. 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. - Front. Ecol. Environ. 4: 80-86.

Grand, J. et al. 2004. A multiscale landscape approach to predicting bird and moth rarity hotspots in a threatened pitch pine-scrub oak community. - Conserv. Biol. 18: 1063-1077.

Hampe, A. and Petit, R. J. 2005. Conserving biodiversity under climate change: the rear edge matters. - Ecol. Lett. 8: 461-467.

Hausner, V. H. et al. 2003. Selecting indicator traits for monitoring land use impacts: birds in northern coastal birch forests. ï Ecol. Appl. 13: 999-1012.

Henle, K. et al. 2004. Predictors of species sensitivity to fragmentation. ï Biodivers. Conserv. 13: 207-251.

Holzkämper, A. et al. 2006. Optimizing landscape configuration to enhance habitat suitability for species with contrasting habitat requirements. - Biol. Conserv. 198: 277-292.

Julliard, R. et al. 2003. Common birds facing global changes: what makes a species at risk? - Global Change Biol. 10: 148-154.

Julliard, R. and Jiguet, F. 2005. Statut de conservation en 2003 des oiseaux communs nicheurs en France selon 15 ans de programme STOC. - Alauda 73: 345-356.

Kotze, D. J. and OôHara, R. B. 2003. Species decline ï but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. - Oecologia 135: 138-148.

Lafranchis, T. 2000. Les papillons de jour en France, Belgique et Luxembourg et leurs chenilles. - Biotope.

Laiolo, P. et al. 2004. Can forest management have season-dependent effects on bird diversity? ï Biodivers. Conserv. 13: 1925-1941.

Loreau, M. et al. 2003. Biodiversity as spatial insurance in heterogeneous landscapes. - Proc. Natl. Acad. Sci. U.S.A. 100: 12765-12770.

McGarigal, K. et al. 2002. Fragstats: spatial pattern analysis program for categorical maps. ï Univ. of Massachusetts.

McGill, B. J. et al. 2006. Rebuilding community ecology from functional traits. - Trends Ecol. Evol. 21: 178-185.

McKinney, M. L. and Lockwood, J. L. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. - Trends Ecol. Evol. 14: 450-453.

Mellado, A. et al. 2008. Biological traits of stream macroinvertebrates from a semi-arid catchment: patterns along complex environmental gradients. - Freshwater Biol. 53: 1-21.

Ohwaki, A. et al. 2007. Butterfly assemblages in a traditional agricultural landscape: importance of secondary forests for conserving diversity, life history specialists and endemics. ï Biodivers. Conserv. 16: 1521-1539.

Paradis, E. et al. 1998. Patterns of natal and breeding dispersal in birds. - J. Anim. Ecol. 67: 518ï536.

Pollard, E. and Yates, T. J. 1993. Monitoring butterflies for ecology and conservation. - Chapman and Hall.

Purtauf, T. et al. 2005. Landscape context of organic and conventional farms: influences on carabid beetle diversity. - Agr. Ecosyst. Environ. 108: 165-174.

Rainio, J. and Niemelä, J. K. 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. - Biodivers. Conserv. 12: 487-506.

Ribera, I. et al. 2001. Effect of land disturbance and stress on species traits of ground beetles assemblages. - Ecology 82: 1112-1129.

Riecken, U. and Raths, U. 1996. Use of radio telemetry for studying dispersal and habitat use of Carabus coriaceus L. - Ann. Zool. Fenn. 33: 109-116.

Samways, M. J. and Lu, S. S. 2007. Key traits in a threatened butterfly and its common sibling: implications for conservation. ï Biodivers. Conserv. 16: 4095-4107.

Sanderson, F. J. et al. 2006. Long-term population declines in Afro-Palearctic migrant birds. - Biol. Conserv. 131: 93-105.

Söderström, B. et al. 2001. Grazing effects on between-year variation of farmland bird communities. ï Ecol. Appl. 11: 1141-1150.

Summerville, K. S. et al. 2006. Species traits as predictors of lepidopteran composition in restored and remnant tallgrass prairies. - Ecol. Appl. 16: 891-900.

Tessier, F. 2000. Catalogue des Coléoptères Carabiques du Lot et Garonne. - Bull. Soc. Linn. Bordeaux 28: 1-56.

Tscharntke, T. et al. 2002. Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. - Ecol. Appl. 12: 354-363.

Tscharntke, T. et al. 2008. Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. - Ecology 89: 944-951.

Turin, H. 2000. De Nederlandse loopkevers. Verspreiding en oecologie (Coleoptera: Carabidae). Nederlandse fauna 3. - Nationaal Natuurhistorisch Museum Naturalis.

van Halder, I. et al. 2008. Importance of semi-natural habitats for the conservation of butterfly communities in landscapes dominated by pine plantations. - Biodivers. Conserv. 17: 1149-1169.

Warren, M. S. et al. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. - Nature 414: 65-69.

Weibull, A. C. et al. 2003. Species richness in agroecosystems: the effect of landscape, habitat and farm management. - Biodivers. Conserv. 12: 1335-1355.

Photo 3. Habitats caractéristiques de la forêt de plantation des Landes de Gascogne. De gauche à droite et de haut en bas : jeunes plantations de pin maritime, plantation mature, parefeu herbacé, îlot feuillu (Inge van Halder).

2.3. Réponses numériques et fonctionnelles des oiseaux insectivores à un défoliateur forestier

2.3.1. Sélection multi-échelles de lôhabitat et écologie du foraging chez la huppe fasciée

Résumé

La conservation des espèces dôoiseaux utilisant de grands domaines vitaux composés dôhabitats complémentaires juxtaposés peut être problématique dans les paysages à rotation rapide comme les forêts de plantation. La huppe fasciée *Upupa epops* est une espèce en déclin en Europe mais encore abondante dans le sud-ouest de la France. Nous avons étudié la sélection multi-échelles de lôhabitat par les huppes dans des plantations de pin, en combinant points dôécoute à lôéchelle du paysage et télémétrie à lôéchelle des domaines vitaux. Nous avons quantifié lôutilisation de lôhabitat en fonction du comportement des individus et caractérisé les sites de óforagingô selon des variables de micro-habitat et lôabondance de la proie principale dans la zone dôétude, la processionnaire du pin *Thaumetopoea pityocampa.* A lôéchelle du paysage, les huppes sélectionnent des mosaïques dôhabitats de grande diversité, incluant fragments et haies de feuillus comme sites de nidification pour cet oiseau cavernicole. A lôéchelle du domaine vital, elles sélectionnent la végétation herbacée rase le long des pistes forestières pour la prospection alimentaire. La végétation herbacée est significativement plus rase et clairsemée sur les sites de óforagingô et lôintensité de prospection alimentaire augmente avec la densité de nids dôhiver de processionnaires. Le succès reproducteur diminue au cours des 3 ans avec lôabondance des processionnaires, ce qui suggère un besoin de complémentation entre sites de óforagingô et de nidification dans les plantations de pins. La conservation de la huppe fasciée passe par le maintien dôhabitats de nidification (îlots feuillus) adjacents aux habitats de prospection alimentaire (zones herbacées rases en lisière des plantations), donc de la diversité des habitats à lôéchelle du paysage.

Abstract

Bird conservation can be challenging in landscapes with high habitat turnover such as planted forests, especially for species that require large home ranges and juxtaposition of different habitats to complete their life cycle. The Eurasian hoopoe *Upupa epops* has declined severely in western Europe but is still abundant in south-western France. We studied habitat selection of hoopoes in pine plantation forests using a multi-scale survey, including point-counts at the landscape level and radio-tracking at the home-range scale. We quantified habitat use by systematically observing bird behaviour and characterized foraging sites according to micro-habitat variables and abundance of the main prey in the study area, the pine processionary moth *Thaumetopoea pityocampa.* At the landscape scale, hoopoes selected habitat mosaics of high diversity, including deciduous woods and hedgerows as main nesting sites. At the home-range scale, hoopoes showed strong selection for short grassland vegetation along sand tracks as main foraging habitats. Vegetation was significantly shorter and sparser at foraging sites than random, and foraging intensity appeared to be significantly correlated with moth winter nest abundance. Nesting success decreased during the three study years parallel to moth abundance. Thus, we suggest that hoopoes need complementation between foraging and breeding habitats to establish successfully in pine plantations. Hoopoe conservation requires the maintenance of adjacent breeding (deciduous woods) and foraging habitats (short swards adjacent to plantation edges), and consequently depends on the maintenance of habitat diversity at the landscape scale.

Introduction

The relevance of heterogeneous habitat mosaics for bird conservation has been recently highlighted with the emergence of the continuum model as a new paradigm in landscape ecology (Manning et al. 2004). This model considers landscape as a mosaic of habitats of different qualities instead of using a binary classification of habitat and non-habitat, as in the classical island biogeography theory (Kupfer et al. 2006). It also predicts that the effects of surrounding matrix habitats may be more important than processes occurring within habitat patches, as demonstrated for birds in different biogeographic areas (Wiens 1995; Wolff et al. 2002; Wethered and Lawes 2003; Tubelis et al. 2004). Edges between matrix and breeding habitats can have positive effects on bird populations because of differences in resource availability and microclimate at edges, and when food is taken outside the breeding habitat (McCollin 1998). In the latter case, species need the complementation of non-substitutable resources in the landscape mosaic to complete their life cycle (Dunning et al. 1992; Brotons et al. 2004; Ouin et al. 2004). In western Europe, habitat complementation at the landscape scale is probably essential for the conservation of several bird species that have been declining at least in part of their European range through the past decades (Burfield and van Bommel 2004): turtle dove (*Streptopelia turtur*, Browne and Aebischer 2003), wryneck (*Jynx torquilla*, Freitag 2004), woodlark (*Lullula arborea*, Bowden 1990), red-backed shrike (*Lanius collurio*, Virkkala et al. 2004) or linnet (*Carduelis cannabina*, Eybert et al. 1995).

Habitat complementation has important implications for bird conservation in heterogeneous landscape mosaics with high turnover in space and time, such as plantation forests (Barbaro et al. 2005; Paquet et al. 2006). Some species of particular conservation concern need the juxtaposition of breeding and foraging resources found in semi-natural habitat patches that may no longer be available in commercial plantation landscapes. The identification of key foraging habitats, especially when distinct from the main breeding habitat, consequently arises as a major issue in bird conservation management. For example, the presence of adjacent semi-natural grasslands is beneficial to farmland birds in mosaic forest-agricultural landscapes, both in northern and southern Europe (Preiss et al. 1997; Pons et al. 2003; Virkkala et al. 2004). Managed grasslands are suitable foraging habitats for open habitat specialists, but also for species such as the eurasian hoopoe (*Upupa epops epops*) nesting in wooded habitats and foraging on grassland seeds or invertebrates

Hoopoes preferably inhabit farmlands with trees or walls where they nest in hollows, and open habitats with short sward structures where they forage on large ground-living insects (Kristin 2001). They also occur in cleared and thinned forests (Camprodon and Brotons 2006), and their bimodal distribution in bird-habitat ordination models suggest that they use multiple habitats (Preiss et al. 1997). The hoopoe is classified as declining in western Europe and France (Olioso and Jourde 1999; Burfield and van Bommel 2004). Food quality and accessibility as well as the availability of suitable nesting cavities are major limiting factors (Martin-Vivaldi et al. 1999; Arlettaz et al. 2000). In western Europe, hoopoes occur in farmlands where they feed mainly on molecrickets (*Gryllotalpa gryllotalpa*) and Lepidoptera larvae (Fournier and Arlettaz 2001). They also inhabit pine plantations, where they specialize in pupae of the pine processionary moth (*Thaumetopoea pityocampa*), which is a serious forest pest (Battisti et al. 2000; Kristin 2001). In south-western France, hoopoes breed in oak forest fragments embedded within a landscape matrix of maritime pine (*Pinus pinaster*) plantation forests (Barbaro et al. 2007). Here, we examine habitat selection by hoopoes at the landscape-scale (i.e., distribution of breeding pairs), at the home-range scale (i.e., habitat use of individual birds), and at the micro-habitat scale (i.e., selection of foraging sites). Specifically, we ask if (i) landscape mosaics occupied by hoopoes show significant differences in habitat composition compared to unoccupied ones; (ii) hoopoe behaviour is different according to habitat within home range; (iii) hoopoe select foraging sites with particular micro-habitat attributes; and (iv) hoopoe foraging intensity is positively related to pine processionary moth abundance.

Methods

Study area

The study took place in the Landes de Gascogne forest, south-western France, a region covering c.10000 km^2 dominated by intensively managed maritime pine plantation forests. Climate, soil composition and current sylvicultural practices are described in Maizeret (2005). The distribution of breeding hoopoes was sampled at two nested scales within the study area. At the landscape-scale, the study site spans c.10000 ha (44°40ôN to 44°44ôN, 0°57ôW to 0°46ôW) and is composed of small (< 5 ha) and isolated patches of oak (mainly *Quercus robur*) woodlands embedded in a matrix of pine plantations of different ages. At the home-range scale, we selected a part of the study site covering 180 ha, including pine stands, clearcuts and oak woodland patches bordered by large maize fields. Grasslands (with *Molinia caerulea*, *Pseudarrhenatherum longifolium*, *Agrostis* *curtisii* and *Ulex minor*) and heathlands (with *Pteridium aquilinum, Ulex europaeus, Erica cinerea, E. scoparia* and *Calluna vulgaris*) occur in recent clearcuts, firebreaks and sand track edges of the study area.

Bird surveys

The distribution of breeding hoopoes was surveyed at the landscape-scale in 2002-2003. Two observers performed 286 point-counts with unlimited distance using a sampling survey stratified by the main habitat types (see below). Points were established at least 400 m apart to avoid double counting (Sutherland et al. 2004). We conducted two 20-min visits before and after mid-May, within 5 h after sunrise and excluding rainy days. Habitat use of individual birds in the 180ha-area was investigated using the territory mapping method. Territory mapping is considered to be the standard method for birds showing territorial behaviour and not ranging widely (Bibby et al. 2000), such as the hoopoe (Kristin 2001). Between 2004 and 2006, hoopoes were monitored twice a week in the morning (9:00 to 11:00) or late afternoon (16:00 to 18:00) from mid-April to mid-July. We drove slowly along the dense network of tracks to survey the whole area, including the interior of pine stands. In this area, understorey is regularly cut for management access and allows the observer to sight birds located as far as 200 m inside the stands from the tracks. All stands were checked carefully with binoculars before driving along the tracks, to locate hoopoes before they were disturbed and to avoid a bias on the detection probability of birds between habitats. We used driving because hoopoes can be more closely approached by car than by a walking observer. Moreover, territory mapping involves locating individual birds as precisely and rapidly as possible to avoid double counting the same birds that may have moved from their initial locations (Bibby et al. 2000). The location and behaviour of every recorded bird were mapped on a Geographic Information System (ArcView, ESRI, Redlands, CA, USA), except birds seen in flight that were not mapped, as well as birds showing any change in behaviour because of the observerȏs presence. The coupling of territory mapping with colour-marking and radio-tagging (see below) allowed us to attribute a large majority of sightings to known individuals, as well as to distinguish adults from fledglings and additional non-breeding individuals (Bibby et al. 2000).

Nesting success

In the 180ha-area, we established 13 specific nestboxes in 2002, in order to monitor breeding parameters. Nestboxes were located only in adequate breeding habitats (i.e., deciduous woodlands or hedgerows) to mimic natural conditions. At the beginning of the study, a breeding population of hoopoes was already established in the area. They nested only in large hollows in deciduous trees (mostly oaks) because cavities are lacking in pine plantations. This population bred continuously in natural cavities during the study with 3 to 4 pairs from 2004 to 2006. The provision of nestboxes provided nesting opportunities for additional pairs, which fluctuated from 4 pairs in 2004 and 3 pairs in 2005 to 6 pairs in 2006. Consequently, the total density of breeding pairs varied from 1 pair/20-45 ha during the study. We monitored breeding parameters (laying date, clutch size, brood size at hatching and number of fledged youngs) for 4 pairs in 2004, 4 pairs in 2005 (including 2 second clutches) and 9 pairs in 2006 (including 3 second clutches). Nestboxes were checked at the critical periods of egg laying, hatching and fledging, and nesting success was calculated only for the 14 successful clutches, by dividing the number of fledglings by clutch size (Martin-Vivaldi et al. 1999).

Ringing and radio-tracking

From 2004 to 2006, we caught 61 fledglings (c.20 days old) and 20 adults, and ringed them with a metal ring and Darvic plastic colour rings using combinations that allowed visual re-identification of individuals. In addition, 15 birds were radio-tagged using tail-mounted 1.3 g-tags (Pip-tags, Biotrack, UK), i.e., < 2 % of body mass, with a life of c.6 weeks and a range of c.1-2 km. Tags were glued on to the central tail feathers, but 8 out of the 15 hoopoes removed the tags by pulling out the rectrice within 24 h following the capture. The remaining 7 birds kept their tags between 2 and 46 days, and 6 were followed long enough to obtain more than 10 direct relocations (Table 1). Radio-tagged birds were relocated every day by approximate triangulation based on signal strength, until the bird was sighted and its precise location mapped (Browne and Aebischer 2003). We used interval sampling at more than 30-min intervals between two consecutive fixes to achieve independence of locations and to avoid bias by relocating birds disturbed by the observer (Sierro et al. 2001). Direct fixes were completed with additional, associated fixes when the bird identity could be confirmed visually (either by colour rings or by direct sighting of birds flying from foraging sites to the nest). This allowed to improve sample size for birds that had lost their transmitters early, and to estimate home ranges for two additional birds that were not tagged in 2005 (Table 1).

Year	Sex	Age	Nest-box	Sighting period	Tracking days	Direct fixes[b]	Associated fixes[b]	Total fixes	Home range (ha)[c]	
									MCP	KER
2004	Fem	-	11	Apr 29-June 7	21	44	6	50	9.77	6.52
2004	Male	2d yr	5	Apr 9-June 2	2	2	28	30	7.52	7.79
2004	Male	2d yr	7	May 17-27	10	12	5	17	14.03	26.46
2004	Fem	-	7	Apr 29-May 27	10	15	4	19	17.37	24.27
2004	Male	2d yr	11	May 17-June 4	18	19	10	29	7.41	7.91
2005	Male	2d yr	-	June 2-3	1	3	1	4	-	-
2005	Male	2d yr	14	Apr 11-May 13	-	0	37	37	11.89	15.29
2005	Male	2d yr	7	Apr 12-July 20	-	0	40	40	12.29	16.90
2006	Male	2d yr	1	Apr 26-May 24	6	21	11	32	15.57	23.93
2006	Male	1st yr	1	May 11-12	1	1	0	1	-	-
2006	Male	2d yr	14	Apr 28-July 20	1	1	39	40	16.63	22.47
2006	Male	2d yr	10	Apr 27-July 20	1	1	30	31	8.82	9.71
2006	Male	2d yr	11	Apr 27-June 14	1	1	27	28	9.46	10.89
2006	Fem	2d yr	11	Apr 26-May 31	12[a]	30	7	37	30.76	21.98
2006	Fem	2d yr	14	Apr 26-June 13	1	6	11	17	7.97	10.43
2006	Male	2d yr	9	Apr 21-June 8	1	3	13	16	9.25	9.88
2006	Male	2d yr	-	Apr 18-June 2	1	6	10	16	12.99	20.99

Table 1 Radio-tracking parameters and home-range sizes for 17 hoopoes. [a]Transmitter failed after 12 days but was still on the bird when re-captured 46 days after; [b]Direct fixes were obtained by relocations of radio-tagged individuals and associated fixes by re-sightings of known individuals; [c]Estimates of home-range sizes calculated by minimum convex polygons (MCP) and fixed kernel density functions (KER).

Habitat use and foraging ecology

Habitat maps were digitized on GIS from colour aerial orthophotographs at the scale 1:25000. We used the following 7 habitat types, with field calibration: mature pine plantation (tree height > 7 m), young pine plantation (tree height < 7 m), deciduous woodland and hedgerow, shrubland and heathland, semi-natural grassland (including herbaceous firebreaks), hay meadow and crop (maize field). We calculated the percentage cover of each habitat and a set of landscape metrics within 400-m radius buffers of 50.3ha around point-counts using Fragstats 3.3 (McGarigal et al. 2002). Previous studies showed that the most significant landscape metrics related to bird distribution were mean patch size (in ha), edge density (total length of all edges between all habitat patches, in m.ha-1) and the Shannon index of habitat diversity (Barbaro et al. 2005). In the 180ha-area, we measured micro-habitat variables in 1-m² quadrats located at 40 foraging sites and 40 random sites in May-June 2006. Foraging sites were located by direct observations of foraging hoopoes and the quadrats were centred on the empty cocoons left by the birds when extracting processionary moth pupae from the ground (Battisti et al. 2000). Control plots were established randomly within the same area using GIS tools to create random points. In both plots, we recorded the distance to the nearest occupied cavity, vegetation height, and percentage cover of the main plant species, bare ground, woody debris, litter, bryophyte, grass and shrub layers (Bowden 1990; Sutherland et al. 2004).

Prey availability

Previous observations of foraging hoopoes in the study area indicated that birds feed mostly on two prey species, which are typically extracted from the first cm of the ground (Kristin 2001): pupae of the pine processionary moth and adult field crickets (*Gryllus campestris*). As moth pupae seemed to be quantitatively the most important prey, we monitored moth populations by counting winter nests in tree crowns (Hodar and Zamora 2004; Battisti et al. 2005). Pine processionary moth larvae live gregariously and build a winter silk nest in the tree crown periphery. Density of winter nests is known to be maximal at pine stand edges rather than within stands, as a result of female moth preference for trees standing out against clear sky. The short swards along stand edges allow the caterpillars to burrow themselves into the upper 5 cm of the soil for pupating, where they are exposed to hoopoe predation (Battisti et al. 2000). We assumed a significant relationship between moth nest density and below-ground pupae abundance per edge. To estimate moth abundance within the 180ha-area, one observer counted all winter nests in the first two tree rows of pine stand edges in early spring of each study year. We did not sample the interior of pine stands because most feeding hoopoes used the herbaceous fringe between a track and a plantation, and food availability should only be measured in habitats where birds can actually forage (Wolda 1990).

Statistical analyses

For binary point-count data, we compared mean landscape attributes for occupied and unoccupied mosaics using two-sample t-tests, and Mann-Whitney U-tests when data had non-normal distributions. We used binomial Generalized Linear Models (GLM) with logit link to relate hoopoe occurrence and landscape variables. Stepwise backward model selection was performed with Akaikeôs Information Criterion using ñstepAICò procedure in R software (Diekötter et al. 2006). For radio-tracking data, home-range sizes were calculated for the 15 individuals with more than 16 relocations (direct plus associated fixes). Among these birds, 8 had more than 30 relocations and thus allowed a reliable estimate of 70-80% of their maximum home-range area (Sutherland et al. 2004). We used two methods to estimate home-range sizes: minimum convex polygon (MCP) and fixed kernel density function with 95% of the fixes. For kernel functions, we used least-squares cross-validation for calculation of the smoothing parameter H (Worton 1989). For habitat use, we compared the proportion of relocations in each habitat within individual home ranges (used habitats) to habitat availability at two levels: within the 180ha-area and within individual home ranges (Aebischer et al. 1993). For each individual, we calculated a forage ratio, using the B_{i1} index of Manly et al. (1972), by dividing the proportion of bird records in a given habitat by the proportion of habitat available, then by dividing the forage ratio for each habitat by the sum of forage ratios for all habitats (Sutherland et al. 2004). We assessed for differences in mean forage ratios between habitats by Kruskal-Wallis H-test. We then used compositional analysis to compared habitat use within home range to habitat availability within total study area, and within individual home ranges (Aebischer et al. 1993). Compositional analysis was performed using the R package ñadehabitatò with missing values replaced by 0.01%, and randomisation tests (1000 permutations) to assess for the significance of habitat selection (Calenge 2006). We compared the proportion of bird having a particular behaviour in each habitat to the proportion of each habitat available by means of G^2 tests and non-parametric Kendall correlation coefficients (Robinet et al. 2003). Micro-habitat variables were log-transformed when necessary to improve normality and data recorded at foraging sites were compared with those measured at the nearest control plot using a paired t-test. We used one-way ANOVA to test for a year effect on prey abundance (number of moth nest per stand edge) and nesting success, and linear regression to relate the log-transformed number of foraging hoopoes to prey abundance. To test for between-year variation in the regression slopes between foraging intensity and prey abundance, we performed an ANCOVA with the year as factor, the number of foraging hoopoes as response variable and prey abundance as covariate.

Results

Habitat selection at the landscape scale

Hoopoes were recorded in half of the 286 point-counts. There was a significant effect of habitat type on hoopoe mean abundance, with significantly higher abundance in deciduous woodlands compared to all other habitats (ANOVA, F-ratio = 5.662, P < 0.0001). Landscape mosaics occupied by breeding pairs had significantly higher habitat diversity and smaller mean patch size than unoccupied mosaics, thus hoopoes tended to select the most heterogeneous parts of the landscape (Table 2). They avoided areas that contained a high proportion of mature pine plantations and favoured areas with more deciduous woods, hedgerows and meadows (Table 2). In addition, the stepwise GLM selection using AIC retained four variables: deciduous woodland, grassland and meadow covers and Shannon index of habitat diversity, but only the latter showed a significant effect on hoopoe occurrence (coefficient = 1.09 ± se 0.34, z-value = 3.21, P < 0.001).

Landscape attributes	Occupied	Unoccupied	*t* and *U* tests	*P*
Landscape structure				
Edge density (m/ha)	229.73 ± 66.26	216.36 ± 71.87	-1.636	ns
Mean patch size (ha)	2.16 ± 1.23	2.61 ± 1.57	2.676	*
Shannon index	1.71 ± 0.37	1.54 ± 0.51	-3.355	**
Habitat cover (%)				
Mature pine	37.81 ± 20.66	45.93 ± 24.69	12152.5	**
Young pine	17.99 ± 17.06	17.11 ± 18.43	9674.5	ns
Deciduous wood	9.47 ± 12.11	8.05 ± 12.72	8681.5	*
Hedgerow	0.32 ± 0.74	0.14 ± 0.43	8469.5	***
Shrubland	15.96 ± 13.06	13.51 ± 13.82	8856.5	ns
Grassland	4.73 ± 5.62	6.24 ± 8.37	11023.0	ns
Meadow	2.97 ± 8.13	0.91 ± 3.12	8821.0	**
Crop	2.29 ± 8.20	2.00 ± 8.29	9396.5	ns

Table 2 Mean ± sd values of landscape attributes measured within 50ha-areas around point-counts for mosaics occupied or unoccupied by hoopoes (t-tests for landscape structure and Mann-Whitney U tests for habitat cover, df = 284, *** P < 0.001, ** P < 0.01, * P < 0.05, ns = not significant)

Habitat selection at the home-range scale

Home-range sizes were estimated for 15 hoopoes (Table 1, Fig. 1), of which 13 were radio-tagged birds. They measured on average 12.78 ha (± sd 5.96; range 7.41-30.76 ha) when calculated with the MCP method, and 15.69 ha (± 7.07; range 6.52-26.46 ha) when calculated with the kernel method, a difference which was not significant (Mann-Whitney test, U = 86.0, P = 0.27). Similarly, for the 6 individuals with more than 10 direct relocations, home-range sizes estimated with total fixes and with direct fixes only were not statistically different (U = 15.5, P = 0.69), and the estimates strictly identical for 4 birds. Home ranges overlapped largely within breeding pairs but generally not between pairs, with few exceptions (Fig. 1). Within home ranges, forage ratios differed significantly among habitats (Kruskal-Wallis test, H = 49.0, df = 5, P < 0.0001). Mean forage ratios were higher for sand tracks and deciduous woodlands and hedgerows than for the other habitats, demonstrating positive selection of these two habitats as compared to their availability (Fig. 2). Compositional analysis showed that habitat selection for the 13 tagged hoopoes differed significantly from random at both levels of habitat availability within total study area (ş = 0.026, P < 0.001) and individual home ranges (ş = 0.025, P < 0.001). At the home range level, the ranking matrix of preferred used habitats gave the following order (>>> indicating significant differences): Sand tracks > Deciduous woods and hedgerows >>> Mature pines > Grasslands >>> Crops > Young pines.

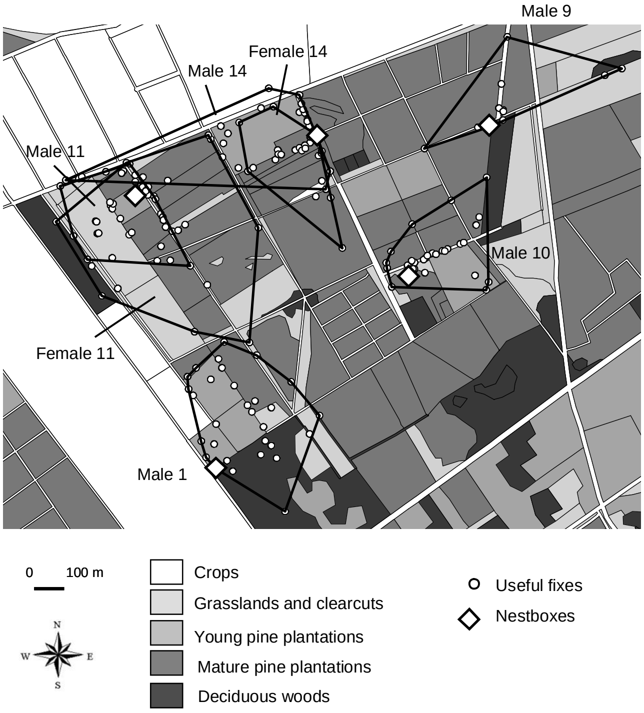


Fig. 1 Home ranges of 7 radio-tagged hoopoes in 2006. White dots indicate fixes used to calculate home-range sizes by means of minimum convex polygons.

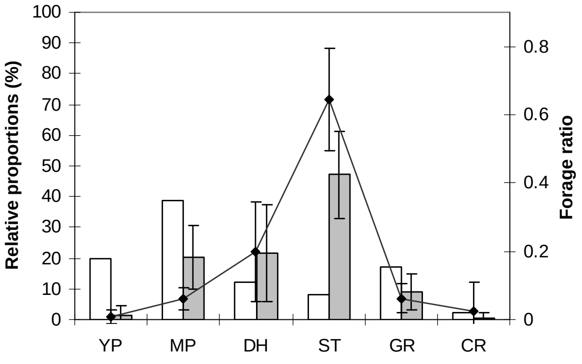
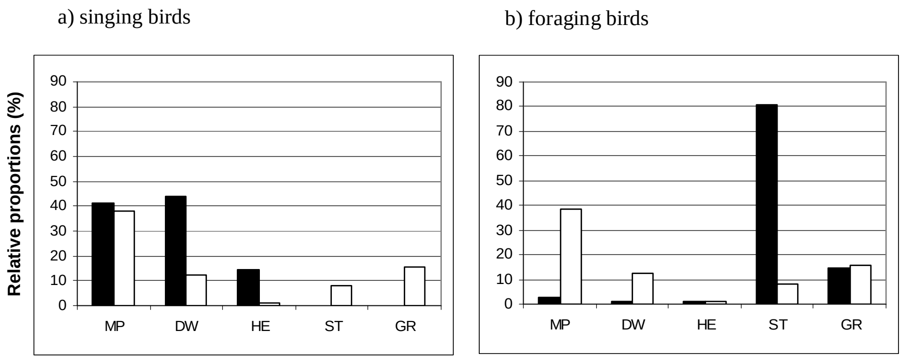


Fig. 2 Relative proportions (%) of habitat types available within the study area (white bars), mean (± sd) proportion of hoopoe relocations per habitat type within home ranges (grey bars) and mean (± sd) forage ratio per habitat type (black line). YP = young pine, MP = mature pine, DH = deciduous woods and hedgerows, ST = sand tracks, GR = grasslands, CR = crops

Habitat use according to behaviour

A total number of 711 hoopoe observations were made between 2004 and 2006 (n = 225 in 2004, n = 142 in 2005 and n = 344 in 2006). Half of the birds were recorded in sand tracks and their herbaceous edges (51%), 17% in mature pine plantations, 14% in oak woods, 9% in hedgerows and 8% in grasslands. Habitat use differed between years ($G^2 = 30.22$, df = 8, $P < 0.0001$), with grasslands being less used in 2004 than in 2005-2006 and sand tracks more used in 2004-2005 than in 2006. The most common behaviour noted was roosting, either in a tree or on the ground (47% of sightings), then foraging (34%), singing (11%) and feeding chicks (8%). Hoopoe behaviour varied significantly among habitats ($G^2 = 455.43$, df = 12, $P < 0.0001$) and among years ($G^2 = 60.09$, df = 6, $P < 0.0001$), with more foraging birds in 2005-2006 than in 2004. Singing hoopoes were recorded in all wooded habitats, including pine plantations (Fig. 3a), while foraging birds were mainly recorded from sand tracks and secondly from grasslands (Fig. 3b). When comparing the proportion of birds with particular behaviour in each habitat to habitat availability in the 180ha-area, we did not find any significant correlations, meaning significant habitat selection according to behaviour (Kendall correlation coefficients, Ű= -0.359 for breeding behaviour, Ű= 0.105 for singing, Ű= 0.200 for foraging and Ű= -0.200 for roosting, all $P > 0.05$).


a) singing birds

b) foraging birds

Fig. 3 Relative proportions (%) of hoopoe behaviour category per habitat type (black bars), compared to habitat availability (white bars) in the 180ha study area: a) singing birds, b) foraging birds (data are pooled over the three study years). GR = grasslands, HE = hedgerows, DW = deciduous woods, MP = mature pine, ST = sand tracks

Small-scale selection of foraging habitats

The mean distance between foraging sites and nests was 271 ± 143 m (range 8-600 m), which was not significantly different from the distance measured between the randomly located plots and the nearest nest (Table 3). Foraging sites were all located in sand track edges adjacent to pine plantations, except one located in a mature pine plantation and four located in grasslands far from plantation edges. Vegetation was significantly shorter (7.4 cm ± 7.1) in foraging sites compared to control plots (23.8 cm ± 15.7). Bare ground (25.7% ± 26.7 vs 12.1% ± 29.3) and bryophytes (17.1% ± 18.2 vs 5.3% ± 13.2) had significantly higher cover than in control plots (Table 3). Vegetation composition at foraging sites also differed from control plots, with cover of bracken Pteridium aquilinum, gorse Ulex europaeus and deciduous shrubs being significantly higher in control plots, and cover of short annual graminoids, dicots and dwarf gorse Ulex minor being higher in foraging sites.

Prey abundance, foraging and nesting success

Moth abundance non-significantly decreased during the study (ANOVA, F = 1.58, df = 2, P = 0.21, n = 90), from an average of 62.3 (± sd 38.2) nests per edge in 2004 to 53.8 (± 31.2) in 2005 and 47.5 (± 26.3) in 2006. There was a significant year effect on hoopoe nesting success (F = 5.21, df = 2, P = 0.03, n = 14), which decreased in parallel to moth abundance from 0.81 (± 0.09) in 2004 to 0.67 (± 0.17) in 2005 and 0.52 (± 0.15) in 2006. In all three years, the log-number of hoopoes observed foraging at a pine plantation edge was significantly and positively correlated to the number of moth winter nests per edge (Fig. 4). This relationship was stronger in 2004 (n = 30 edges, $r^2 = 0.452$, $P < 0.0001$) than in 2005 (n = 39, $r^2 = 0.273$, $P < 0.001$) and 2006 (n = 40, $r^2 = 0.218$, $P < 0.002$). Results of ANCOVA showed a significant prey abundance effect (F = 43.19, df = 1, $P < 0.0001$) on hoopoe foraging intensity when taking into account the covariation between year and prey abundance. However, the interaction effect between year and prey abundance was not significant (F = 0.06, df = 2, P = 0.94) i.e., the slopes of the three regression models were not significantly different. The overall year effect was however significant (F = 10.91, df = 2, $P < 0.0001$), indicating that the intercepts differed according to year, in parallel to the variations in hoopoe density (Fig. 4).

Micro-habitat variables	Foraging sites	Random sites	*t*-test	*P*
Distance to the nearest nest (m)	271.5 ± 143.0	254.4 ± 133.7	-0.881	ns
Vegetation height (cm)	7.4 ± 7.1	23.8 ± 15.7	4.271	***
Bare ground (%)	25.7 ± 26.7	12.1 ± 29.3	-6.139	***
Woody debris (%)	1.8 ± 3.9	2.5 ± 2.9	1.828	ns
Litter (%)	8.1 ± 12.2	20.5 ± 27.3	1.966	ns
Bryophyte cover (%)	17.1 ± 18.2	5.3 ± 13.2	-3.756	***
Grass cover (%)	34.0 ± 24.8	41.8 ± 30.9	-0.270	ns
Shrub cover (%)	11.3 ± 14.3	17.2 ± 22.4	1.123	ns
Pteridium aquilinum (%)	0.3 ± 0.5	6.3 ± 10.3	4.392	***
Molinia caerulea (%)	3.5 ± 12.2	6.2 ± 16.6	1.159	ns
Pseudarrhenatherum longifolium (%)	7.9 ± 14.4	11.3 ± 11.8	1.751	ns
Short annual graminoids (%)	11.0 ± 15.6	6.4 ± 15.9	-2.204	*
Dicots (%)	2.0 ± 3.2	0.6 ± 2.2	-3.156	**
Calluna vulgaris (%)	6.2 ± 14.1	4.5 ± 12.8	-1.281	ns
Erica cinerea (%)	2.7 ± 5.3	4.0 ± 10.3	-0.924	ns
Erica scoparia (%)	0.7 ± 3.2	1.6 ± 3.6	1.784	ns
Ulex minor (%)	2.2 ± 3.4	1.2 ± 5.2	-2.962	**
Ulex europaeus (%)	0.3 ± 1.6	4.9 ± 12.1	4.177	***
Deciduous shrubs (%)	0.4 ± 0.9	5.1 ± 8.1	3.607	***

Table 3 Mean ± sd values of micro-habitat attributes measured in 1-m^2 quadrats centred on 40 hoopoe feeding locations and 40 randomly distributed plots (paired t-tests, df =39, *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns = not significant)

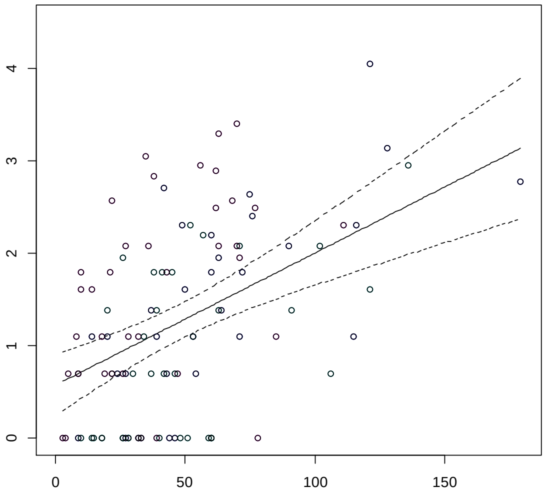


Fig. 4 Linear mixed model linking the log-transformed abundance of foraging hoopoes *Upupa epops* to winter nest abundance of *T. pityocampa* along pine plantation edges in south-western France ($t = 4.95$; $P < 0.0001$).

Discussion

Habitat use and landscape complementation

The present study demonstrated that resource complementation between habitats at the landscape-scale was a keystone factor for this breeding population of hoopoes. Birds showed a preference for landscape mosaics with high habitat diversity. They selected particularly deciduous woodlands and hedgerows for the availability of deep nesting cavities in old oaks. At the home-range scale, hoopoes likewise showed a preference for habitat mosaics combining mature pine plantations, deciduous woods, hedgerows, grasslands and sand tracks, but only sand tracks and deciduous woods and hedgerows were selected more than expected from their availability. Deciduous woods and hedgerows were typical breeding sites, while foraging birds occurred mostly on sand track edges, and sometimes on grasslands. At a finer scale, foraging hoopoes selected microsites with short and sparse vegetation dominated by bryophytes, annual graminoids, dicots and dwarf gorse. Habitat selection in birds is known to be a hierarchical process acting at multiple scales (Wiens 1995). For instance, owls choose their habitats according to trophic resources at a large scale, and according to breeding and roosting requirements at a smaller scale (Martinez and Zuberogoitia 2004). Similarly, choughs (*Pyrrhocorax pyrrhocorax*) use grazed habitats at a coarse scale and, at a finer scale, areas with the shortest swards for foraging (Whitehead et al. 2005).

Our results suggest multi-scale habitat selection at three nested spatial scales: (i) at the landscape scale, breeding hoopoes select oak woodlands embedded in a matrix of pine plantations and open habitats, (ii) at the home-range scale they prefer areas with breeding and foraging habitats in close vicinity, and (iii) at the micro-habitat scale, foraging birds select short and sparse swards along plantation-track edges. Thus, landscape mosaics with high habitat diversity are favoured because they fulfil both breeding and foraging requirements. As landscape complementation and supplementation are widespread mechanisms of multi-habitat use, they have important implications for bird conservation in mosaic landscapes (Wiens 1995; Brotons et al. 2004; Tubelis et al. 2004). In pine plantation forests of western Europe, several other threatened insectivorous birds would benefit from increasing habitat diversity at the landscape-scale through supplementation or complementation of resources, including nightjar (*Caprimulgus europaeus*, Sierro et al. 2001), wryneck (Freitag 2004), woodlark (Bowden 1990), or mistle thrush (*Turdus viscivorus*, Pons et al. 2003).

Foraging and prey availability

Foraging habitat selection results from an interaction between food abundance and accessibility, mediated by vegetation structure (Morris et al. 2001). As a result, the question arises if hoopoes feed on habitat edges because of higher prey abundance or higher accessibility compared to stand interiors? For example, nightjars did not use pine plantations as much as oak scrublands despite similar moth abundance in the two habitats because dense understorey in plantations prevent birds from foraging in flight (Sierro et al. 2001). Like other ground gleaners or probers, hoopoes feed preferably in short sward structures with c.25% bare ground. They generally avoid the interior of plantations stands because of dense understorey, but they can use them when mechanical cutting creates short vegetation or small gaps (Camprodon and Brotons 2006). Dense vegetation and impenetrable soils make arthropods inaccessible by probing or gleaning (McCracken and Tallowin 2004), and shorter and sparser swards are therefore preferred by most ground insectivores (Bowden 1990; Browne and Aebischer 2003; Whitehead et al. 2005). Hoopoes are able to use foraging sites located far from nesting cavities (Arlettaz et al. 2000; Kristin 2001). In our study area, the distance between the nest and suitable foraging sites did not seem to be a limiting factor since hoopoes undertook foraging trips of up to 600 m from the nest. Mean foraging distance was 272 m, larger than the one observed in other ground insectivorous birds such as wryneck (115 m, Freitag 2004) or woodlark (118 m, Bowden 1990).

The hoopoe is a brood reduction strategist able to adjust clutch size to prey availability by selective starvation of the youngest chicks (Martin-Vivaldi et al. 1999). The influence of food availability and its accessibility on breeding success is therefore critical (Fournier and Arlettaz 2001). As a specialist predator, the hoopoe is likely to respond to fluctuations in prey abundance (Crawford and Jennings 1989; Sherry 1990), as suggested by nesting success decreasing in parallel to moth abundance. Lepidopterous pupae and larvae are the main preys of many insectivorous forest birds (Glen 2004). The distribution of pine processionary moth is the main factor for the occurrence of another specialist predator, the great spotted cuckoo (*Clamator glandarius*, Hoyas and Lopez 1998). However, in western Europe, only the hoopoe can feed on buried moth pupae during the breeding season, because of its long curved bill and unique foraging technique among forest insectivorous birds (Kristin 2001). Although hoopoes commonly feed on pine processionary moth in Spain and Italy, the main prey in Switzerland is the molecricket (Arlettaz et al. 2000; Battisti et al. 2000). The decrease in moth abundance observed during the study coincided with an increase in grassland use and foraging time, which suggests that hoopoes may switch to alternative orthopteran preys (field crickets), in years of low moth density. However, as the nutritional value of moth pupae compared to field crickets is not documented, the relative importance of the two preys in the study area and their among-years variations remain to be investigated (Fournier and Arlettaz 2001).

Implications for conservation

The long-term conservation of the hoopoe in mosaic landscapes dominated by pine plantations depends on the maintenance of habitat diversity or its restoration by planting or regenerating oak woodland patches embedded in the pine plantation matrix. An appropriate management of the fringes between tracks and pine stands is also critical to allow hoopoes to access their preys (either moth pupae or field crickets) and will benefit other ground foraging birds (McCracken and Tallowin 2004), as well as plants and arthropods (Mullen et al. 2003). Edges between mature plantations and clearcuts may also provide suitable foraging sites if they are bordered by a short herbaceous strip both favourable to caterpillar burrowing and hoopoe probing. Moreover, previous studies have shown that clear-cutting in plantation forests lead to the establishment of a specific bird assemblage involving several threatened species (Barbaro et al. 2005; Paquet et al. 2006). As nest site availability, together with prey availability, is a limiting factor for the hoopoe in plantation forests, we advocate the use of nestboxes to increase breeding density or restore populations in areas where cavities are lacking. Hoopoes generally respond to the establishment of nestboxes within a few years (Arlettaz et al. 2000; Kristin 2001). Moreover, breeding pairs tend to aggregate in the study area (Barbaro et al. 2007), although spatial aggregation may be caused by potentially confounding factors such as environmental heterogeneity (Cornulier and Bretagnolle 2006) or intra-specific social interactions (Martinez and Zuberogoitia 2004). In the hoopoe, displaying males tend to aggregate spontaneously where they expect to find females, and non-paired males frequently help to feed incubating females and chicks of other males (Martin-Vivaldi et al. 2002). We therefore suggest that the establishment of a dense network of nestboxes will allow the clumping of breeders in loose colonies and would increase social interactions in hoopoe populations.

In addition, the use of nestboxes may also be a tool for promoting biological control of pest insects in pine plantation forests. Predation of pine processionary moth by insectivorous birds may maintain moth populations at low densities, despite interactions with other causes of mortality such as parasitoid insects (Crawford and Jennings 1989; Battisti et al. 2000; Glen 2004). The increase of pine processionary moth populations with climate warming and the consequent potential threats to forest health and biodiversity (Hodar and Zamora 2004; Battisti et al. 2005) may be therefore mitigated by an increase in the density of functional insectivores such as the hoopoe (Jones et al. 2005). Conservation management in production forests should actually aim at maintaining or restoring native vegetation patches and corridors within a complex landscape matrix to enhance the functional diversity of species (Fischer et al. 2006). The hoopoe is an emblematic example of a threatened keystone species that may be favoured by such management recommendations in plantation forests.

References

Aebischer NJ, Robertson PA, Kenward RE (1993) Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313-1325

Arlettaz R, Fournier J, Zbinden N (2000) Evolution démographique (1979-1998) d'une population témoin de Huppe fasciée Upupa epops en Valais et stratégie de conservation ciblée. Nos Oiseaux 47:19-27

Barbaro L, Pontcharraud L, Vetillard F, Guyon D, Jactel H (2005) Comparative responses of bird, carabid, and spider assemblages to stand and landscape diversity in maritime pine plantation forests. Ecoscience 12:110-121

Barbaro L, Rossi JP, Vetillard F, Nezan J, Jactel H (2007) The spatial distribution of birds and carabid beetles in pine plantation forests: the role of landscape composition and structure. J Biogeogr 34:652-664

Battisti A, Bernardi M, Ghiraldo C (2000) Predation by the hoopoe on pupae of Thaumetopoea pityocampa and the likely influence on other natural enemies. Biocontrol 45:311-323

Battisti A, Stastny M, Netherer S, Robinet C, Schopf A, Roques A, Larsson S (2005) Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. Ecology 15:2084-2096

Bibby CJ, Burgess ND, Hill DA, Mustoe S (2000) Bird census techniques. Academic Press, London

Bowden CGR (1990) Selection of foraging habitats by woodlarks (Lullula arborea) nesting in pine plantations. J Appl Ecol 27:410-419

Brotons L, Herrando S, Martin JL (2004) Bird assemblages in forest fragments within Mediterranean mosaics created by wild fires. Landscape Ecol 19:663-675

Browne SJ, Aebischer NJ (2003) Habitat use, foraging ecology and diet of Turtle Doves Streptopelia turtur in Britain. Ibis 145:572-582

Burfield I, van Bommel, F (2004) Birds in Europe: population estimates, trends and conservation status. BirdLifeInternational, Cambridge

Calenge C (2006) The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecol Model 197: 516-519.

Camprodon J, Brotons L (2006) Effects of undergrowth clearing on the bird communities of the Northwestern Mediterranean Coppice Holm oak forests. Forest Ecol Manag 221:72-82

Cornulier T, Bretagnolle V (2006) Assessing the influence of environmental heterogeneity on bird spacing patterns: a case study with two raptors. Ecography 29:240-250

Crawford HS, Jennings DT (1989) Predation by birds on spruce budworm Choristoneura fumiferana: functional, numerical, and total responses. Ecology 70:152-163

Diekötter T, Walther-Hellwig K, Conradi M, Suter M, Frankl R (2006) Effects of landscape elements on the distribution of the rare bumblebee species Bombus muscorum in an agricultural landscape. Biodivers Conserv 15:57-68

Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological processes that affect populations in complex landscapes. Oikos 65:169-175

Eybert MC, Constant P, Lefeuvre JC (1995) Effects of changes in agricultural landscape on a breeding population of linnets Acanthis cannabina L. living in adjacent heathland. Biol Conserv 74:195-202

Fischer J, Lindenmayer DB, Manning AD (2006) Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. Front Ecol Environ 4:80-86

Fournier J, Arlettaz R (2001) Food provision to nestlings in the Hoopoe Upupa epops: implications for the conservation of a small endangered population in the Swiss Alps. Ibis 143:2-10

Freitag A (2004) Measuring food availability for an insectivorous bird: the case study of wrynecks and ants. In: van Hemden H, Rothschild M (eds) Insect and bird interactions. Intercept, Andover

Glen DM (2004) Birds as predators of lepidopterous larvae. In: van Hemden H, Rothschild M (eds) Insect and bird interactions. Intercept, Andover

Hodar JA, Zamora R (2004) Herbivory and climatic warming: a Mediterranean outbreaking caterpillar attacks a relict, boreal pine species. Biodivers Conserv 13:493-500

Hoyas J, López F (1998) Distribución del críalo según la abundancia de procesionaria del pino. Quercus 149:20-22

Jones GA, Sieving KE, Jacobson SK (2005) Avian diversity and functional insectivory on north-central Florida farmlands. Conserv Biol 19:1234-1245

Kristin A (2001) Family Upupidae (Hoopoe). In: del Hoyo J, Elliott A, Sargatal J (eds) Handbook of the birds of the world, vol. 6, Mousebirds to Hornbills. Lynx Edicions, Barcelona

Kupfer JA, Malanson GP, Franklin SB (2006) Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. Global Ecol Biogeogr 15:8-20

McCollin D (1998) Forest edges and habitat selection in birds: a functional approach. Ecography 21:247-260

McCracken DI, Tallowin JR (2004) Swards and structure: the interactions between farming practices and bird resources in lowland grasslands. Ibis 146:108-114

McGarigal K, Cushman SA, Neel MC, Ene E (2002) Fragstats: spatial pattern analysis program for categorical maps. Computer software program, University of Massachusetts, Amherst

Maizeret C (2005) Les Landes de Gascogne. Delachaux et Niestlé, Paris

Manly BJF, Miller P, Cook LM (1972) Analysis of a selective predation experiment. Am Nat 106:719-736

Manning AD, Lindenmayer DB, Nix HA (2004) Continua and Umwelt: novel perspectives on viewing landscapes. Oikos 104:621-628

Martinez JA, Zuberogoitia I (2004) Habitat preferences for long-eared owls Asio otus and little owls Athene noctua in semi-arid environments at three spatial scales. Bird Study 51:163-169

Martin-Vivaldi M, Palomino JJ, Soler M, Soler JJ (1999) Determinants of reproductive success in the Hoopoe Upupa epops, a hole-nesting non-passerine bird with asynchronous hatching. Bird Study 46:205-216

Martin-Vivaldi M, Martinez JG, Palomino JJ, Soler M (2002) Extrapair paternity in the Hoopoe Upupa epops: an exploration of the influence of interactions between breeding pairs, non-pair males and strophe length. Ibis 144:236-247

Morris AJ, Whittingham MJ, Bradbury RB, Wilson JD, Kyrkos A, Buckingham DL, Evans AD (2001) Foraging habitat selection by yellowhammers (Emberiza citrinella) nesting in agriculturally contrasting regions in lowland England. Biol Conserv 101:197-210

Mullen K, Fahy O, Gormally M (2003) Ground flora and associated arthropod communities of forest road edges in Connemara, Ireland. Biodivers Conserv 12:87-101

Olioso G, Jourde P (1999) Huppe fasciée Upupa epops. In: Rocamora G, Yeatman-Berthelot D (eds) Oiseaux menacés et à surveiller en France. Société d'Etudes Ornithologiques de France, LPO, Paris

Ouin A, Aviron S, Dover J, Burel F (2004) Complementation/supplementation of resources for butterflies in agricultural landscapes. Agric Ecosyst Environ 103:473-479

Paquet JY, Vandevyvre X, Delahaye L, Rondeux J (2006) Bird assemblages in a mixed woodland-farmland landscape: the conservation value of silviculture-dependant open areas in plantation forest. Forest Ecol Manag 227:59-70

Pons P, Lambert B, Rigolot E, Prodon R (2003) The effects of grassland management using fire on habitat occupancy and conservation of birds in a mosaic landscape. Biodivers Conserv 12:1843-1860

Preiss E, Martin JL, Debussche M (1997) Rural depopulation and recent landscape changes in a Mediterranean region: consequences to the breeding avifauna. Landscape Ecol 12:51-61

Robinet O, Bretagnolle V, Clout M (2003) Activity patterns, habitat use, foraging behaviour and food selection of the Ouvéa Parakeet (Eunymphicus cornutus uvaeensis). Emu 103:71-80

Sherry TW (1990) When are birds dietary specialized? Distinguishing ecological from evolutionary approaches. Stud Avian Biol 13:337-352

Sierro A, Arlettaz R, Naef-Daenzer B, Strebel S, Zbinden N (2001) Habitat use and foraging ecology of the nightjar Caprimulgus europaeus in the Swiss Alps: towards a conservation scheme. Biol Conserv 98:325-331

Sutherland WJ, Newton I, Green RE (2004) Bird ecology and conservation: a handbook of techniques. Oxford University Press, Oxford

Tubelis DP, Cowling A, Donnelly C (2004) Landscape supplementation in adjacent savannas and its implications for the design of corridors for forest birds in the central Cerrado, Brazil. Biol Conserv 118:353-364

Virkkala R, Luoto M, Rainio K (2004) Effects of landscape composition on farmland and red-listed birds in boreal agricultural-forest mosaics. Ecography 27:273-284

Wethered R, Lawes MJ (2003) Matrix effects on bird assemblages in fragmented Afromontane forest in South Africa. Biol Conserv 114:327-340

Whitehead S, Johnstone I, Wilson J (2005) Choughs Pyrrhocorax pyrrhocorax breeding in Wales select foraging habitat at different spatial scales. Bird Study 52:193-203

Wiens JA (1995) Habitat fragmentation: island vs landscape perspectives on bird conservation. Ibis 137:97-104

Wolda H (1990) Food availability for an insectivore and how to measure it. Stud Avian Biol 13:38-43

Wolff A, Dieuleveut T, Martin JL, Bretagnolle V (2002) Landscape context and little bustard abundance in a fragmented steppe: implications for reserve management in mosaic landscapes. Biol Conserv 107:211-220

Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164-168

Photo 4. Huppe fasciée *Upupa epops* adulte en óforagingô dans un bord de piste enherbée, Cestas, Gironde, juin 2006 (Julien Nezan).

2.3.2. Réponses hivernales des oiseaux généralistes à un défoliateur forestier

Résumé

La question du rôle contributif des interactions prédateur-proie à la limitation des pullulations dôinsectes forestiers fait encore débat. Peu de travaux se sont intéressés aux réponses numériques hivernales des oiseaux insectivores généralistes à la densité de chenilles hivernantes dôun défoliateur forestier majeur, la processionnaire du pin. Nous avons testé les effets de la structure et de la composition forestière aux échelles de la parcelle et du paysage sur la densité de chenilles et les communautés dôoiseaux hivernants, incluant des prédateurs généralistes. Nous avons échantillonné la densité de nids de processionnaire et les communautés dôoiseaux pendant deux hivers consécutifs le long de 25 transects linéaires situés dans des pinèdes de montagne sur un gradient altitudinal dans les Préalpes françaises. La sévérité de lôhiver affecte négativement à la fois la densité de chenilles et lôabondance et la richesse totales des oiseaux. La densité de processionnaires augmente dans les expositions sud et avec la fragmentation forestière, en particulier la densité de lisières. Les communautés dôoiseaux hivernants sont plus influencées par la fragmentation du paysage que les variables locales, à part la densité de nids de processionnaires. Lôabondance totale des oiseaux augmente avec la densité de processionnaires, mais seulement pendant lôhiver le plus froid, tandis que celle de la mésange charbonnière *Parus major* augmente avec cette densité, quelque soit la sévérité de lôhiver. Les réponses numériques hivernales des oiseaux dépendent plus de la composition du paysage que de la structure et de la composition forestière à lôéchelle de la parcelle. La conservation de la diversité fonctionnelle des oiseaux nicheurs et hivernants à lôéchelle du paysage devrait augmenter les opportunités de contrôle biologique des insectes ravageurs en forêt de montagne.

Abstract

The challenging question of predator-prey interactions contributing or not to limit insect outbreaks in forest ecosystems is still ongoing. Winter numerical responses of generalist insectivorous birds to overwintering larvae of a key pine defoliator, the pine processionary moth, has received little attention to date. Here, we tested the effects of forest structure and composition at stand and landscape scales on overwintering moth density and winter bird communities, including generalist moth predators. We assessed moth nest density and bird communities during two consecutive winters on 25 linear transects along an elevation gradient in mountain pine forests of the southern French Prealps. We found that winter severity significantly decreased both moth density and total bird abundance and richness. Pine processionary moth density increased with south-facing aspects and forest fragmentation, especially edge density, at the landscape scale. Winter bird communities were influenced more by forest fragmentation at the landscape scale than stand-scale variables, except moth density. Total bird abundance increased significantly with moth density only in the colder winter. Great tit *Parus major* abundance also increased significantly with moth density, but irrespective of winter severity. Winter bird numerical responses were mediated primarily by landscape composition, and secondarily by forest stand structure and composition. We suggest that landscape-scale conservation of bird functional diversity in both breeding and wintering seasons would increase opportunities for biological control of pest insects in mountain forests.

Introduction

Ecological theory predicts that outbreak frequency and magnitude of forest pest insects might be modified by concomitant changes in the abundance of their natural enemies (Klemola et al., 2002; Jepsen et al., 2008; Barbosa et al., 2012). However, actual changes in predator-prey interactions are still unclear due to the complexity of interactions involved (Bretagnolle and Gillis, 2010). A model case study is the pine processionary moth *Thaumetopoea pityocampa*, the main defoliator of south-european pine forests (Hódar and Zamora, 2004; Battisti et al., 2005). The pine processionary moth has been actively and rapidly spreading northwards and upwards in Europe in the last decades, winter temperature being its main limiting factor (Battisti et al., 2005). The threats constituted by this key pest insect to Mediterranean and European pine forests include a loss of biodiversity associated to isolated pine woodlands at the southern edge of their distributions (Hódar and Zamora, 2004), and a loss of wood economical value when repeated defoliations occur (Jacquet et al., 2012). Another important problem for human and domestic animal health is the easy wind dispersion of urticating setae released by late-instar overwintering larvae, which can cause serious reactions and allergy (Battisti et al., 2011). Overall, these problems can lead to controversial insecticide spraying over large forest areas (Cayuela et al., 2011). The relative role of pathogens, parasitoids and predators on the regulation of cyclic population outbreaks of pest herbivorous insects has been extensively debated (Klemola et al., 2002; Jepsen et al., 2008; Barbosa et al., 2012). The key functional role of vertebrate natural enemies such as birds and small mammals in keeping herbivorous insect populations at low densities is widely acknowledged (Crawford and Jennings, 1989; Glen, 2004). As a consequence, there has been a recent focus on ecosystem services provided by predatory birds in respect to insect herbivory control (Wenny et al., 2011). Yet, this focus is offset by another debate on the role of insect outbreaks as a natural disturbance for the long-term and large-scale conservation of forest biodiversity (Müller et al., 2008). Indeed, the spatio-temporal distribution of an invasive or outbreaking herbivorous insect is a major, although often overlooked, biotic factor driving the occurrence of insectivorous forest birds (Crawford and Jennings, 1989; Patten and Burger, 1998; Haney, 1999; Gale et al., 2001; Unno, 2002; Hogstad, 2005; Edworthy et al., 2011). In temperate forests of the Northern hemisphere, the bird guild of canopy-gleaners (e.g., Parulinae warblers in northern America or Paridae tits in Europe) often show significant numerical responses to outbreaking Lepidoptera and increase their density during peak tree defoliation (Diaz et al., 1998; Patten and Burger, 1998; Haney, 1999).

Generalist and specialist birds have different effects on prey outbreaks because of distinct responses to prey density (Klemola et al., 2002; Unno, 2002). When a pest insect with strong adaptations to avoid predation such as *T. pityocampa* is involved, the complementary feeding and foraging strategies in time and space of specialist and generalist birds allow an efficient predation throughout all life stages (Barbaro and Battisti, 2011; Nixon and Roland, 2012). Specialist birds such as the Eurasian hoopoe *Upupa epops* can have a strong impact at the pupal stage of *T. pityocampa* locally, but they need habitat complementation at the landscape scale (Barbaro and Battisti, 2011). Generalist avian predators can also be useful for the biological control of *T. pityocampa*, particularly because they tend to reach higher density and require lower habitat quality than specialists (Klemola et al., 2002; Symondson et al., 2002). Among the generalist predators of the pine processionary moth, the most regular are Paridae tits, and especially the great tit *Parus major* (Gonzalez-Cano, 1981). Habitat quality and forest tree diversity influence forest stand selection by the moth, but also the functional responses of generalist birds and the overall efficiency of avian predation (Jactel and Brockerhoff, 2007; Nixon and Roland, 2012). The seasonal patterns of relative predation rates on different life cycles of pest Lepidoptera by generalist predators has received little attention to date (Unno, 2002; Nixon and Roland, 2012). In particular, knowledge on winter numerical responses of bird communities to overwintering insects is lacking (Carrascal et al., 2013), even though winter predation has proved critical to herbivorous arthropods (Barber and Wouk, 2012). Moreover, there is virtually no information on how forest fragmentation and landscape composition would mediate generalist bird responses to a key defoliator such as the pine processionary moth. The main objective of the present work is therefore to analyse the effect of landscape composition on winter bird numerical responses to *T. pityocampa* on a gradient of elevational expansion in the southern French Alps. We further tested to what extent (i) *T. pityocampa* winter abundance will decrease with increased winter severity and forest fragmentation; and (ii) bird communities and numerical bird responses to the moth will be affected by winter severity and mediated by landscape- and local-scale habitat composition of mountain pine forests.

Methods

Study area

The study site was located in the UNESCOôs Man and the Biosphere (MAB) Reserve of the Mont Ventoux in southeastern France (46°10ôN; 5°19ôE; Vaucluse district). The Mont Ventoux is a calcareous mountain peaking at 1912 m asl on the southern Prealps. The climate is supra-mediterranean, with high summer temperatures and marked summer drought at lower elevations (mean rainfall June-August, 170-180 mm; mean annual rainfall, 950-1000 mm; mean annual temperature, 9.2°C). The current forest mostly results from a massive afforestation with conifer plantations (mainly Corsican pine *Pinus nigra* ssp *laricio* and Atlas cedar *Cedrus atlantica*) in the late 19th century. We selected 25 pine forest stands distributed along an elevational gradient of decreasing *T. pityocampa* density, ranging from 400 to 1400 m asl on the north-western slope of the Mont Ventoux. The maximal elevation actually reached by the moth during the study was a winter nest found on a mountain pine *Pinus uncinata* at 1350 m in March 2009. The stands were selected according to several local factors expected to influence moth distribution, including main pine species, elevation, aspect, and proximity to an adjacent open habitat (Stastny et al., 2006; Dulaurent et al., 2011; Hódar et al., 2012). Forest stand composition was dominated by Aleppo pine *Pinus halepensis* and holm oak *Quercus ilex* at lower elevation, Corsican and Scots pine *P. sylvestris* at mid-elevation, and mountain pine, beech *Fagus sylvatica* and silver fir *Abies alba* at higher elevation. The forest was dense overall but interspersed with patches of lower pine tree density, agricultural openings and dry grassland-shrub mosaics dominated by *Buxus sempervirens* and *Juniperus communis*.

Bird and pine processionary moth sampling

During two consecutive years, two observers (LB and SB) sampled bird communities using 250m-long linear transects. All birds heard and seen were recorded and affected to 4x10 m-large strips on each side of the transect (i.e., up to 40 m on each side). Linear transects were used rather than point-counts because they were more suitable to survey birds outside their breeding season and matched the sampling methods used to record *T. pityocampa* winter nest density (see below). Birds were sampled in the morning of days without high wind or rain in April 2008 and March 2009. We estimated species detection probabilities with uniform detection function and cosine adjustment using Distance 6.0 software (Thomas et al., 2010). For the 18 most frequent species (51% of species), raw bird densities were highly correlated with density estimates accounting for species detectabilities ($R^2 = 0.82$). We hence used raw abundance data for further analyses. The density of *T. pityocampa* winter nests was measured on the same 250 m-long linear transects as birds (up to 10 m on each side). The winter nests of *T. pityocampa* were easy to locate because of their large size and obvious white color against blue sky on a sunny day; hence winter nest density can be considered a relevant proxy for true population density (Samalens and Rossi, 2011).

Stand and landscape variables

Meteorological data were obtained from HOBO® Pro v2 data loggers located at the upper range of the elevational gradient in the study site (1115 m asl). Data loggers monitored daily mean and minimal temperatures (T_{mean} and T_{min}; ŬC) and relative humidity (RH; %) from December 1st to March 31st during the two consecutive winters of 2008 and 2009. For each transect, we recorded 10 stand variables including elevation, aspect, dominant tree species (Scots pine stands, pure Corsican pine stands, mixed Corsican pine stands), mean tree height, percent cover of canopy and understorey trees, shrub, grasses and bare ground, and stratification diversity index. We measured mean tree height and the percent covers of vegetation layers with an ultrasound telemeter. For the landscape-scale variables, we mapped the study site in ArcView 3.2 (ESRI, Redlands) using the BD Ortho aerial imagery of the French National Geographic Institute from 2001. We exported circular buffers of 500- and 1000-m radius centred in the middle of the linear transects in raster format of 1-m pixel size from the vector land cover map. For each buffer, we computed 9 metrics to quantify landscape structure (i.e. edge density, mean patch area and perimeter / area ratio, habitat diversity index) and composition (% habitat covers: dense and clear forest, shrubland, agricultural land and rocky areas).

Data analysis

We first performed a Principal Component Analysis (PCA) on stand and landscape variables for a preliminary selection of predictive variables. To avoid multicollinearity in multi-model selection, we tested continuous variables for pairwise correlations > 0.65 using Pearson coefficients (Grueber et al., 2011). We also tested the effect of buffer scales and found that 500 m always performed better than 1000 m for explanatory landscape variables. We tested for a year effect (i.e., winter severity) on mean and minimum winter temperatures and relative humidity by means of Mann-Whitney non-parametric tests. Yet, we tested the effects of stand and landscape variables on winter nest density of the pine processionary moth. The number of *T. pityocampa* winter nests was log (x+1)-transformed to improve normality. We used multi-model inference within a hierarchical framework to analyse the effects of stand and landscape-level predictors on moth nest density (Grueber et al., 2011). We performed linear mixed models (Zuur et al., 2009) with multi-model selection by first testing the best performing model at the stand level (i.e., using all stand variables); and second the best model at the landscape level (500m) using the stand variables selected in the best previous model and all landscape variables. The initial set of stand variables included year, elevation, aspect, mean tree height, stratification diversity index and dominant tree species. The initial set of landscape variables included edge density, dense forest, clear forest and shrubland covers within 500 m-buffers around transect centers. Forest stand was defined as a random effect for all models to take into account repeated sampling periods for a given transect (Zuur et al., 2009; Grueber et al., 2011). The models were finally ranked according to their φAICc (< 3) at both stand and landscape levels with MuMIn R-package (Barton, 2012).

Winter bird communities were analyzed by Non-Metric Multidimensional Scaling (NMDS) of the data table including the 21 most abundant (>5 ind.) species x 50 sites. NMDS is a non-linear multivariate ordination method based on Bray-Curtis dissimilarities between species and sites (Oksanen 2011). We performed log (x+1) transformation of bird species abundances before NMDS analysis. We used the vegan R-package with the function ómetaMDSô for species ordination by NMDS and the function óenvfitô to calculate correlations between ordination axes and stand and landscape variables, where significance is based on 999 random permutations of the data table (Oksanen 2011). We performed Generalized Linear Mixed Models (GLMM) fitted with a Poisson distribution and using a log link function and Laplace approximation for total bird species abundance and richness and individual species abundance (Zuur et al., 2009). We modelled individual abundances for the 9 most abundant species, including *Fringilla coelebs*, *Periparus ater*, *Erithacus rubecula*, *Lophophanes cristatus*, *Regulus ignicapillus*, *Phylloscopus collybita*, *Cyanistes caeruleus*, *Certhia brachydactyla* and *Parus major*. We used the same multi-model selection procedure than previously by first testing the best model at the stand level, and second, the best model at the landscape level with best stand predictors conserved. We also included in the initial models at the stand level the interaction between year and *T. pityocampa* winter density, which was significant only for total bird abundance. To avoid confounding effects of forest habitat and moth density on individual bird responses to the moth, we systematically tested for non-significance of interactions between moth density and habitat variables. Forest stand was defined as a random intercept effect for all GLMMs (Zuur et al., 2009; Grueber et al., 2011). We finally ranked the best models combining variables selected at the stand and landscape levels with φAICc < 3. For individual species, we only present below the best models obtained after selection procedure. GLMMs were systematically checked for data overdispersion in model residuals. We used the R-package nlme for LMMs and lme4 for GLMMs (Bates et al., 2011; Pinheiro et al., 2012) and the MuMIn R-package to rank the final models with φAICc < 3 (Barton, 2012).

Results

Winter severity

The mean daily temperature (T_{mean}) was 2.75 ± 0.28°C during the winter of 2008 (from December 1st to March 31st), and 1.17 ± 0.28°C during the winter of 2009. The minimum daily temperature (T_{min}) was 0.61 ± 0.27°C and -0.95 ± 0.27°C and the relative humidity (RH) was 72.80 ± 1.59 % and 76.03 ± 1.51 % during the winters of 2008 and 2009, respectively. A significant year effect was observed on T_{mean} ($Z = 3.94$, $P < 0.001$) and T_{min} ($Z = 3.98$, $P < 0.001$), but not on RH. The winter of 2009 was therefore significantly colder than the one of 2008 and overall much snowier, with late spring snowfalls.

Scale	Model	Model predictors	k	AICc	φAICc	w_i
Stand		Initial model (stand) :				
		year + aspect + elevation + tree species + tree height + stratification diversity	10	145.8	3.00	0.09
	41	year + aspect	7	142.8	0	0.40
	45	year + aspect + tree species	9	142.8	0	0.40
	42	year + aspect + elevation	8	145.7	2.85	0.10
	46	year + aspect + elevation + species	10	145.8	3.00	0.09
Landscape		Initial model (stand + landscape):				
		year + aspect + edge density + clear forest + dense forest + shrubland	11	151.1	9.22	0.00
	45	year + aspect + edge density	8	141.9	0	0.32
	41	year + aspect	7	142.8	0.98	0.20
	61	year + aspect + edge density + shrubland	9	144.7	2.81	0.08
	47	year + aspect + edge density + dense forest	9	144.8	2.99	0.07

Table 1 Top linear mixed models (φAICc < 3) on log-transformed *T. pityocampa* nest density as response variable, stand and landscape scale variables as fixed effects and forest stand as random effect. AICc is the Akaike information criterion adjusted for sample size; φAICc is the difference in AICc between a given model and the best model having the lowest AICc score; k is the number of model parameters and wi is the AICc weight for a given model.

Pine processionary moth density

Winter severity significantly affected *T. pityocampa* nest density (Linear Mixed Model; F = 10.17; P < 0.004), with twice less nests per ha in 2009 than in 2008 on average (49.6 ± 14.4 in 2008 and 18.8 ± 6.4 in 2009). As expected, pine processionary moth density also decreased significantly with elevation (F = 18.65; P < 0.0003), was higher in south-facing slopes (F = 22.11; P < 0.001) and in pure Corsican pine stands (F = 18.57; P < 0.001), in both years. The winter nest density of *T. pityocampa* decreased significantly with dense forest cover (F = 9.39; P < 0.006) and increased significantly with overall forest fragmentation at the landscape level, especially with clear forest cover and edge density (F = 17.79; P < 0.0003 and F = 20.51; P < 0.0002 respectively; Fig. 1). At the stand scale, the best model included year and aspect, showing the predominant role of climate-related factors at the local scale (Table 2). At the landscape scale, these stand-level variables were conserved when considering the best model, which finally included year, aspect and edge density (Table 1).

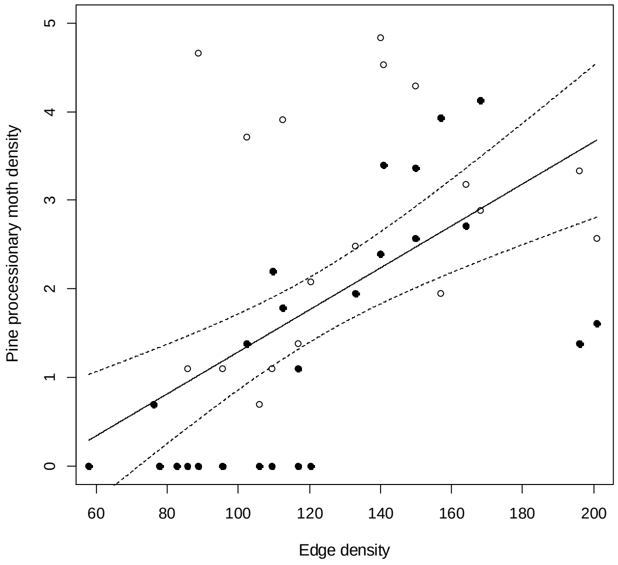


Fig. 1 Linear mixed model linking log-transformed density of the pine processionary moth to edge density at 500 m-landscape scale. Plain black and dashed lines are the estimates of linear predictors and 95% confidence intervals of LMM. White dots = winter 2008; black dots = winter 2009.

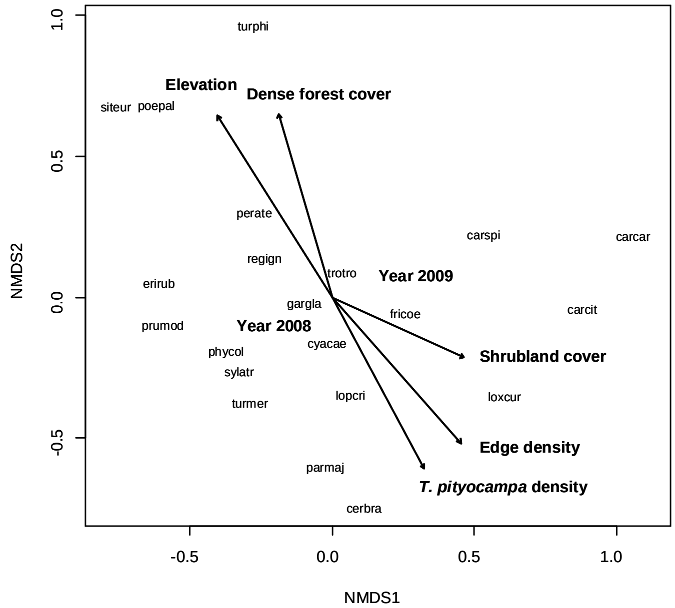


Fig. 2. NMDS ordination biplot of 21 bird species x 50 plots. Stand and landscape variables with highest correlations with ordination axes are shown (P < 0.05). Species codes use the first three letters of genus and species scientific names respectively, as follows: turphi = *Turdus philomelos.*

Ordination of winter bird communities

We recorded 982 individual birds of 35 species overall. The 5 dominant species (with > 50 individuals) were in decreasing order *Fringilla coelebs, Periparus ater, Erithacus rubecula, Lophophanes cristatus* and *Regulus ignicapillus*. The ordination of winter bird communities was conducted on a subsample of the 21 most abundant and frequent species by NMDS (Fig. 2). The most significant stand and landscape variables related to the ordination of bird communities were respectively elevation ($R^2 = 0.35$; $P < 0.001$), moth nest density ($R^2 = 0.29$; $P < 0.001$), edge density ($R^2 = 0.28$; $P < 0.001$), dense forest cover ($R^2 = 0.28$; $P < 0.002$) and year ($R^2 = 0.11$; $P < 0.007$) (Fig. 2). Other stand variables, i.e., mean tree height and stratification diversity index, were not significant. The colder winter of 2009 was characterized by a higher abundance of several fringillids including red crossbill Loxia curvirostra, Eurasian siskin *Carduelis spinus* and citril finch *C. citrinella* (Fig. 2).

Winter bird abundance and richness

Total bird abundance was significantly lower in the colder winter of 2009 (mean bird density per ha = 11.5 ± 1.1 in 2008 vs 8.4 ± 1.0 in 2009; Poisson GLMM; $z = -4.96$; $P < 0.0001$). Total bird abundance also increased significantly with *T. pityocampa* nest density ($z = 4.33$; $P < 0.0001$) but only in the colder winter, as shown by the significant interaction between year and the log-transformed moth abundance ($z = 2.31$; $P < 0.02$). The best model obtained by multi-model inference at the stand level included year, *T. pityocampa* density and mean tree height as significant variables. After adding landscape variables, the final model obtained included year, T. pityocampa density, clear forest and dense forest covers (Table 2). Mean bird species richness recorded on linear transects was also significantly lower in the colder winter (9.2 ± 0.6 in 2008 vs 7.0 ± 0.6 in 2009; $z = -2.71$; $P < 0.01$), but the effect of *T. pityocampa* density was not significant. The best final model for species richness included year, dense forest and clear forest covers.

Model	Model predictors	k	AICc	φAICc	w_i
	Initial model (stand + landscape):				
	year + log PPM + tree height + edge density + clear forest + dense forest + shrubland	9	173.5	7.72	0.007
84	year + log PPM + clear forest + dense forest	6	165.8	0	0.336
88	year + log PPM + edge density + clear forest + dense forest	7	168.0	2.18	0.113
116	year + log PPM + clear forest + dense forest + shrubland	7	168.1	2.35	0.104
92	year + log PPM + tree height + clear forest + dense forest	7	168.3	2.51	0.096

Table 2 Top Poisson generalized linear mixed models with φAICc < 3 after multimodel inference for stand and landscape variables as fixed effects and forest stand as random effect on total bird abundance. Log PPM is the log-transformed abundance of *T. pityocampa* winter nests. AICc is the Akaike information criterion adjusted for sample size; φAICc is the difference in AICc between a given model and the best model having the lowest AICc score; k is the number of model parameters and wi is the AICc weight for a given model.

Numerical responses of individual bird species

We performed multi-model selection for the 9 most abundant bird species, based on an initial model with the same set of stand and landscape variables (Table 3). Winter severity (year effect) affected significantly individual abundances for 6 species, while pine processionary moth density was selected in final best models for 4 species, including great tit *Parus major*, blue tit *Cyanistes caeruleus*, short-toed treecreeper *Certhia brachydactyla* and chaffinch *Fringilla coelebs* (Table 3). The other stand variables were selected in best models for 2 species (tree height, tree species and stratification diversity) and clear forest and dense forest covers were the most influential landscape predictors, for respectively 4 and 3 species (Table 3). For the main generalist moth predator, *Parus major*, there was a significant effect of *T. pityocampa* winter nest density ($z = 3.16$; $P < 0.002$; Fig. 3). However, year effect (i.e., winter severity) did not affect significantly great tit abundance. The best model at the stand level included only moth density, and the best model for landscape-scale variables also included clear forest, dense forest and shrubland covers (Table 3). The interaction terms between moth density and landscape variables were not significant for any species, thus accounting for the absence of confounding effects between moth abundance and habitat variables.

Bird species	Model	Model predictors	k	AICc	w_i
Erithacus rubecula	41	year + tree species	5	92.7	0.118
Phylloscopus collybita	37	year + stratification diversity	4	64.8	0.100
Regulus ignicapillus	89	year + tree height + tree species	6	72.0	0.120
Parus major	28	log PPM + clear forest + dense forest + shrubland	6	56.4	0.192
Cyanistes caeruleus	21	log PPM + stratification diversity	4	86.9	0.160
Periparus ater	109	year + edge density + dense forest + shrubland	6	75.1	0.082
Lophophanes cristatus	40	year + edge density + clear forest + dense forest	6	65.5	0.519
Certhia brachydactyla	10	log PPM + clear forest	4	57.2	0.221
Fringilla coelebs	90	year + log PPM + tree height + clear forest	6	105.1	0.169

Table 4 Top Poisson generalized linear mixed models after multimodel inference for stand and landscape variables as fixed effects and forest stand as random effect on the 9 most abundant bird species. Log PPM is the log-transformed abundance of *T. pityocampa* winter nests. AICc is the Akaike information criterion adjusted for sample size; k is the number of model parameters and wi is the AICc weight for a given model.

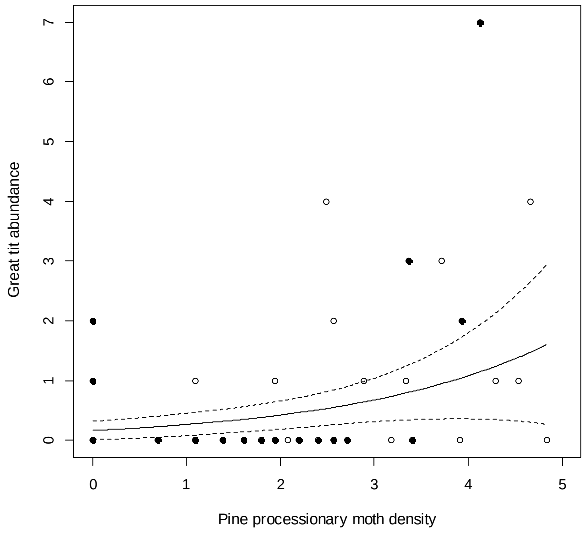


Fig. 3 Poisson generalized linear mixed model linking great tit *Parus major* abundance to log-transformed density of the pine processionary moth. Plain black and dashed lines are the estimates of linear predictors and 95% confidence intervals of Poisson GLMM. White dots = winter 2008; black dots = winter 2009.

Discussion

Winter severity and forest fragmentation affect moth density

The present work highlights the important effects of winter severity and forest fragmentation on the pine processionary moth. *T. pityocampa* is a social Lepidoptera that overwinters at the late-instar larval stage and formerly had a circum-mediterranean range distribution (Hódar and Zamora, 2004; Battisti et al., 2005). The increase in minimum winter temperatures has been the main factor responsible for the current expansion of *T. pityocampa* along latitudinal and elevational gradients in western Europe (Battisti et al., 2005). Climatic effects on *T. pityocampa* mortality at the local habitat scale are well-known, especially the negative effect of minimal daily temperatures, while high sunlight conditions increase larval growth rates because of higher daytime temperature inside the nest (Battisti et al., 2005). Here, we found that the effects of winter severity on overwintering nest density of *T. pityocampa* were mediated by forest habitat structure and composition at both local and landscape scales. Most notably, aspect (south-facing slopes) and stand tree composition (pure Corsican stands) at the local scale, as well as edge density at the landscape scale had the strongest positive effects on winter nest density. This is consistent with previous studies that demonstrated a higher sensitivity of pure Corsican stands to infestations by the pine processionary moth (Stastny et al., 2006; Hódar et al., 2012).

Moreover, the positive edge effect on late-instar pupae survival (Dulaurent et al., 2011) scales up into positive edge effects on *T. pityocampa* distribution in continuous forest landscapes interspersed with open habitats (Samalens and Rossi, 2011). An effect of forest tree diversity, albeit not tested here, is also likely to influence moth distribution both at the stand and landscape scales (Jactel and Brockerhoff, 2007).

Winter bird numerical responses to the moth

Our work provides empirical evidence for a significant increase of winter bird abundance to the density of pine processionary moths during a cold winter. Such an increase does not imply only a direct effect of moth density on bird abundance, but also a potential effect of the same habitat variables on both overwintering birds and moths. However, the lack of significant individual effects of stand-level variables, except mean tree height, on winter bird abundance suggests that moth density is a key environmental factor in bird winter habitat that could be used as a visual cue by forest birds to indicate more suitable habitat conditions favouring survival in winter (Carrascal et al., 2012). Moreover, direct field observations tend to prove that moth winter nests are actually predated by great tits using a particular feeding method (Gonzalez-Cano, 1981). The presence of tits is also used by other forest passerines to indicate higher habitat quality and food availability and may gather mixed-species foraging flocks in the same areas (Forsman et al., 2009). Few studies to date had demonstrated significant numerical responses of generalist insectivorous birds to *T. pityocampa* seasonal abundance (see a review in Barbaro and Battisti, 2011). Here, we found that total bird abundance and the abundance of the main generalist avian predator, the great tit Parus major, significantly increased with nest density of *T. pityocampa.* Outbreaking populations of Lepidoptera are considered to have escaped controlling factors (Barbosa et al., 2012). One of the factors involved, together with interacting demographic processes and climatic variables, could actually be avian predation (Barbosa et al., 2012). Indeed, both numerical and functional responses of generalist insectivorous birds to pest Lepidoptera outbreaks have been documented in various temperate forest ecosystems (Crawford and Jennings, 1989; Patten and Burger, 1998; Haney, 1999; Gale et al., 2001; Hogstad, 2005). The respective role of specialist vs generalist predators on the efficiency of biological control for pest Lepidoptera have been extensively discussed (Symondson et al., 2002). Generalist predators are generally considered to significantly contribute to maintain low population levels and potentially decrease the frequency and magnitude of insect outbreaks (Klemola et al., 2002; Glen, 2004; Barbosa et al., 2012).

Among generalist insectivorous birds, the great tit *Parus major* is the most significant generalist avian predator of *T. pityocampa* (Barbaro and Battisti, 2011). Great tits are actually key generalist predators of Lepidoptera larvae able to switch on a particular resource temporarily available by locating rapidly a local increase in food availability, including during wintertime (Diaz et al., 1998; Sanz, 2001; Unno, 2002; Carrascal et al., 2012). This behaviour, whether it is a learning behaviour or an evolved behavioural adaptation, allows them to feed on palatable parts of otherwise urticating prey (Gonzalez-Cano, 1981). They tend to forage preferentially on a few tree species with high total biomass, and to select the largest prey items (Diaz et al., 1998; Sanz, 2001). Moreover, their winter distribution is driven by food availability and accessibility (Brotons and Herrando, 2003; Carrascal et al., 2012), at least as much as in spring and summer (Diaz et al., 1998). Winter food availability also determines the spatial variation in species richness of some bird foraging guilds, especially for stable and predictable resources not affected by snowfalls (Carrascal et al., 2012). Large aggregated *T. pityocampa* larvae within easily detectable winter nests may therefore constitute an attractive prey source for great tits in winter. However, feeding on urticating larvae requires significant handling time because the bird needs to remove the head capsule to eat only the inner parts of the larvae (Gonzalez-Cano, 1981). A temporary specialization of great tits during winter on a predictable and abundant food resource (Carrascal et al., 2013) may therefore explain the numerical responses observed here. The other mechanisms potentially involved in the observed bird responses include the use of *T. pityocampa* winter nests as visual cues by other foraging insectivorous birds. For example, moth nests can provide additional resources such as predatory ants and other arthropods attracted by dead moth larvae, or silken threads used for nest buildings in early spring by several species, including the chaffinch *Fringilla coelebs* (Barbaro and Battisti, 2011). Moreover, the mixed flocks leaded by foraging tits are indicators of habitat quality for other forest insectivorous birds (Forsman et al., 2009). Great tits are flock leaders in cooperative winter foraging flocks and small insectivorous followers participating to these flocks could therefore be able to increase their own foraging rates and feeding efficiency (Sridhar et al., 2009).

Landscape composition mediates bird winter abundance

A striking result from the present study is the combination of winter severity (year effect), *T. pityocampa* density and landscape composition variables for shaping bird numerical responses. As demonstrated by previous studies on bird communities in the same study area, bird species richness did not differ significantly between pure and mixed forest stands, and between native Scots pine vs introduced Corsican pine stands (Archaux and Bakkaus, 2007). Moreover, bird richness does not change significantly with elevation in mountain forests (Schwenk et al., 2010), most likely because a large turnover in species composition between broadleaved and conifer-associated birds compensates for a loss in species richness on the elevational gradient (Archaux and Bakkaus, 2007). Here we found that landscape-level factors such as forest fragmentation (edge density) and the relative proportions of open habitats and dense and clear forests affected more winter bird distribution than stand-scale variables. At the stand level, the key factor affecting bird responses was actually *T. pityocampa* density. These results therefore support our initial hypothesis that landscape fragmentation and composition would mediate winter bird responses to the pine processionary moth as an aggregated food resource temporarily exploited by some insectivorous birds, especially during cold winters. Forest fragmentation and especially edge effects actually favor both *T. pityocampa* survival (Dulaurent et al., 2011) and bird foraging in winter (Brotons and Herrando, 2003). Moreover, forest habitat quantity and diversity at the landscape scale are also likely to promote insectivorous bird survival in winter, by providing more potential food resources during a critical period within a smaller spatial area (Siffczyk et al., 2003; Carrascal et al., 2012). Such a positive numerical response of winter bird communities to *T. pityocampa* raises the question of the pine processionary moth being as much a keystone species for biodiversity as a pest defoliator in mountain forests (Müller et al., 2008).

Conclusion

The present study suggests that adequate landscape-level planning and management of forests may enhance generalist avian predation and biological pest control by conservation of functional bird diversity (Tscharntke et al., 2007). It may also contribute to limit the development of *T. pityocampa* outbreaks and impede the negative effects of intensive management of pine forests by insecticide spraying, especially in recreational areas such as MAB Reserves (Sanz, 2001; Cayuela et al., 2011). The numerical response of generalist insectivorous birds to in newly-colonized areas may help to slow down the northwards and upwards moth expansion observed with climate change (Battisti et al., 2005). However, the slow response of bird communities to climate warming in the southern Alps (Archaux and Bakkaus, 2007), together with the recent expansion of Corsican pines above the timberline (Piermattei et al., 2012), both question the evolution of such predator-prey interactions under fast climate change.

References

Archaux, F., Bakkaus, N., 2007. Relative impact of stand structure, tree composition and climate on mountain bird communities. Forest Ecol. Manag. 247, 72-79.

Barbaro, L., Battisti, A., 2011. Birds as predators of the pine processionary moth (Lepidoptera: Notodontidae). Biol. Control 56, 107-114.

Barber, N.A., Wouk, J., 2012. Winter predation by insectivorous birds and consequences for arthropods and plants in summer. Oecologia 170, 999-1007.

Barbosa, P., Letourneau, D., Agrawal, A., 2012. Insect outbreaks revisited. John Wiley & Sons, Chichester.

Barton, K., 2012. Package óMuMInô. Model selection and model averaging based on information criteria. R package version 1.7.11.

Bates, D., Maechler, M., Bolker, B., 2011. lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-39.

Battisti, A., Stastny, M., Netherer, S., Robinet, C., Schopf, A., Roques, A., Larsson, S., 2005. Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. Ecol. Appl. 15, 2084ï 2096.

Battisti, A., Holm, G., Fagrell, B., Larsson, S., 2011. Urticating hairs in arthropods: their nature and medical significance. Annu. Rev. Entomol. 56, 203ï 220.

Bretagnolle, V., Gillis, H., 2010. Predatorï prey interactions and climate change. In: Moller, A.P., Fiedler, W., Berthold, P. (Eds.) Effects of climate change on birds. Oxford Univ Press, New York, pp. 227-248.

Brotons, L., Herrando, S., 2003. Effect of increased food abundance near forest edges on flocking patterns of coal tit Parus ater winter groups in mountain coniferous forests. Bird Study 50, 106ï 111.

Carrascal, L.M., Seoane, J., Villén-Pérez, S., 2013. Temperature and food constraints in wintering birds: an experimental approach in montane Mediterranean oakwoods. Community Ecol. 13, 221-229.

Carrascal, L.M., Villén-Pérez, S., Seoane, J., 2012. Thermal, food and vegetation effects on winter bird species richness of Mediterranean oakwoods. Ecol. Res. 27, 293ï 302.

Cayuela, L., Hódar, J.A., Zamora, R., 2011. Is insecticide spraying a viable and cost-efficient management practice to control pine processionary moth in Mediterranean woodlands? Forest Ecol. Manag. 261, 1732ï 1737.

Crawford, H.S., Jennings, D.T., 1989. Predation by birds on spruce budworm Choristoneura fumiferana: functional, numerical, and total responses. Ecology 70, 152ï 163.

Diaz, M., Illera, J.C., Atienza, J.C., 1998. Food resource matching by foraging tits Parus spp. during spring-summer in a Mediterranean mixed forest: evidence for an ideal free distribution. Ibis 140, 654-660.

Dulaurent, A.M., Porté, A.J., van Halder, I., Vétillard, F., Menassieu, P., Jactel, H., 2011. A case of habitat complementation in forest pests: pine processionary moth pupae survive better in open areas. Forest Ecol. Manag. 261, 1069ï 1076.

Edworthy, A.B., Drever, M.C., Martin, K., 2011. Woodpeckers increase in abundance but maintain fecundity in response to an outbreak of mountain pine bark beetles. Forest Ecol. Manag. 261, 203ï 210.

Forsman J.T., Hjernquist M.B., Gustafsson L., 2009. Experimental evidence for the use of density based interspecific social information in forest birds. Ecography 32, 539ï 545.

Gale, G.A., DeCecco, J.A., Marshall, M.R., McClain, W.R., Cooper, R.J., 2001. Effects of gypsy moth defoliation on forest birds: an assessment using breeding bird census data. J. Field Ornithol. 72, 291-304.

Glen, D.M., 2004. Birds as predators of lepidopterous larvae. In: van Hemden, H., Rothschild, M. (Eds.), Insect and bird interactions. Intercept, Andover, pp. 89-106.

Gonzalez Cano, J.M., 1981. Predacion de procesionaria del pino por vertebrados en la zona de Mora de Rubielos (Teruel). Boletin de la Estacion Central de Ecologia 10, 53-77.

Grueber, C.E., Nakagawa, S., Laws R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. J. Evol. Biol. 24, 699-711.

Haney, J.C., 1999. Numerical response of birds to an irruption of elm spanworm (Ennomos subsignarius [Hbn.]; Geometridae: Lepidoptera) in old-growth forest of the Appalachian Plateau, USA. Forest Ecol. Manag. 120, 203-217.

Hódar, J.A., Zamora, R., 2004. Herbivory and climatic warming: a Mediterranean outbreaking caterpillar attacks a relict, boreal pine species. Biodivers. Conserv. 13, 493ï 500.

Hódar, J.A., Zamora, R., Cayuela, L. 2012. Climate change and the incidence of a forest pest in Mediterranean ecosystems: can the North Atlantic Oscillation be used as a predictor? Climatic Change 113, 699ï 711.

Hogstad, O., 2005. Numerical and functional responses of breeding passerine species to mass occurrence of geometrid caterpillars in a subalpine birch forest: a 30-year study. Ibis 147, 77ï 91.

Jacquet, J.S., Orazio, C., Jactel, H., 2012. Defoliation by processionary moth significantly reduces tree growth: a quantitative review. Ann. Forest Sci. 69, 857-866.

Jactel, H., Brockerhoff, E.G., 2007. Tree diversity reduces herbivory by forest insects. Ecol. Lett. 10, 835-848.

Jepsen, J.U., Hagen, S.B., Ims, R.A., Yoccoz, N.G., 2008. Climate change and outbreaks of the geometrids Operophtera brumata and Epirrita autumnata in subarctic birch forest: evidence of a recent outbreak range expansion. J. Anim. Ecol. 77, 257ï 264.

Klemola, T., Tanhuanpia, M., Korpimaki, E., Ruohomaki, K., 2002. Specialist and generalist natural enemies as an explanation for geographical gradients in population cycles of northern herbivores. Oikos 99, 83-94.

Müller J., Bussler H., Gossner M., Rettelbach T., Duelli P., 2008. The European spruce bark beetle Ips typographus in a national park: from pest to keystone species. Biodivers. Conserv. 17, 2979-3001.

Nixon A.E., Roland J., 2012. Generalist predation on forest tent caterpillar varies with forest stand composition: an experimental study across multiple life stages. Ecol. Entomol. 37, 13ï 23.

Oksanen, J., 2011. Multivariate analysis of ecological communities in R: vegan tutorial. R package vs 2.0-1.

Patten, M.A., Burger, J.C., 1998. Spruce budworm outbreaks and the incidence of vagrancy in eastern North American wood-warblers. Can. J. Zool. 76, 433-439.

Piermattei, A., Renzaglia, F., Urbinati, C., 2012. Recent expansion of Pinus nigra Arn. above the timberline in the central Apennines, Italy. Ann. Forest Sci. 69, 509ï 517.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core team, 2012. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-103.

Samalens J.C., Rossi J.P., 2011. Does landscape composition alter the spatiotemporal distribution of the pine processionary moth in a pine plantation forest? Popul. Ecol. 53, 287ï 296.

Sanz, J.J., 2001. Experimentally increased insectivorous bird density results in a reduction of caterpillar density and leaf damage to Pyrenean oak. Ecol. Res. 16, 387ï 394.

Schwenk, W.S., Strong, A.M., Sillett, T.S., 2010. Effects of bird predation on arthropod abundance and tree growth across an elevational gradient. J. Avian Biol. 41, 367-377.

Siffczyk, C., Brotons, L., Kangas, K., Orell, M., 2003. Home range size of willow tits: a response to winter habitat loss. Oecologia 136, 635ï 642.

Sridhar, H., Beauchamp, G., Shanker, K., 2009. Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. Anim. Behav. 78, 337-347.

Stastny, M., Battisti, A., Petrucco-Toffolo, E., Schlyter, F., Larsson, S., 2006. Host-plant use in the range expansion of the pine processionary moth, Thaumetopoea pityocampa . Ecol. Entomol. 31, 481-490.

Symondson, W.O.C., Sunderland K.D., Greenstone M.H., 2002. Can generalist predators be effective biocontrol agents? Annu. Rev. Entomol. 47, 561-594.

Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L., Bishop, J.R.B., Marques, T.A., Burnham, K.K., 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. J. Appl. Ecol. 47, 5-14.

Tscharntke, T., Bommarco, R., Clough, Y., Crist, T.O., Kleijn, D., Rand, T.A., Tylianakis, J.A., van Nouhuys, S., Vidal, S., 2007. Conservation biological control and enemy diversity on a landscape scale. Biol. Control 43, 294ï 309.

Unno, A., 2002. Tree species preferences of insectivorous birds in a Japanese deciduous forest: the effect of different foraging techniques and seasonal change of food resources. Ornithol. Sci. 1, 133ï 142

Wenny, D.G., DeVault, T.L., Johnson, M.D., Kelly, D., Sekercioglu, C.H., Tomback, D.F., Whelan, C.J., 2011. The need to quantify ecosystem services provided by birds. Auk 128, 1-14.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R. Springer, New York

Photo 5. Vue du site dőétude, versant Nord de Mont Ventoux, Vaucluse, juin 2008 (Luc Barbaro).

2.4. Effets directs et indirects de lôinsectivorie avienne en forêt

2.4.1. Effets de lisière et de surface sur les assemblages dôoiseaux et lôinsectivorie dans les forêts natives fragmentées

Résumé

Les effets confondus de lisière et de surface sont difficiles à démêler dans les paysages fragmentés et requièrent lôutilisation de protocoles appropriés. Nous avons examiné les effets de la surface du fragment forestier et de la position du relevé en lisière ou en intérieur sur les assemblages dôoiseaux natifs et exotiques dans la péninsule de Banks (Ile du Sud, Nouvelle-Zélande). Nous avons aussi mesuré expérimentalement avec des leurres en plasticine lôinfluence de la surface du fragment et de la lisière forestière sur lôintensité dôinsectivorie avienne. Les assemblages dôoiseaux ont été échantillonnés par points dôécoute de 15 minutes appariés en lisière et en intérieur dans 13 fragments forestiers de surface variant entre 0.5 et 141 ha. Lôinsectivorie avienne a été mesurée par le taux dôattaque des oiseaux insectivores sur des leurres en plasticine modelés en forme dôune chenille de lépidoptère polyphage natif. Il y a des effets de lisière significatifs, mais pas dôeffets de surface, sur la richesse, lôabondance et la composition de lôavifaune. Les oiseaux exotiques sont plus abondants en lisière mais il nôy a pas dôeffet de lisière ou de surface significatifs sur la richesse et lôabondance des oiseaux natifs. Le taux de prédation des leurres augmente avec la fragmentation car lôinsectivorie est plus forte à la fois dans les fragments de petite taille et les lisières forestières. La prédation par les oiseaux augmente significativement avec la richesse en oiseaux insectivores et lôabondance des oiseaux en prospection alimentaire. La coexistence dôespèces natives et exotiques dans les paysages néo-zélandais en mosaïque favorise la diversité fonctionnelle et la complémentarité des traits de vie au sein des assemblages dôoiseaux prédateurs. Cette coexistence se traduit par une insectivorie des oiseaux plus grande dans les petits fragments forestiers en raison dôeffets additifs de lisière et de surface.

Abstract

Disentangling the confounded effects of edge and area in fragmented landscapes is a recurrent challenge for landscape ecologists, requiring the use of appropriate study designs. Here, we examined the effects of forest fragment area and plot location at forest edges vs interiors on native and exotic bird assemblages on Banks Peninsula (South Island, New Zealand). We also experimentally measured with plasticine models how forest fragment area and edge vs interior location influenced the intensity of avian insectivory. Bird assemblages were sampled by conducting 15 min point-counts at paired edge and interior plots in 13 forest fragments of increasing size (0.5 - 141 ha). Avian insectivory was measured as the rate of insectivorous bird attacks on plasticine models mimicking larvae of a native polyphagous moth. We found significant effects of edge, but not of forest patch area, on species richness, abundance and composition of bird assemblages. Exotic birds were more abundant at forest edges, while neither edge nor area effects were noticeable for native bird richness and abundance. Model predation rates increased with forest fragmentation, both because of higher insectivory in smaller forest patches and at forest edges. Avian predation significantly increased with insectivorous bird richness and foraging bird abundance. We suggest that the coexistence of native and exotic birds in New Zealand mosaic landscapes enhances functional diversity and trait complementation within predatory bird assemblages. This coexistence results in increased avian insectivory in small forest fragments through additive edge and area effects.

Introduction

The biological control of forest insect pests by insectivorous birds is considered a major ecosystem service provided by biodiversity (Wenny et al. 2011). Avian insectivory contributes to the regulation of insect populations and their associated damages on plants, wood or fruit production (Wearing and McCarthy 1992; Mols and Visser 2002; Skoczylas et al. 2007; Philpott et al. 2009). In forest ecosystems, such a reduction in herbivory favours seedling survival and enhances forest regeneration (Simonetti et al. 2007; Giffard et al. 2012). However, this beneficial role of insectivorous birds may be threatened by temporal and spatial mismatches due to climate warming and native forest fragmentation, which may either increase or decrease the frequency and magnitude of insect outbreaks (Tscharntke et al. 2007; Bretagnolle and Gillis 2010). The fragmentation of native habitats affects both species patch occupancy and species interactions through the trophic chain length (Ewers and Didham 2006). Habitat fragmentation is expected to increase frequency or magnitude of ecological processes, including species interactions. Such altered processes in fragmented habitats are defined as hyperdynamic (Laurance 2002). Fragmentation actually involves several inter-related albeit distinct components with synergistic or antagonistic effects on species communities and interactions, such as overall habitat loss, reduced patch area and increased edge effects (Parker et al. 2005; Ewers et al. 2007; Fletcher et al. 2007; Banks-Leite et al. 2010). These components of fragmentation are therefore expected to influence both the composition of bird and insect communities in remaining native forest patches and the intensity of bird insectivory, i.e., the consumption rates of herbivorous insects by insectivorous birds (González-Gómez et al. 2006; Skoczylas et al. 2007). Bird species responses to forest patch size and edge effects may also differ according to their native or exotic origin, which can be reflected in their distinct life-histories and habitat preferences (Cassey 2001; van Heezik et al. 2008).

The native forests of New Zealand have experienced a long history of fragmentation and are nowadays occurring throughout much of the country as forest patches of various sizes within a landscape matrix dominated by exotic grasslands and pine plantations (Clout and Gaze 1984; Deconchat et al. 2009; Burns et al. 2011). Together with predation by introduced mammals, the loss of habitat due to the clearing of natural forest and the expansion of agriculture and other modified land cover resulted in major extinction events among the native avifauna (Holdaway 1989). These massive extinctions were accompanied by introductions of many bird species, mainly of European but also North American, Asian and Australian origin, in the New Zealand countryside before 1907 (Veltman et al. 1996). Among these alien species, 28 out of 137 that were released have successfully established, and their introduction success is correlated with initial population size and characteristics such as nonmigratory behaviour and high reproductive capacity (Veltman et al. 1996; Maitner et al. 2012). Invasion success in introduced birds is also known to be higher for small-bodied species, habitat generalists, and gregarious foragers (Veltman et al. 1996; Cassey 2001). In New Zealand, omnivorous or granivorous passerines foraging in open habitats clearly dominate among the successful invaders (Robertson et al. 2007). Interestingly, these successful invaders include several species which now have an unfavourable conservation status in their native region, including skylark (*Alauda arvensis*) and yellowhammer (*Emberiza citrinella*) (MacLeod et al. 2009). By contrast, New Zealandôs native forest habitats are less prone to colonization by exotic birds and other species. This is generally attributed to the greater invasibility of disturbed habitat and, especially for insects, the large phylogenetic distance between native New Zealand plants and the original host plants of introduced arthropods (Brockerhoff et al. 2010). Because life-history strategies often differ between native and exotic components of species assemblages, they are likely to be affected differently by edge effects and the distribution of native and exotic habitats at both local and landscape scales (Clout and Gaze 1984; Ewers et al. 2007; van Heezik et al. 2008).

The present work aims at disentangling the effects of forest fragment area and edge vs interior location on both bird assemblages sampled by point-counts and experimentally measured avian insectivory. We quantified avian insectivory using plasticine models mimicking larvae of a native polyphagous moth, the common forest looper (*Pseudocoremia suavis* Butler, Lepidoptera: Geometridae) (Berndt et al. 2004). Outbreaks of this species are known to cause occasional defoliations in pine plantations (Berndt et al. 2004), which may increase in the future with climate warming and development of new exotic plantations within mosaic landscapes mixing native and exotic habitats (Tscharntke et al. 2007; Brockerhoff et al. 2010). Plasticine models were successfully used to measure relative larval predation rates across habitats in tropical and temperate forest ecosystems (Loiselle and Farji-Brenner 2002; Koh and Menge 2006; Skoczylas et al. 2007; Mäntylä et al. 2008b). This technique allows replicating experiments at the landscape scale, and the observed predation rates has been shown to correlate well with bird foraging activity in a density-dependent way (González-Gómez et al. 2006). Here, we used the guidelines provided by Fletcher et al. (2007) to build a study design allowing to disentangle area and edge effects per se, by measuring bird abundance using point-counts and by assessing avian predation rates using plasticine models at the same distances from the nearest edge (0 and 50 m) in forest fragments of different sizes. We used the distance of 50 m to define forest interiors because this was above the depth of edge influence generally considered for vegetation structure and composition (Harper et al. 2005). Moreover, forest interior birds have been shown to increase significantly above an approximate threshold of 50 m from the edge (Brand and George 2001). We further hypothesized that: (i) native and exotic bird assemblages are differently affected by fragmentation of native forests through additive or synergistic effects of area and edge (Ewers et al. 2007; Deconchat et al. 2009); (ii) increasing fragmentation of native forests modifies the intensity of avian insectivory measured by model predation rates, in relation to both fragment area and edge effects (González-Gómez et al. 2006; Skoczylas et al. 2007).

Methods

Study sites

The study area was the volcanic Banks Peninsula located on the east coast of the South Island, New Zealand (43.74°S; 172.86°E), covering an area of ca. 1000 km² and peaking at 920 m asl (Wilson 2008). Banks Peninsula was almost entirely forested until the arrival of European settlers in ca. 1840 which was followed by rapid and large-scale deforestation leading to 90% deforestation by the early 20th century (Wilson 2008). Recently there has been a considerable increase of regenerating native scrub and forests, notably in reserve areas and along streams (Wilson 2008). However, old-growth native forests remaining today represent only ca. 1% of their pre-human extent (ca. 800 ha) and the main native forests are currently regenerating kanuka (*Kunzea ericoides*), and mixed hardwood forests (Wilson 2008). The main other habitats are exotic grasslands mostly grazed by sheep and covering ca. 50% of the area; exotic shrublands dominated by gorse (*Ulex europaeus*) and broom (*Cytisus scoparius*); and exotic plantation forests, mainly of *Pinus radiata*, covering ca. 2% of the present area. Within the study area, we selected 13 native forest fragments ranging in size from 0.5 to 141 ha and located in various protected areas, including scenic reserves (Fig.1). The main native tree and shrub species that were encountered in native forest fragments were *Melicytus ramiflorus, Macropiper excelsum, Pseudopanax arboreus, Pseudowintera colorata, Pittosporum tenuifolium, Alectryon excelsus, Coprosma rotundifolia, C. robusta, Griselinia littoralis, Myrsine australis, Plagianthus regius* and *Hebe salicifolia.* The only introduced tree species commonly recorded, although infrequent, was *Sambucus nigra.*

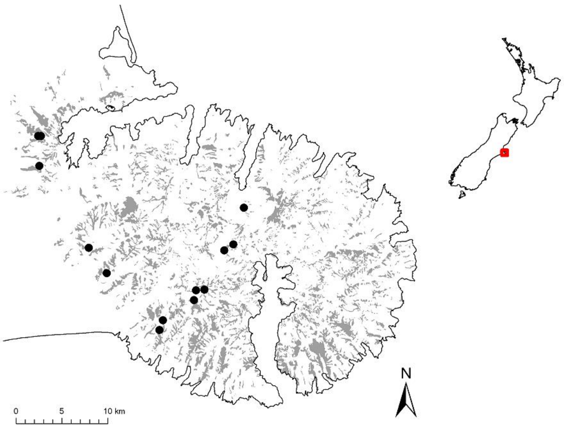


Fig. 1 Location map of Banks Peninsula (Canterbury, South Island, New Zealand). Black dots indicate plot locations and grey area shows the distribution of native forests.

Bird assemblages

Bird assemblages were sampled during the austral summer of 2010-2011 by the same observer (LB) using 15 min point-counts at paired edge and interior plots located at 50 m from the nearest forest edge in each of the 13 forest fragments (n = 26 plots). For the smallest forest patch (0.5 ha), the interior plot was located at 50 m from the sampled edge but due to the small size of the patch the other edges were closer to the interior plot (ca 35-40 m), while still holding a typical interior bird assemblage. Counts were performed twice in the season, the first visit in mid-January and the second in early February 2011, between 8 am and 12 pm during days without rain or high wind. To maintain species detectability comparable between edges and interiors, we limited bird counts to a 25 m-radius around the observer, which is considered a distance allowing a high probability of contact among forest passerines (close to 1) given their easy auditory detectability (Brotons and Herrando 2003). Bird species abundances used in further analyses were the maximum number of individuals recorded between the two visits.

To measure avian foraging intensity at the species assemblage level, we recorded individual birds observed in foraging activity during 10-minute periods after point-counts were carried out (Brotons and Herrando 2003). Foraging intensity was estimated as the number of birds observed in foraging activity at least once during the recording period (González-Gómez et al. 2006). Here again, we paid special attention to keep bird detectability comparable between edges and interiors by selecting similar understorey structures and densities at all plots surveyed (Brotons and Herrando 2003). Moreover, it was easy to obtain both auditory and visual contacts with the species recorded in foraging activity, particularly because the most frequent native species, i.e., bellbird (*Anthornis melanura*), silvereye (*Zosterops lateralis*) and fantail (*Rhipidura fuliginosa*) are very confident and not disturbed by the presence of humans (Higgins et al. 2006). We attributed bird species to native vs exotic sub-assemblages and to their main trophic guilds (Higgins et al. 2006; Barbaro and van Halder 2009). Birds were classified as insectivorous when invertebrate prey represents a significant part of the diet during summer (i.e., during the study period from mid-January to mid-February). The insectivorous bird guild included 8 native and 6 introduced species (Table 1). We included the mainly nectarivore bellbird in the insectivorous guild since invertebrates represent ca. 30-40% of the diet during its breeding period (Murphy and Kelly 2003).

Species name	Scientific name	Status	Trophic guild	Freq	Abun	Edge	Interior	Forag
New Zealand pigeon	*Hemiphaga novaeseelandiae*	Endemic	Granivorous	22	36	14	22	0
Shining cuckoo	*Chrysococcyx lucidus*	Native	Insectivorous	3	3	2	1	0
Sacred kingfisher	*Halcyon sancta*	Native	Omnivorous**	2	2	1	1	0
Rifleman	*Acanthisitta chloris*	Endemic	Insectivorous	1	1	0	1	0
Silvereye	*Zosterops lateralis*	Native	Insectivorous	19	60	39	21	14
Grey warbler	*Gerygone igata*	Endemic	Insectivorous	19	37	16	21	9
Brown creeper	*Mohoua novaeseelandiae*	Endemic	Insectivorous	5	15	5	10	8
New Zealand fantail	*Rhipidura fuliginosa*	Native	Insectivorous	18	37	15	22	11
Tomtit	*Petroica macrocephala*	Endemic	Insectivorous	6	8	2	6	4
Bellbird	*Anthornis melanura*	Endemic	Insectivorous*	26	94	40	54	22
Sulphur-crested cockatoo	*Cacatua galerita*	Exotic	Granivorous	1	4	4	0	0
Blackbird	*Turdus merula*	Exotic	Insectivorous*	21	40	17	23	0
Song thrush	*Turdus philomelos*	Exotic	Insectivorous	18	31	14	17	2
Dunnock	*Prunella modularis*	Exotic	Insectivorous	2	2	0	2	0
House sparrow	*Passer domesticus*	Exotic	Granivorous	2	7	7	0	5
Chaffinch	*Fringilla coelebs*	Exotic	Insectivorous*	8	22	20	2	7
Redpoll	*Carduelis flammea*	Exotic	Granivorous	18	49	37	12	0
Goldfinch	*Carduelis carduelis*	Exotic	Granivorous	3	8	8	0	0
Greenfinch	*Carduelis chloris*	Exotic	Granivorous	3	5	5	0	0
Yellowhammer	*Emberiza citrinella*	Exotic	Insectivorous*	12	17	17	0	3
Starling	*Sturnus vulgaris*	Exotic	Insectivorous*	4	14	10	4	1
Australian magpie	*Gymnorhina tibicen*	Exotic	Omnivorous	6	8	8	0	0
Total abundance of native species					293	134	159	68
Total abundance of exotic species					207	147	60	18
Total abundance of all bird species combined					500	281	219	86

Table 1 Total frequency and abundance of bird species recorded by point-counts and foraging observations. Status and diet according to Murphy and Kelly (2003); Higgins et al. (2006) and Barbaro and van Halder (2009). *Main diet during the breeding season (austral summer); **Forest-dwelling individuals are mostly insectivorous. Freq = Total species frequency; Abun = Total species abundance; Edge = Total species abundance at edge plots; Interior = Total species abundance at interior plots; Forag = Total number of foraging birds recorded.

Avian insectivory

In each of the 13 forest fragments, we selected 3 individual shrubs within the understorey at both the edge and interior plots (n = 3 x 2 x 13 = 78 individual shrubs). Each selected shrub was used as a support for artificial larvae mimicking Pseudocoremia suavis, a native polyphagous geometrid whose larvae are active throughout summer, naturally feeding on various native tree and shrub species (Berndt et al. 2004). Due to the high tree and shrub species diversity in New Zealand forests, it was not possible to control for the shrub species used. Instead, we used a few different species in proportion to their abundance within the understorey, with the most abundant species being mahoe (*Melicytus ramiflorus*, n = 29), kawakawa (*Macropiper excelsum*, n = 10), five-finger (*Pseudopanax arboreus*, n = 9), horopito (*Pseudowintera colorata*, n = 6) and kohuhu (*Pittosporum tenuifolium*, n = 5).

On each of the 78 individual shrubs, we attached 5 larvae modelled in light green plasticine with thin metal wires (Ø = 0.5 mm) on the external part of branches of the target shrub at ca. 2 m height (n = 30 models per forest fragment; n = 390 models for total plots). Each caterpillar was modelled to the approximate size and appearance of a bright green 5th or 6th-instar larva of *Pseudocoremia suavis*, i.e., L = ca. 20-30 mm, Ø = ca. 2-3 mm (Berndt et al. 2004). We measured model predation rates as the number of models attacked by birds (obvious bill markings) or mammals (obvious teeth markings) after 10 days in the field. We used a 10-day period to capture the most significant period of predator response in accordance with previous studies showing a peak in model predation rates by birds within 4-9 days after the larvae were installed (Posa et al. 2007; Mäntylä et al. 2008b). It was always possible to distinguish between attack markings caused by predatory birds or mammals. Mammal markings were all attributable to two introduced pests, the house mouse (*Mus musculus*) and the common brushtail possum (*Trichosurus vulpecula*). We did not observe any signs of attack by predatory arthropods.

Data analysis

The multivariate analysis of bird assemblages was performed by non-metric multidimensional scaling (NMDS) on the species-plot data table (26 plots x 16 species). NMDS (function metaMDS in vegan R-package) is a non-linear ordination method based on dissimilarities that allows finding the optimal ordination of species and sites (Oksanen 2011). We used Bray-Curtis distances as dissimilarity index for the species data table after log (x+1) transformation of species abundances. A non-parametric MANOVA was used to test for the joint effects of forest fragment area and location (edge vs interior plots) on the ordination of bird species assemblages (Oksanen 2011). The function adonis of the vegan R-package performs this non-parametric method fitting linear models to distance matrices, and the significance is obtained from a random permutation test on the data table (Oksanen 2011). To take into account the nestedness of the experimental design (paired edges and interior plots for a given forest fragment), we included forest fragment identity as a random effect (Oksanen 2011).

As for bird assemblages, the nested data structure resulting from the study design required the use of mixed models to analyze abundance and richness data (Zuur et al. 2009). Linear mixed models (LMM) were performed on total, insectivore and native bird species richness and abundance. Residuals of all LMMs were checked in order to meet the assumptions of normality and homoscedasticity. We used generalized linear mixed models (GLMM) on exotic species abundance and richness, single species abundances and numbers of foraging birds per species, fitted with a Poisson distribution and using a log link function and Laplace approximation for count data (Zuur et al. 2009). For the model predation rates, we used GLMMs with a binomial distribution for proportional data, i.e., the number of attacked models out of 15 models per plot (Zuur et al. 2009). We additionally tested with a binomial GLMM for an effect of the supporting shrub species on model predation rates with shrub species as a fixed effect and plot location nested within forest patch as random effects. As shrub species had no significant effect, we analysed model predation rates at the plot level. In all mixed models, forest fragment area and plot location (edge vs interior) were the fixed effects while the forest patch (accounting for replication between edge and interior plots within a given patch) was the random effect. For all GLMMs, the significance of each fixed effect (area, location and their interaction) was tested by comparing model deviances fitted with and without each effect with a G^2 test (Zuur et al. 2009). GLMMs were systematically checked for data overdispersion and spatial autocorrelation in model residuals. We did not find any significant data overdispersion or spatial structure in model residuals tested with Moranôs correlograms (see Supplementary material). We used R-packages ncf for correlograms, nlme for LMMs and lme4 for GLMMs (Bates et al. 2011; Pinheiro et al. 2012). The function predictSE.mer in AICcmodavg R-package was used to compute intercepts and slopes of GLMMs and their 95% confidence intervals (Mazerolle 2011).

Results

Bird assemblages

We recorded a total number of 500 bird individuals of 22 species of which 10 were native or endemic and 12 were exotic species (10 introduced from Europe and 2 from Australia) (Table 1). The most abundant species were, in decreasing order: bellbird, silvereye, redpoll (*Carduelis flammea*), blackbird (*Turdus merula*), grey warbler (*Gerygone igata*) and fantail. Most native species we encountered have a predominantly insectivorous diet, except New Zealand pigeon (*Hemiphaga novaeseelandiae*). By contrast, introduced species have mostly a mixed granivorous-insectivorous diet except for sulphur-crested cockatoo (*Cacatua galerita*) and Australian magpie (*Gymnorhina tibicen*) (Table 1). The 16 most abundant (8 native and 8 exotic) species were retained for the analysis of bird assemblages by NMDS. The species removed were very rare (Ò3 individuals) or infrequent (Ò2 plots) in the data set and included sulphur-crested cockatoo, dunnock (*Prunella modularis*), house sparrow (*Passer domesticus*), shining cuckoo (*Chrysococcyx lucidus*), sacred kingfisher (*Halcyon sancta*) and rifleman

(*Acanthisitta chloris*) (Table 1). The optimal ordination of species and sites obtained by NMDS (stress = 18.92) is shown in Fig. 2.

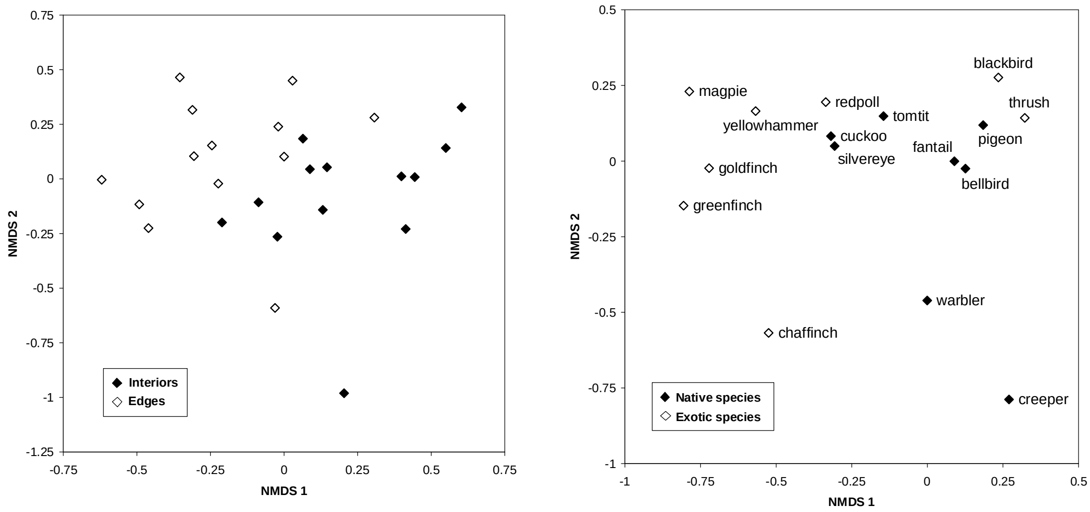


Fig. 2 NMDS ordination biplots of a) edge (white diamonds) and interior (black diamonds) plots (n = 26) and b) native (black diamonds) and exotic (white diamonds) bird species (n = 16; stress = 18.92). The effect of edge vs interior plot location is significant according to a non-parametric MANOVA with 200 random permutations (F = 5.42; P < 0.005).

The effects of edge vs interior location and forest patch area on species ordination were tested by a non-parametric MANOVA using 200 random permutations, with forest patch as a random effect. There was a significant effect of location (edge vs interior) on bird assemblages ($F_{1,22} = 5.42$; $P < 0.005$), as well as a significant area effect ($F_{1,22} = 1.93$; $P < 0.005$), but the interaction term location × area interaction was not significant. The NMDS ordination biplot was clearly separating edges from forest interiors, with the exotic species most associated with open habitats at the upper left corner of the biplot: Australian magpie, goldfinch (*Carduelis carduelis*) and greenfinch (*C. chloris*) (Fig. 2). Most exotic species were associated with edges and most native species primarily associated with interiors, with the noticeable exceptions of the native silvereye associated with edge plots, and introduced blackbird and song thrush (*Turdus philomelos*) to interiors.

Mixed model	Response variable	df	Area	Location	Area×location	Best model	AIC
LMM	Total bird abundance	1, 11	0.1137	0.0357 *	0.2063	Location	177.97
	Total bird richness	1, 11	0.1262	0.0042 **	0.1066	Location	111.65
	Insectivore abundance	1, 11	0.2642	0.4209	0.4821	Area	164.32
	Insectivore richness	1, 11	0.2255	0.1006	0.2838	Location	97.05
	Native bird abundance	1, 11	0.5859	0.5565	0.5597	Location	154.25
	Native bird richness	1, 11	0.4641	0.5500	0.1229	Area	96.18
Poisson GLMM	Exotic bird abundance	1, 11	0.0788	< 0.0001***	0.1913	Area + Location	47.84
	Exotic bird richness	1, 11	0.3283	0.0011 **	0.8585	Location	16.89
	Silvereye *Zosterops lateralis*	1, 11	0.4141	0.0192 *	0.0536	Area × Location	46.99
	Chaffinch *Fringilla coelebs*	1, 11	0.0102 *	0.0004***	0.9940	Area + Location	34.59
	Redpoll *Carduelis flammea*	1, 11	0.7261	0.0003 ***	0.3250	Location	48.98
Binomial GLMM	Total model predation	1, 11	0.0015 **	0.0298 *	0.7824	Area + Location	49.20
	Avian model predation	1, 11	0.0004***	0.0999	0.3642	Area + Location	46.13
	Rodent model predation	1, 11	0.4622	0.2114	0.6071	Location	30.96

Table 2 P-values from linear mixed models (LMM) on total, native and insectivore abundance and richness, generalized linear mixed models (GLMM) on exotic abundance and richness and single species abundances (Poisson GLMM) and larval predation rates (binomial GLMM). Forest patch area, plot location (forest edge vs interior) and interaction area × location are the fixed effects and forest patch is the random effect. Significances of GLMMs were tested by deviance comparisons between models fitted with and without the effects of area × location, area and location, and z-values for each significant effect are indicated in the text. For each response variable, the best model based on AIC values is also indicated.

Bird species richness and abundance

Total bird species richness and abundance were significantly higher at forest edges than in interiors while forest patch area had no significant effect except on exotic bird abundance (Table 2). Native species were markedly dominant at interior plots, while exotic species were slightly dominant at edge plots (Fig. 3). Exotic species richness and abundance were significantly higher at forest edges than interiors (Fig. 3 and Table 2). The positive edge effect (i.e., greater abundance at edges) was therefore largely attributable to the exotic component of the local bird assemblages. Moreover, there was also a trend to have more exotic birds in smaller forest fragments (Table 2). Forest patch area and edge vs interior location had no significant effect on native and insectivore bird richness and abundance (Table 2). A significant individual species response to edges was noticeable for three species, one native, the silvereye, and the two most frequent exotic fringillids, redpoll and chaffinch (*Fringilla coelebs*). The silvereye was significantly less abundant at forest interiors than edges (Poisson GLMM; $z = -2.85$; $P < 0.005$, see Table 2 for model deviance comparisons). Redpoll and chaffinch were also less abundant at forest interiors than edges ($z = -3.34$; $P < 0.001$ and $z = -3.03$; $P < 0.003$ respectively). Overall, there were non-significant trends for positive edge responses in most introduced passerines with a mixed seed-insect or omnivorous diet, including goldfinch, greenfinch, magpie, house sparrow, starling (*Sturnus vulgaris*) and yellowhammer. By contrast, endemic species such as bellbird, brown creeper (*Mohoua novaeseelandiae*), New Zealand pigeon, tomtit (*Petroica macrocephala*) and grey warbler tended to be more abundant at interiors, although not significantly. There was also a trend for insectivorous exotics such as blackbird or song thrush to be more abundant at interior plots where they were virtually the only exotic species that were regularly observed (Fig. 2). Edge effects were thus a predominant driver for bird assemblages, especially for the exotic sub-assemblage. Forest patch area appeared to have no significant separate effects, although exotic species tended to increase with decreasing forest patch area.

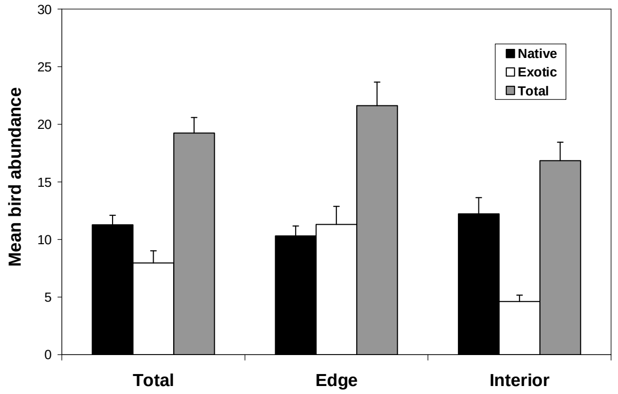


Fig. 3 Mean abundance (± SE) of native birds (black bars), exotic birds (white bars) and all bird species combined (grey bars) for edge, interior and all plots combined. See Table 2 for significant effects.

Foraging birds

Overall, we recorded 86 individual birds in foraging activity at edge and interior plots of the 13 forest fragments (Table 1). Foraging activity was higher for native birds ($n = 68$) than exotics ($n = 18$), and the species most often encountered in foraging activity were bellbird, silvereye, and fantail, three native species (Table 1). A lower foraging activity for exotic birds in native forest fragments is not surprising since most exotics tend to forage outside forest habitats, due to their predominantly granivorous or mixed diets (with the exception of *Turdus* spp.). Total and native foraging bird abundance and richness did not differ between edges and interiors, and fragment area had no significant effect. However, there was a trend for higher foraging activity of native birds at forest interiors than edges ($n = 40$ vs 28), especially for bellbird, fantail and brown creeper. By contrast, all foraging exotic birds were observed at edge plots. The foraging activity of brown creeper significantly increased with decreasing fragment area ($z = -2.09$; $P < 0.05$ and $G^2 = 5.18$; $P < 0.02$ for model deviance comparison), while the foraging activity of silvereye was lower at interiors than edges ($z = -1.90$; $P < 0.05$ and $G^2 = 4.86$; $P < 0.03$ for model deviance comparison).

Model predation rates

Out of a total number of 390 caterpillar models, 61 showed obvious attack markings (15.6%) of which the majority (46) was attributable to predatory birds (11.8%). We observed both bird and mouse attacks on the same model twice, resulting in 17 attack markings caused by predatory mammals (4.4%): 15 attacks by house mouse and 2 attacks by brushtail possum. The effect of supporting shrub species on model predation rates was not significant according to binomial GLMMs with plot location nested within forest patch as random effects ($G^2 = 7.98$; $P = 0.157$; $G^2 = 6.46$; $P = 0.264$; $G^2 = 4.16$; $P = 0.527$ for total, bird, and mouse predation models respectively). Total, bird, and mouse predation rates were on average higher at edge plots than interiors (Fig. 4), but this edge effect was only significant for total predation rate ($z = -2.15$; $P < 0.05$; see Table 2 for deviance comparisons). Forest fragment area had a significant negative effect on total and avian predation rates whereas the area × location interaction was not significant (binomial GLMMs; $z = -2.93$; $P < 0.005$ for total attacks; $z = -2.06$; $P < 0.05$ for bird attacks; see Table 2 and Fig. 5a). Moreover, avian predation rates were positively correlated with insectivorous bird richness ($z = 2.77$; $P < 0.006$) and abundance ($z = 2.93$; $P < 0.003$), as well as foraging bird richness ($z = 3.99$; $P < 0.0006$) and abundance ($z = 4.47$; $P < 0.0001$; Fig. 5b). Significance of all models was tested by deviance comparisons including a complete model with the œdge vs interior locationô factor which was not significant for any models.

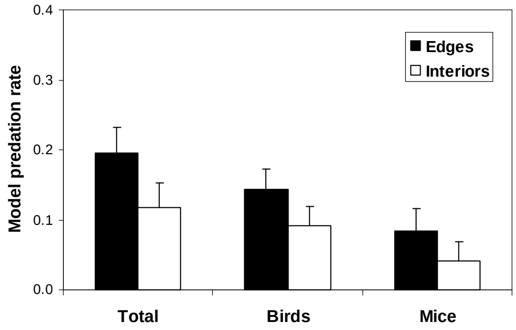


Fig. 4 Mean model predation rates (± SE) attributable to birds, mice and all predators combined at edge (black bars) and interior plots (white bars). See Table 2 for significant effects.

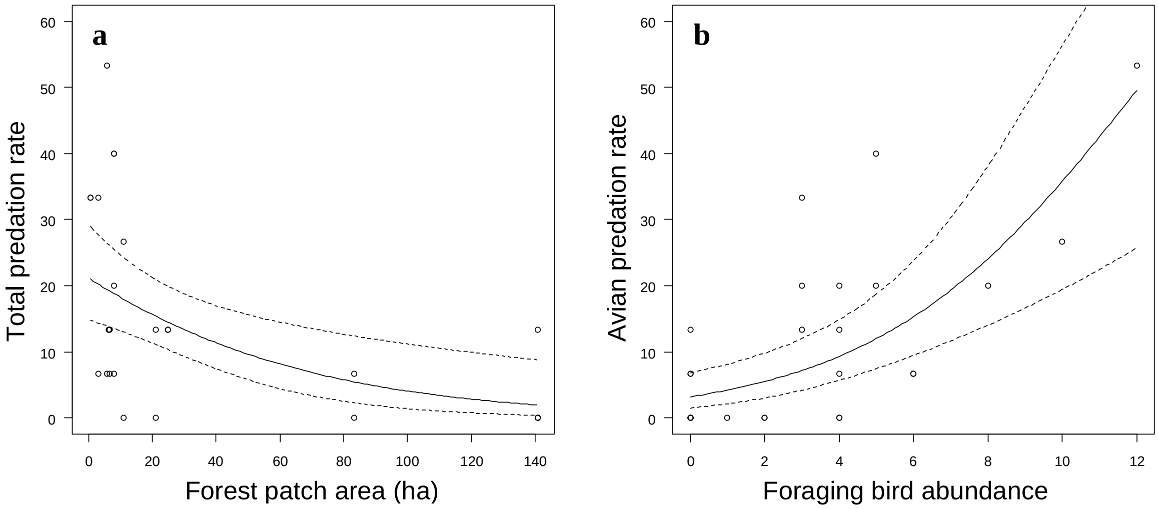


Fig. 5 Binomial generalized linear mixed models relating a) total predation rate and forest fragment area ($z = -2.92$; $P < 0.003$); and b) avian predation rate and foraging bird abundance ($z = 4.47$; $P < 0.0001$). Plain black and dashed lines are the estimates of linear predictors and 95% confidence intervals of GLMMs respectively.

Discussion

Disentangling edge effects from area effects when analysing how fragmentation affects bird communities and their interactions with other components of forest biodiversity is a growing concern in landscape ecology and requires the use of appropriate study designs. In the present work, we found significant effects of forest edge on the composition of bird assemblages and single species abundances recorded by point-counts on the one hand; and of forest patch area on avian insectivory measured by model predation rates on the other hand. These distinct but complementary responses observed for avian assemblages and insectivory produced additive effects of edge and area in a landscape context of heavily fragmented native forests. Edge and area effects may also become synergistic if edge effects increase disproportionately with decreasing size of forest patches (Ewers et al. 2007; Banks-Leite et al. 2010). However, edge effects that are distinct and independent from strict area effects have also been documented (Parker et al. 2005; Fletcher et al. 2007). Here, increased abundance of exotic birds at forest edges, compared to interiors, was associated with increased larval predation at edges, together with a higher silvereye foraging activity. Avian insectivory measured by model predation rates also increased significantly with decreasing patch area, probably due to a high foraging activity of native birds in interiors of small forest patches.

Area effects

Native birds remaining in the currently fragmented New Zealand landscape are expected to be less sensitive to native forest fragmentation than species that are already extinct (Cassey 2001; Deconchat et al. 2009). The landscape matrix surrounding native forest patches is likely to provide complementary or supplementary resources to native birds that can use small dispersed forest patches due to higher mobility compared with other taxa (González-Gómez et al. 2006; Haslem and Bennett 2011; Herrera et al. 2011). On the contrary, exotic birds introduced from Europe and Australia are mainly open-habitat generalists, social foragers and highly productive species (Veltman et al. 1996; Maitner et al. 2012). With the notable exception of the chaffinch and two European turdids, the blackbird and the song thrush, they seldom colonize the interiors of large native forests because of distinct habitat requirements (Deconchat et al. 2009; MacLeod et al. 2009). Both blackbird and song thrush are insectivorous ground probers foraging on the forest ground on leaf-litter and below-ground arthropods (Barbaro and van Halder 2009). It is likely that this foraging niche is now competition-free in present Banks Peninsula forests due to historical extinction of large ground-probing endemics (Holdaway 1989; Wilson 2008). Moreover, native New Zealand forests are not very prone to invasion by exotic invertebrates (Brockerhoff et al. 2010), and most exotic birds do not penetrate far into native forests since they depend on feeding resources provided by adjacent agricultural habitats in winter (MacLeod and Till 2007). Interestingly, we found higher avian predation rates in smaller forest patches independently of strict edge effects. A few previous studies had also demonstrated higher avian insectivory or frugivory measured experimentally in small and isolated native forest patches of temperate ecosystems (González-Gómez et al. 2006; Herrera et al. 2011). Both studies attributed this increase to higher abundance of insectivorous or frugivorous birds in isolated patches, where the negative effects of matrix composition and isolation are reduced by high bird mobility. In tropical ecosystems, bird insectivory measured by model predation rates also increased with the degree of forest disturbance (Posa et al. 2007). However, predatory arthropods and mammals are generally more responsible than birds for the majority of observed predation rates in tropical forest experiments (Loiselle and Farji-Brenner 2002). A mechanism likely to explain increased avian insectivory in smaller fragments is the higher light reflectance in sunnier understorey conditions of fragmented forests vs large forest stands (Mäntylä et al 2008a). This may allow UV-sensitive bird vision to detect prey more easily and consequently contribute to aggregative responses of insectivorous birds in small forest fragments (Mäntylä et al 2008a).

Edge effects

Although edge effects are often counfounded with strict area effects in landscape ecology studies, pure independent effects of edges have also been detected (Parker et al 2005; Ewers and Didham 2006; Fletcher et al. 2007). However, landscape configuration, matrix composition and habitat patch size all interact with edges, having generally synergistic effects by increasing frequency and magnitude of ecological processes in fragmented habitats (Laurance 2002; Ewers and Didham 2006; Fletcher et al. 2007; Banks-Leite et al. 2010). At least in temperate ecosystems, forest edges can harbour richer bird assemblages than forest interiors because of three main mechanisms: (i) dispersing birds tend to concentrate at edges; (ii) food availability is higher and microclimate more favourable at edges; and (iii) birds find complementary resources on each side of the forest edge (Van Wilgenburg et al. 2001; Brotons and Herrando 2003; Ries et al. 2004). The second mechanism may be relevant to explain the higher use of edges by insectivorous birds, especially if the expected higher productivity of plants in sunnier edge conditions causes higher larval abundance on these more productive edge-grown leaves (Barber and Marquis 2011). However, this assumption has not always been demonstrated in the field, since avian insectivory can be higher at edges despite higher herbivory on plants located in forest interiors (Skoczylas et al. 2007). Moreover, the effect of avian predation on herbivore abundance and leaf damage was not significantly different between trees grown in sun and shade conditions (Barber and Marquis 2011). The third mechanism is the most likely responsible for the observed use of native forest edges by exotic birds in the present study, since species such as chaffinch, greenfinch, redpoll, yellowhammer or starling use both forest patches for breeding or roosting and adjacent open habitats for foraging (MacLeod and Till 2007). On the contrary, all native species and introduced turdids, blackbird and song thrush, tend to use forest interiors as much as, or more than edges, probably because leaf-litter arthropods and other key resources are typically forest edge-avoiders (Van Wilgenburg et al. 2001). Also, some species may show a seasonal variation of edge preference or avoidance in interaction with prey accessibility mediated by understory structure (Murphy and Kelly 2003; Whelan and Maina 2005). In the present study, the only native species preferring forest edges is the silvereye, a recent self-colonizer from Australia having larger habitat tolerance than strictly endemic New Zealand birds (Robertson et al. 2007; Deconchat et al. 2009). Silvereyes are known to be very efficient predators of pest Lepidoptera larvae in New Zealand apple orchards (Wearing and McCarthy 1992).

Positive effects of forest edges have been previously demonstrated on two main ecosystem services provided by birds: avian insectivory (Skoczylas et al. 2007), and avian seed dispersal depending on the extent of adjacent native habitats (Zamora et al. 2010). Increased skink predation by birds has also been found at forest edges in Australia (Anderson and Burgin 2008). However, there was no significant edge effect on larval predation rates in neotropical forest fragments (Koh and Menge 2006). In the present work, we suggest that edge-increasing predation patterns were partly masked by the co-occurrence of native and exotic bird sub-assemblages having distinct life-histories, foraging methods and habitat preferences. Habitat filtering may consequently be more important than interspecific competition to explain the present coexistence of native and exotic birds in New Zealand mosaic landscapes (Maitner et al. 2012). Edge preference or avoidance actually depends on bird traits such as biogeographic origin, trophic guild, body size or breeding productivity (Ewers and Didham 2006; Barbaro and van Halder 2009; Vetter et al. 2011). For example, the endemic bellbird is likely to select alternatively forest edges and interiors for foraging, depending on seasonal variation in the availability of the main components of its diet, namely nectar, honeydew, fruits and invertebrates (Murphy and Kelly 2003). This may explain why bellbirds successfully survived native forest fragmentation on Banks Peninsula by exploiting resources found in other elements of the landscape matrix, such as flowers of New Zealand flax (*Phormium* spp) and other nectar-producing plants (Murphy and Kelly 2003; Deconchat et al. 2009). Such a neutral response to fragmentation has also been shown for most neotropical nectarivores (Banks-Leite et al. 2010; Vetter et al. 2011). Other native birds still common on Banks Peninsula may also benefit from such landscape complementation or supplementation of resources; for example New Zealand pigeon, shining cuckoo, sacred kingfisher, brown creeper and grey warbler are all able to use exotic pine plantation forests to some degree (Clout and Gaze 1984; Deconchat et al. 2009).

Conclusions

The present work emphasizes how native birds, exotic birds and avian insectivory measured with plasticine models have distinct and complementary responses to the two main components of native forest fragmentation, i.e., edge and area effects. Our findings suggest that an increased functional diversity of predatory birds through the coexistence of native and exotic insectivores results in enhanced effective insectivory in smaller forest fragments. This pattern is consistent with the fact that functional richness increases avian predation rates through life-trait complementation among predatory birds (Philpott et al. 2009). Such coexistence may also contribute to maintain ecosystem services provided by birds in New Zealand native forests (Clout and Hay 1989; Murphy and Kelly 2003; Wenny et al. 2011), especially in changing mosaic landscapes of native and exotic forests and open habitats (Tscharntke et al. 2007; Zamora et al. 2010; Burns et al. 2011). However, further functional extinction of keystone endemics will strongly affect ecosystem services, as demonstrated by reduced bird pollination of native shrubs in the mainland compared to island sanctuaries (Anderson et al. 2011). Also, the consequence of increased larval predation at edges by both native and exotic birds, together with introduced mice, may have a long-term negative effect for the conservation of declining endemic Lepidoptera (Brockerhoff et al. 2010). Measuring avian predation rates on the long-term by using replicated artificial larvae across habitats may be a relevant and cost-effective way of monitoring the effects of climate and land use changes on a major trophic interaction involving birds and insects at the landscape scale.

References

Anderson L, Burgin S (2008) Patterns of bird predation on reptiles in small woodland remnant edges in peri-urban north-western Sydney, Australia. Landscape Ecol 23:1039ï 1047

Anderson SH, Kelly D, Ladley JJ, Molloy S, Terry J (2011) Cascading effects of bird functional extinction reduce pollination and plant density. Science 331:1068-71

Banks-Leite C, Ewers RM, Metzger JP (2010) Edge effects as the principal cause of area effects on birds in fragmented secondary forest. Oikos 119:918ï 926

Barbaro L, van Halder I (2009) Linking bird, carabid beetle and butterfly life-history traits to habitat fragmentation in mosaic landscapes. Ecography 32:321-333

Barber NA, Marquis RJ (2011) Light environment and the impacts of foliage quality on herbivorous insect attack and bird predation. Oecologia 166:401ï 409

Bates D, Maechler M, Bolker B (2011) lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-39.

Berndt LA, Brockerhoff EG, Jactel H, Weis T, Beaton J (2004) Biology and rearing of Pseudocoremia suavis, an endemic looper (Lepidoptera: Geometridae) with a history of outbreaks on exotic conifers. New Zeal Entomol 27:73-82

Brand LA, George TL (2001) Response of passerine birds to forest edge in coast redwood forest fragments. Auk 118:678-686

Bretagnolle V, Gillis H (2010) Predatorï prey interactions and climate change. In: Moller AP, Fiedler W, Berthold P (eds) Effects of climate change on birds. Oxford Univ Press, New York, pp 227-248

Brockerhoff EG, Barratt BIP, Beggs JR, Fagan LL, Kay MK, Phillips CB, Vink CJ (2010) Impacts of exotic invertebrates on New Zealandôs indigenous species and ecosystems. New Zeal J Ecol 34:158-174

Brotons L, Herrando S (2003) Effect of increased food abundance near forest edges on flocking patterns of Coal Tit Parus ater winter groups in mountain coniferous forests. Bird Study 50:106ï 111

Burns BR, Floyd CG, Smale MC, Arnold GC (2011) Effects of forest fragment management on vegetation condition and maintenance of canopy composition in a New Zealand pastoral landscape. Austral Ecol 36:153ï 166

Cassey P (2001) Determining variation in the success of New Zealand land birds. Global Ecol Biogeogr 10:161ï 172

Clout MN, Gaze PD (1984) Effects of plantation forestry on birds in New Zealand. J Appl Ecol 21:795ï 815

Clout MN, Hay JR (1989) The importance of birds as browsers, pollinators and seed dispersers in New Zealand forests. New Zeal J Ecol 12:27ï 33

Deconchat M, Brockerhoff EG, Barbaro L (2009) Effects of surrounding landscape composition on the conservation value of native and exotic habitats for native forest birds. Forest Ecol Manage 258:S196ï S204

Ewers RM, Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biol Rev 81:117-142

Ewers RM, Thorpe S, Didham RK (2007) Synergistic interactions between edge and area effects in a heavily fragmented landscape. Ecology 88:96ï 106

Fletcher RJ, Ries L, Battin J, Chalfoun AD (2007) The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined? Can J Zool 85:1017-1030

Giffard B, Corcket E, Barbaro L, Jactel H (2012) Bird predation enhances tree seedling resistance to insect herbivores in contrasting forest habitats. Oecologia 168:415ï 424

González-Gómez PL, Estades CF, Simonetti JA (2006) Strengthened insectivory in a temperate fragmented forest. Oecologia 148:137-143

Harper KA, Macdonald SE, Burton PJ, Chen JQ, Brosofske KD., Saunders SC, Euskirchen ES, Roberts D, Jaiteh MS, Esseen PA (2005) Edge influence on forest structure and composition in fragmented landscapes. Conservation Biology 19:768-782

Haslem A, Bennett AF (2011) Countryside vegetation provides supplementary habitat at the landscape scale for woodland birds in farm mosaics. Biodivers Conserv 20:2225ï 2242

Herrera JM, Garcia D, Morales JM (2011) Matrix effects on plant-frugivore and plant-predator interactions in forest fragments. Landscape Ecol 26:125ï 135

Higgins PJ, Peter JM, Cowling SJ (eds) (2006) Handbook of Australian, New Zealand and Antarctic Birds. Volume 7: Boatbill to Starlings. Oxford University Press, Melbourne

Holdaway RN (1989) New Zealandôs pre-human avifauna and its vulnerability. New Zeal J Ecol 12:11-25

Koh LP, Menge DNL (2006) Rapid assessment of Lepidoptera predation rates in neotropical forest fragments. Biotropica 38:132-134

Laurance WF (2002) Hyperdynamism in fragmented habitats. J Veg Sci 13:595ï 602

Loiselle BA, Farji-Brenner A.G. (2002) Whatôs up? An experimental comparison of predation levels between canopy and understory in a tropical wet forest. Biotropica 34:327-330.

MacLeod CJ, Till A (2007) Crop use by introduced bird species in winter in relation to crop structure and seed resources. Bird Study 54:80ï 86

MacLeod CJ, Newson SE, Blackwell G, Duncan RP (2009) Enhanced niche opportunities: can they explain the success of New Zealandôs introduced bird species? Diversity Distrib 15:41ï 49

Maitner BS, Rudgers JA, Dunham AE, Whitney KD (2012) Patterns of bird invasion are consistent with environmental filtering. Ecography 35:614-623

Mäntylä E, Klemola T, Sirkiä P, Laaksonen T (2008a) Low light reflectance may explain the attraction of birds to defoliated trees. Behav Ecol 19:325-330

Mäntylä E, Alessio GA, Blande JD, Heijari J, Holopainen JK, Laaksonen T, Piirtola P, Klemola T (2008b) From plants to birds: higher avian predation rates in trees responding to insect herbivory. PLoS ONE 3:e2832.

Mazerolle MJ (2011) AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 1.15.

Mols CMM, Visser ME (2002) Great tits can reduce caterpillar damage in apple orchards. J Appl Ecol 39:888-899

Murphy DJ, Kelly D (2003) Seasonal variation in the honeydew, invertebrate, fruit and nectar resource for bellbirds in a New Zealand mountain beech forest. New Zeal J Ecol 27:11-23

Oksanen J (2011) Multivariate analysis of ecological communities in R: vegan tutorial. R package version 2.0-1.

Parker TH, Stansberry BM, Becker CD, Gipson PS (2005) Edge and area effects on the occurrence of migrant forest songbirds. Conserv Biol 19:1157-1167

Philpott SM, Soong O, Lowenstein JH, Pulido AL, Lopez DT, Flynn DFB, DeCleck F (2009) Functional richness and ecosystem services: bird predation on arthropods in tropical agroecosystems. Ecol Appl 19:1858ï 1867

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core team (2012) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-103

Posa MRC, Sodhi NS, Koh LP (2007) Predation on artificial nests and caterpillar models across a disturbance gradient in Subic Bay, Philippines. J Trop Ecol 23:27ï 33

Ries L, Fletcher RJ, Battin J, Sisk TD (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. Annu Rev Ecol Evol Syst 35:491-522

Robertson CJR, Hyvonen P, Fraser MJ, Pickard CR (2007) Atlas of bird distribution in New Zealand 1999ï 2004. The Ornithological Society of New Zealand, Wellington

Simonetti JA, Grez AA, Celis-Diez JL, Bustamante RO (2007) Herbivory and seedling performance in a fragmented temperate forest of Chile. Acta Oecol 32:312-318

Skoczylas DR, Mutha NZ, Niesenbaum RA (2007) Contribution of insectivorous avifauna to top down control of Lindera benzoin herbivores at forest edge and interior habitats. Acta Oecol 32:337-342

Tscharntke T, Bommarco R, Clough Y, Crist TO, Kleijn D, Rand TA, Tylianakis JA, van Nouhuys S, Vidal S, (2007) Conservation biological control and enemy diversity on a landscape scale. Biol Control 43:294ï 309

van Heezik Y, Smyth A, Mathieu R (2008) Diversity of native and exotic birds across an urban gradient in a New Zealand city. Landscape Urban Plan 87:223ï 232

Van Wilgenburg SL, Mazerolle DF, Hobson KA (2001) Patterns of arthropod abundance, vegetation and microclimate at boreal forest edge and interior in two landscapes: implications for forest birds. Ecoscience 8:454-461

Veltman CJ, Nee S, Crawley MJ (1996) Correlates of introduction success in exotic New Zealand birds. Am Nat 147:542-557

Vetter D, Hansbauer MM, Végvári Z, Storch I (2011) Predictors of forest fragmentation sensitivity in Neotropical vertebrates: a quantitative review. Ecography 34:1-8

Wearing CH, McCarthy K (1992) Predation of codling moth Cydia pomonella L. by the silvereye Zosterops lateralis (Latham). Biocontrol Sci Techn 2:285-295

Wenny DG, DeVault TL, Johnson MD, Kelly D, Sekercioglu CH, Tomback DF, Whelan CJ (2011) The need to quantify ecosystem services provided by birds. Auk 128:1-14

Wilson HD (2008) Vegetation of Banks Peninsula. In: Winterbourn M, Knox G, Burrows C, Marsden I (eds) The natural history of Canterbury, University of Canterbury Press, Christchurch, pp 251ï 278

Whelan CJ, Maina GG (2005) Effects of season, understorey vegetation density, habitat edge and tree diameter on patch-use by bark-foraging birds. Funct Ecol 19:529ï 536

Zamora R, Hodar JA, Matias L, Mendoza I (2010) Positive adjacency effects mediated by seed disperser birds in pine plantations. Ecol Appl 20:1053-1060

2.4.2. Effet indirect de la prédation par les oiseaux sur la résistance des plantules aux insectes herbivores

Résumé

Lôhypothèse de résistance par association prédit que la végétation environnante influence à la fois les communautés dôinsectes herbivores et leurs ennemis naturels, mais lôeffet des arbres de la canopée sur lôherbivorie des plantules a été jusquôà présent peu étudié. Un des mécanismes possibles de la résistance par association est lôimpact indirect dôennemis naturels comme les oiseaux insectivores sur lôherbivorie des insectes, bien quôil ne soit pas clairement établi dans quelle mesure de telles cascades trophiques sont influencées ou non par la composition végétale. Nous avons comparé lôeffet de lôexclusion expérimentale des oiseaux sur les dégâts foliaires causés par les insectes sur des plantules de trois espèces transplantées dans trois types dôhabitats forestiers. Lôexclusion des oiseaux affecte lôherbivorie des insectes de manière espèce-spécifique : les dégâts foliaires augmentent sur le bouleau *Betula pendula* mais pas sur les chênes *Quercus robur* et *Q. ilex*. Le type dôhabitat forestier influence à la fois lôintensité dôherbivorie et lôeffet de lôexclusion des oiseaux. Les plantules de feuillus présentent moins de dégâts foliaires dans les plantations de pins que dans les boisements feuillus, en accord avec lôhypothèse de concentration de la ressource. En accord avec lôhypothèse des ennemis naturels, lôeffet indirect de lôexclusion des oiseaux sur les dégâts foliaires nôest significatif que dans les plantations de pins, suggérant que les oiseaux insectivores nôont un effet sur lôherbivorie des plantules que sous des arbres non-congénériques. Bien que la richesse et lôabondance des oiseaux soit supérieure dans les boisements feuillus, il semble quôils ne puissent contrôler efficacement les insectes herbivores sur des plantules de la même espèce que les arbres de la canopée.

Abstract

Neighbouring plants are expected to influence both the insect herbivore communities and their natural enemies according to the associational resistance hypothesis. However this has rarely been tested for the effects of canopy trees on herbivory of seedlings. One possible mechanism responsible for associational resistance is the indirect impact of natural enemies on insect herbivory, such as insectivorous birds. But it remains unclear to what extent such trophic cascades are influenced by the composition of plant associations (i.e., identity of óassociatedô plants). Here, we compared the effect of bird exclusion on insect leaf damage for seedlings of three broadleaved tree species in three different forest habitats. Exclusion of insectivorous birds affected insect herbivory in a species-specific manner: leaf damage increased on *Betula pendula* seedlings whereas bird exclusion had no effect for two oaks (*Quercus robur* and *Q. ilex*). Forest habitat influenced both the extent of insect herbivory and the effect of bird exclusion. Broadleaved seedlings had lower overall-leaf damage within pine plantations than within broadleaved stands, consistent with the resource concentration hypothesis. The indirect effect of bird exclusion on leaf damage was only significant in pine plantations, but not in exotic and native broadleaved woodlands. Our results support the enemies hypothesis which predicts that the effects of insectivorous birds on insect herbivory on seedlings are greater beneath non-congeneric canopy trees. Although bird species richness and abundance were greater in broadleaved woodlands, birds were unable to regulate insect herbivory on seedlings in forests of more closely related tree species.

Introduction

The relative importance of different mechanisms regulating patterns of insect herbivory in plant communities is still a matter of debate. In particular, insect herbivory is thought to depend on intrinsic plant resistance traits as a given plant species may experience different rates of herbivory depending on the identity and concentration of neighbouring plants. This is one of the principles of the ñassociational resistanceò theory (Barbosa et al. 2009). Two main hypotheses have been proposed to explain associational resistance: the resource concentration hypothesis and the natural enemies hypothesis (Root 1973; Russell 1989). The resource concentration hypothesis states that the likelihood of a plant being located by herbivores, i.e., its apparency (Karban 2010), is influenced by the relative abundance and the nature of neighbouring plants. In more diverse plant communities, a given host plant is proportionally less frequent and can be hidden by neighbouring non-host plants. The natural enemies hypothesis suggests that richer plant assemblages offer a greater array of complementary food and habitat resources that benefit natural enemies which can, in turn, control herbivores more effectively (Root 1973; Russell 1989). It has been suggested that the resource concentration hypothesis may account for a significant part in the reduction of damage from specialized herbivores within diverse plant communities (Finch and Collier 2000; Björkman et al. 2010). In particular, the association of non-congeneric plant species with contrasting morphological or semiochemical traits can greatly reduce the ability of host-specific herbivores to locate, colonize and exploit their host plants (Jactel and Brockerhoff 2007). However, while some studies observed clearly reduced insect herbivory in more diverse forests (Jactel and Brockerhoff 2007), others found no clear evidence for this (Vehviläinen et al. 2006). Depending on the presence of host tree species in mixed forest, there can even be an opposite effect (Vehviläinen et al. 2007) that may be attributable to associational susceptibility (Barbosa et al. 2009). Most previous studies on this subject focussed on canopy trees but the same issues apply to seedlings and saplings which represent a critical developmental stage for forest regeneration. Interestingly, similarly varying responses of insect herbivory were observed on young trees along tree diversity gradients or underneath other adult tree species, with examples of higher (White and Whitham 2000; Schuldt et al. 2010) or lower damage (Maetô and Fukuyama 1997; Sobek et al. 2009). Tree seedlings can be expected to experience a higher risk of insect herbivore spillover from conspecific canopy trees (Maetô and Fukuyama 1997; Pigot and Leather 2008), according to the Janzen ï Connell hypothesis (Norghauer et al. 2010).

Surprisingly few studies have investigated the role of natural enemies in controlling insect herbivory on tree seedlings along ecological gradients (Riihimäki et al. 2005; Kaitaniemi et al. 2007; Sobek et al. 2009). These provide some support for the occurrence of top-down control of forest insects by natural enemies, which may be tree species-dependent. However, these studies only focused on predatory insects. Vertebrates predators, such as birds (Bock et al. 1992), lizards (Dial and Roughgarden 1995) and bats (Kalka et al. 2008), can significantly reduce populations of herbivorous arthropods and indirectly limit damage and/or promote vegetation growth (Mooney et al. 2010; Mäntylä et al. 2011). However, the indirect effect of predators on plant biomass via a trophic cascade is highly variable due to compensation effects at the herbivore or plant levels (Pace et al. 1999). In temperate forests, insectivorous birds are among the most important predators of herbivorous insects, especially Lepidoptera and Hymenoptera (Holmes et al. 1979; Glen 2004). Several studies have reported an increase of leaf damage when insectivorous birds were experimentally excluded using caged plants (Atlegrim 1989; Marquis and Whelan 1994; Sipura 1999; Mazía et al. 2004; Van Bael et al. 2008), whereas others reported more limited effects (Forkner and Hunter 2000; Low and Connor 2003). Insectivorous birds are considered as an element of indirect plant defences (Price et al. 1980) with many documented top-down effects on insect herbivores (Whelan et al. 2008). The identity of the focal plant species may be important to explain both the influence of natural enemies (Vehviläinen et al. 2008) such as insectivorous birds and the effect of host concentration on insect herbivory. Plants differ in their physical characteristics (e.g., architecture, foliage structure), which provides insectivorous birds with a wide variety of distinct foraging substrates, which, in turn, may influence trophic cascades (Marquis and Whelan 1996; Whelan 2001). Plant species also present different constitutive defences (Sipura 1999) or volatile organic compounds (Mäntylä et al. 2008) that have been demonstrated to affect both insect herbivory and insectivorous bird foraging.

In this study, we investigated the importance of bird predation and host resource concentration as mechanisms affecting insect herbivory. We designed a manipulative experiment in the Landes de Gascogne forest, the largest pine plantation forest in Europe. Previous studies in such forests have shown that deciduous trees at the understorey level or as remnants of natural forests provide key resources or habitat to several insect and bird taxa in this context of conifer plantations (Barbaro et al. 2005; Brockerhoff et al. 2008; van Halder et al. 2008). To improve the management of planted forests for the benefit of biodiversity, it is therefore important to know more about how stand composition may affect the impact of insect damage on these broadleaved species at their most susceptible developmental stages, i.e. seedlings and saplings (Vásquez et al. 2007). We tested the effect of the identity of the plant species by comparing the level of insect herbivory on seedlings of three native broadleaved species: silver birch (*Betula pendula*), pedunculate oak (*Quercus robur*) and holm oak (*Quercus ilex*). We then examined the resource concentration hypothesis, and, more specifically, the importance of taxonomic similarity between seedlings and canopy tree species, by experimentally planting seedlings of these native broadleaved trees within three forest habitats: native broadleaved, exotic broadleaved, and native conifer habitat. We hypothesized that deciduous seedlings planted within stands composed of conspecific deciduous tree species would experience higher leaf damage than when they are planted into conifer stands. To test the enemies hypothesis we estimated the effect of removing bird predation on insect herbivory by planting seedlings within bird exclosure cages. We hypothesized that bird predation would be higher in pine stands where deciduous seedlings represent sources of alternative prey.

Methods

Study site

The study was carried out in the Landes de Gascogne forest, south-western France, a region covered by ca 10 000 km^2 of planted forests of native maritime pine *Pinus pinaster*. The climate is thermo-Atlantic and soils are podzols established on several meters of sandy deposit. The study sites are located ca 40 km south of Bordeaux (44°44ô N, 00°46ô W) near the field research centre of the French National Institute for Agricultural Research (INRA). This area is dominated by a mosaic of maritime pine plantations of different ages with small deciduous forest remnants. These woodlands are dominated by native pedunculate oak *Quercus robur* and silver birch *Betula pendula* with scattered holm oaks *Q. ilex*. A few plantations of exotic oak species (red oak *Q. rubra* and Bartramôs oak *Q. heterophylla*) also occur in the area. The understorey vegetation is relatively species-poor, due to both nutrient-poor acidic soils and intensive stand management. Dominant understorey species are common bracken (*Pteridium aquilinum*), various herbaceous species such as *Molinia cærulea* and *Pseudarrhenaterum longifolium*, dwarf and common gorse (*Ulex minor, U. europaeus*), heather species (*Erica scoparia, E. cinerea, Calluna vulgaris*), glossy buckthorn (*Frangula alnus*) and European honeysuckle (*Lonicera periclymenum*).

Experimental design

To test for an effect of contrasting forest habitats, we selected 20 stands comprising six stands of maritime pine, six stands of exotic oaks (*Q. rubra* or *Q. heterophylla*) and eight native woodlands dominated by *Q. robur* and *B. pendula*. In these 20 stands, we established two experimental units to compare two treatments: control and bird exclusion. Both treatments were located in the same stand but 5-10 m from each other to avoid any potential disturbance by birds foraging in control areas. The bird exclosure was a cage measuring of 100 × 100 × 100 cm fenced off with wire netting (15 × 15 mm mesh). This treatment allowed insects to access seedlings while excluding all insectivorous birds including the smallest species recorded from the experimental plots (wren, *Troglodytes troglodytes*, and firecrest, *Regulus ignicapillus*). In the control treatment, seedlings were left uncaged so that herbivorous insects were left exposed to bird predation. A comparison of the microclimatic conditions between treatments was undertaken at the beginning of the experiment (using Hobo, Onset Computer Corporation, Bourne, USA). This showed that exclusion cages had no significant effect on soil humidity, air temperature and relative humidity (Wilcoxon matched-pairs signed-ranks tests). In March 2007, two seedlings of silver birch *B. pendula*, *Q. robur* and *Q. ilex* were transplanted together as an experimental unit of six seedlings. Seedlings were one year old and had the same south-western France origin. They were planted ca 40cm apart from each other and the position of each species was randomly assigned. Experimental units were protected by an exclusion cage (cage treatment) or left uncaged (control). The same paired design was replicated in the 20 experimental forest stands, for a total of 240 transplanted seedlings (2 seedlings × 3 species × 2 experimental units × 20 stands).

Herbivory measures

Nondestructive assessments of insect herbivory were performed by visual inspection of all leaves on every seedling. Damaged leaf area was estimated using transparent plastic grids of two different mesh sizes (0.25 cm^2 and 1 cm^2). The smaller grid was used on leaves smaller than 6 cm^2 for greater accuracy. A percentage of Leaf Area Removed (LAR) was calculated for each leaf and averaged per seedling. Intact leaves were recorded as 0 % LAR. Within the same unit, the two seedlings of the same species were considered as pseudo-replicates and their herbivory rates were averaged. The response variable was therefore calculated as the percent LAR per species for each experimental unit. Herbivory measures were performed during two growth seasons (2007 and 2008), with assessments in May (early season) and July (mid-season) and a final assessment in September 2008.

Bird censuses

Bird communities were censused in nine of the sampled stands, providing three representative replicates of the three forest habitats. We used the point-count method with two visits during early and late breeding seasons of 2007. We recorded all birds heard and seen during the two 20 minute-visits and used the maximal abundance across the two visits for a given species to obtain species richness and abundance for each stand (see Barbaro et al. 2005). We classified all the species recorded according to their diet and foraging guild (Barbaro and van Halder 2009) and kept for further analyses only the insectivorous species likely to forage on the experimental seedlings.

Statistical analyses

To compare herbivory rates between seedling species and forest habitats, linear mixed-model analyses (Pinheiro and Bates 2004) were performed with the procedure lme (R software) using LAR estimated in the control treatment at each period of assessment as response variables. We used fixed effects for seedling species, forest habitat and their interaction and a random effect for forest stand within forest habitat. To test the effect of bird exclusion on herbivory rates according to forest habitats, we performed a second set of linear mixed-model analyses. We used fixed effects for forest habitat, bird exclusion treatment and their interaction and a random effect for forest stand within forest habitat. Analyses were performed on LAR values for each seedling species and each date of assessment separately. Repeated-measures analysis was not used to avoid confounding within-year and between-year repeated measures. In all linear mixed-models, LAR data were arc-sine transformed to meet the assumptions of normality and homoscedasticity, which were verified by graphical analyses and Shapiro-Wilk tests on model residuals. Multiple comparisons were conducted to test for difference between seedling species or forest habitats using Tukeyôs HSD test.

Insectivorous bird richness and abundance were analysed by Kruskal-Wallis rank sum tests followed by Behrens-Fisher multiple comparisons to test for difference between the three forest habitats. Ultimately, we estimated the magnitude of the effect of bird exclusion on LAR in seedlings throughout the two years of assessments (i.e., the difference in LAR between control and exclusion cage treatments). We tested how this magnitude varied with seedling species and forest habitat (Nagawa and Cuthill 2007) by calculating Hedgeôs effect size (d) for each combination of seedling species × forest habitat, using stands within habitat types as replicates. All censuses were pooled following the method proposed by Borenstein et al. (2009) for repeated measurements within a study. For each combination of seedling species × forest habitat, mean LAR values were averaged across the five censuses dates. The averaged standard deviation was calculated as the mean standard deviations in each date weighted by the correlation coefficients between dates. The effect size was calculated as

$$d = J\left[\left(\mathrm{X}_{BE} - \mathrm{X}_{CTL}\right)/S\right]$$

with XBE representing the mean LAR per species and forest habitat in the bird exclusion treatment, XCTL the mean LAR for the control treatment, S the pooled standard deviation and J a factor that corrects for potential bias due to small sample sizes (Hedges and Olkin 1985).

An effect size was considered as significantly different from zero if its bias-corrected bootstrap confidence interval did not bracket the null value (based on 9999 iterations). Meta-analyses were carried out using METAWIN 2.0 software (Rosenberg et al. 2000).

Results

Seedling species response to insect herbivory

The three seedling species exhibited significantly different defoliation levels (LAR) in the control treatment for all the five assessment periods over the two study years (F = 18.64, 45.74, 16.82, 10.26 and 21.34 respectively, P < 0.01). Quercus ilex seedlings were less damaged (7.5 ± 0.6 % mean LAR ± SE) than the deciduous species, Q. robur (17.8 ± 1.1 %) and B. pendula (20.2 ± 1.7 %). The two deciduous species did not show any significant difference in LAR, except in July 2007 when B. pendula seedlings were more damaged than Q. robur seedlings (|z| = 3.17, P = 0.005) and in May 2008 when Q. robur seedlings were more damaged than B. pendula (|z| = 3.78, P = 0.001). Due to the strong seedling species effect on insect herbivory, further analyses on the effects of forest habitat and bird exclusion were therefore conducted for each species separately.

Effect of forest habitat on insect herbivory

Forest habitat had a significant effect on insect herbivory in the control treatment where birds were not excluded but this effect differed between the three seedling species and the five periods of assessment. LAR in *B. pendula* seedlings was significantly lower in pine plantations than in exotic and native oak and birch woodlands only in May 2007 (Table 1 and Fig. 1). For *Q. ilex* seedlings, no effect of forest habitat on herbivory was detected in 2007 but in May and September 2008, insect herbivory was significantly lower within pine plantations than within native oak and birch woodlands (Fig. 1 and Table 1). Herbivory was intermediate within exotic oak woodlands. Forest habitat had a strong effect on herbivory for *Q. robur* seedlings in 2007, LAR being consistently lower within pine plantations than within native oak woodlands (Fig. 1 and Table 1). Again herbivory rates were intermediate within exotic oak woodlands. These trends persisted in May and July 2008 but differences were not significant because of large between-stand variations.

Date	Forest Habitat	*Betula pendula*	*Quercus robur*	*Quercus ilex*
May 2007	Pine vs Native	0.55	2.54 *	0.15
	Pine vs Exotic	1.49	1.80	1.26
	Exotic vs Native	1.05	0.62	1.50
July 2007	Pine vs Native	0.80	2.54 *	1.86
	Pine vs Exotic	0.43	2.09	1.68
	Exotic vs Native	1.26	0.30	0.06
May 2008	Pine vs Native	2.59 **	2.11	2.44 *
	Pine vs Exotic	3.96 ***	1.92	0.41
	Exotic vs Native	1.64	0.07	2.00
July 2008	Pine vs Native	1.38	2.00	2.29
	Pine vs Exotic	0.46	1.70	1.48
	Exotic vs Native	0.82	0.17	0.71
September 2008	Pine vs Native	1.65	0.34	3.23 **
	Pine vs Exotic	0.72	0.11	1.28
	Exotic vs Native	0.83	0.22	1.87

Table 1 Results of Tukeyôs HSD tests of the effects of forest habitat on Leaf Area Removed (LAR %) by herbivorous insects for three seedling species. Values show |z|-statistics for each comparison and significant effects are shown in bold: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$. (Pine = pine plantations; Native = native deciduous woodlands and Exotic = exotic deciduous woodlands)

Effect of forest habitat on insectivorous bird communities

Forest habitat had a significant effect on insectivorous bird richness and abundance (Kruskal-Wallis $H = 6.83$, $P = 0.033$ and $H = 6.54$, $P = 0.038$, respectively). More bird species and individuals occurred in exotic and native deciduous woodlands than in pine plantations (multiple comparisons all significant $P < 0.001$). Native deciduous woodlands had the highest mean richness (R ± SE) and abundance (A ± SE) of insectivorous birds ($R = 14.7 \pm 0.7$ and $A = 29.0 \pm 2.0$), exotic deciduous woodlands were intermediate ($R = 13.3 \pm 0.3$ and $A = 23.3 \pm 1.3$) whereas pine plantations had the lowest richness and abundance ($R = 9.7 \pm 0.3$ and $A = 19.5 \pm 0.6$).

Effect of bird exclusion on insect herbivory

For *B. pendula* seedlings, mixed-models analyses showed that herbivory rates in the bird exclusion treatment were significantly higher than in the control treatment in July 2007 and May 2008 (Table 2). Values of LAR were about 50% higher in July 2007 and twice as high in May 2008, and, although non-significantly, apparently higher in the bird exclusion treatment at the other assessment periods (Fig. 2). For none of the five periods of herbivory measure, the bird exclosure × forest habitat interaction term was not significant, indicating that these two effects operate independently of each other. Bird predation therefore contributed to reduced insect herbivory in birch seedlings. In contrast, we never observed any significant effect of bird exclusion on insect herbivory in *Q. robur* and *Q. ilex* seedlings (Table 2), except in May 2007 on *Q. robur* seedlings. The bird exclosure × forest habitat interaction term was significant due to a significant effect of forest habitat on herbivory in the control treatment (see Table 1) with no significant effect of bird exclosure.

Date	Treatment	*Betula pendula*	*Quercus robur*	*Quercus ilex*
May 2007	FH	1.25	2.83	1.04
	BE	0.45	0.23	2.80
	FH × BE	0.02	3.67 *	0.99
July 2007	FH	2.43	2.06	4.11 *
	BE	6.32 *	2.24	0.04
	FH × BE	1.20	0.44	1.24
May 2008	FH	2.97	3.47	7.11 **
	BE	8.65 **	0.01	0.83
	FH × BE	0.56	0.16	0.05
July 2008	FH	1.59	1.61	5.10 *
	BE	0.03	1.79	0.49
	FH × BE	0.75	0.75	0.13
September 2008	FH	8.10 **	0.05	5.14 *
	BE	0.02	0.04	0.79
	FH × BE	2.42	0.31	0.30

Table 2 Mixed-model analyses for the effect of bird exclusion (BE) and forest habitat (FH) on Leaf Area Removed (LAR %) by herbivorous insects on three seedling species (*B. pendula, Q. robur* and *Q. ilex*). Values show F-statistics for each model and significant effects are shown in bold: ** P < 0.01, * P < 0.05

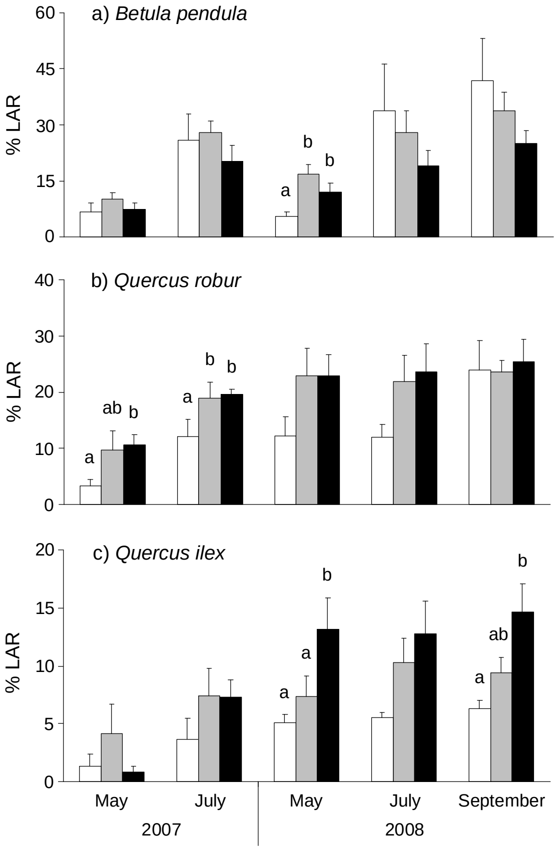


Fig. 1 Mean (+ SE) percent Leaf Area Removed (% LAR) by insects in control treatment on a) *Betula pendula,* b) *Quercus robur* and c) *Quercus ilex* seedlings planted in pine plantations (white bars), exotic woodlands (grey bars) and native woodlands (black bars), at the five assessment dates. Analyses were performed separately for each seedling species and each assessment date and different letters above bars indicate significant differences between forest habitats (at P < 0.05).

Overall effect of forest habitat on bird insectivory

Insect herbivory on the three seedling species showed different responses to bird exclusion when data for all assessment periods were pooled (Fig. 3a). In *B. pendula* seedlings, LAR was significantly higher in bird exclusion cages than in control treatment (d+ = 0.55 with Bias CI = 0.34 to 0.69) indicating that bird predation reduced insect herbivory throughout the two years of measures. For the two oak species, there was no significant effect of bird exclusion on LAR (d+ = -0.02 with Bias CI = -0.31 to 0.51 for *Q. robur* and d+ = 0.16 with Bias CI = -0.24 to 0.35 for *Q. ilex*). Forest habitat also influenced the effect of bird exclusion on insect herbivory in a similar way for the three seedling species as they shared the same gradient of response with higher bird insectivory within pine plantations than within native and exotic deciduous stands (Fig. 3b). Within pine plantations, bird exclusion had a significant effect on insect herbivory with higher damage in bird exclusion cages irrespective of the seedling species (d+ = 0.56 with Bias CI = 0.40 to 0.77). Conversely, there was no significant effect of bird exclusion in native (d+ = 0.24 with Bias CI = -0.05 to 0.55) or exotic deciduous woodlands (d+ = 0.14 with Bias CI = -0.49 to 0.33), irrespective of the seedling species (Fig. 3b).

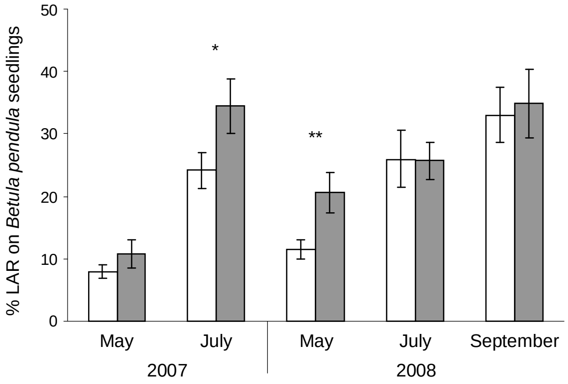


Fig. 2 Mean (± SE) percent Leaf Area Removed (% LAR) by insects in control (white bars) and bird exclusion (grey bars) treatments on *Betula pendula* seedlings, irrespective of the forest habitat. Stars above bars indicate significant differences between treatments (** $P < 0.01$, * $P < 0.05$).

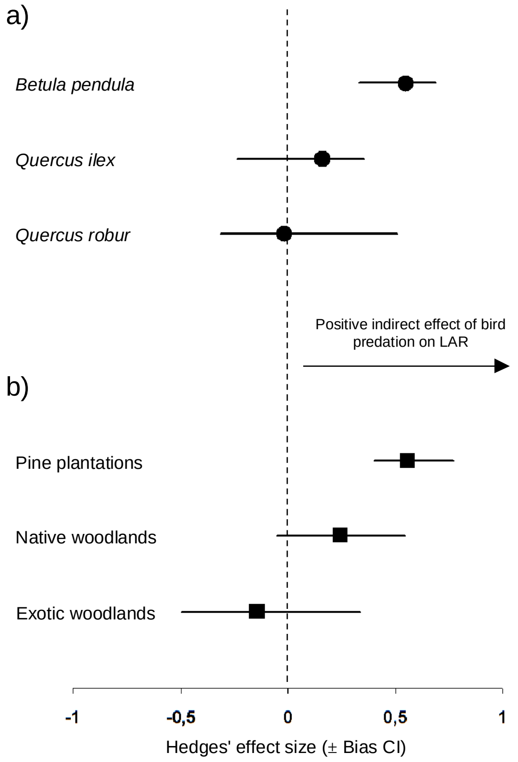


Fig. 3 Mean (± bias-corrected bootstrap Confidence Interval) effect size of bird exclusion on Leaf Area Removed (LAR) a) by seedling species irrespective of the forest habitat and b) by forest habitat irrespective of the seedling species. A positive effect size indicates higher LAR in the bird exclusion treatment than in control (i.e. true bird predation effect) and was considered significant if the confidence interval did not bracket zero.

Discussion

The resource concentration hypothesis

Our results provide new experimental evidence for the importance of resource concentration in the regulation of insect herbivory, a mechanism of associational resistance (Root 1967). For the three broadleaved species tested, seedlings under non-broadleaved canopy trees (maritime pines) were less damaged than those planted within stands of broadleaved tree species. These results are consistent with previous observations of lower insect damage on seedlings or saplings grown in mixed stands than in pure stands of the same canopy species (Batzer et al. 1987; Keenan et al. 1995), and with decreased insect damage on beech and *Acer* saplings with higher abundance of conspecific adult trees (Maetô and Fukuyama 1997; Pigot and Leather 2008; Sobek et al. 2009). The Janzen-Connell hypothesis predicts that seedlings growing close to mother trees suffer from more damage or higher mortality than seedlings growing farther away (Lemen 1981; Norghauer et al. 2010). The resource concentration hypothesis also predicts that specialized herbivores are more likely to find a host plant in stands where this particular species is more abundant (Root 1973). Our results are consistent with both hypotheses: insect herbivory on seedlings was higher beneath a canopy of congeneric trees (i.e., on oak seedlings within native deciduous woodlands dominated by oaks) and lower when the host plant abundance decreased (i.e., on oak seedlings within pine plantations). It is noteworthy that we observed the most significant associational resistance in *Quercus* seedlings which is a genus abundant in the canopy of deciduous woodlands. By contrast, associational susceptibility was the least in *B. pendula*, a species much less frequent in the study area. Seedlings of this rare species probably recruited mainly generalist herbivores, which could increase the risk of associational susceptibility (White and Whitham 2000). Associational susceptibility seems to be most prevalent when the herbivore species is highly polyphagous because generalist herbivores may benefit from mixed forests with multiple host tree species, whereas specialist herbivores are limited by the amount of suitable host trees (Jactel and Brockerhoff 2007). Oak seedlings were more likely to be colonized by specialized oak feeders, which could have led to increased associational resistance.

The natural enemies hypothesis

Associational resistance may also be provided by natural enemy populations which benefit from greater resources provided by plant associations and can therefore provide control of herbivores more effectively (Russell 1989; Barbosa et al. 2009). Changes in the composition of dominant canopy species assemblages or along tree diversity gradients have been shown to increase species richness and abundance of natural enemies such as predatory ants (Riihimäki et al. 2005), staphylinids (Vehviläinen et al. 2008) or birds (Greenberg et al. 1997). In tropical agroecosystems, arthropod abundance decreased when bird species richness increased (Philpott et al. 2009) and bird predation is enhanced by higher floristic diversity (Perfecto et al. 2004). Our study also provides experimental evidence of the natural enemies hypothesis since the more diversified association between seedlings and canopy species (broadleaved tree seedlings within pine stands) resulted in more intense bird predation. Surprisingly, in our experiment, pine plantations had lower insectivorous bird richness and abundance compared to deciduous woodlands, although we found a higher effect of bird predation in pine plantations than in deciduous woodlands. Some authors found no difference in indirect effect of insectivorous birds on plant damage within different forest stand types while bird abundance varied significantly between stands (Greenberg et al. 2000; Barber and Marquis 2009). Conversely, González-Gómez et al. (2006) found that bird insectivory on seedlings, as measured by larval predation, was similar in exotic pine plantations and native forest fragments although bird abundance was lower in plantations. We hypothesized that broadleaved tree seedlings may have provided new feeding resources for insectivorous birds in the pine stands. Conversely, in deciduous woodlands where insect herbivores are likely to be more abundant, the effect of bird predation may have been weakened by a dilution process.

Effect of seedling identity on trophic cascades

In our study, the effects of insectivorous birds affected insect herbivory in the three seedling species differently, and irrespective of the observed effect of contrasting forest habitat. Bird exclusion led to a significant increase of insect herbivory on B. pendula seedlings whereas no effect was detected for the two oak species, Q. robur and Q. ilex. The identity of the plant species is therefore important as it influences the indirect effect of bird predation. Bird predation decreased insect leaf damage on many woody species such as *Vaccinium myrtillus* (Atlegrim 1989), *Quercus alba* (Marquis and Whelan 1994) or *Nothofagus pumilio* (Mazía et al. 2004). Conversely, no effect of bird predation on insect herbivory was detected on *Quercus prinus* and *Q. rubra* (Forkner and Hunter 2000) or *Salix lemonii* (Low and Connor 2003). To explain these differences it has been proposed that bird predation effects would be negligible for plant species that show low average herbivore load. Insectivorous birds seem to prefer foraging on trees where arthropods are more abundant (Bridgeland et al. 2010) and then respond in a density-dependent way to herbivore population dynamics (Sipura 1999). Our results are consistent with this hypothesis: bird predation effect is stronger on *B. pendula* seedlings which were on average more damaged than the oak species. Antiherbivore defences may also dampen the indirect effect of predators: the effect of bird insectivory was stronger on *Salix phylicifolia* than on *Salix myrsinifolia*, a willow species with higher concentrations of phenolic glycosides and hence lower insect abundance (Sipura 1999). In our study, the evergreen species *Q. ilex* was less damaged than the deciduous species. Species with long lifespan leaves are less palatable because of important allocation to antiherbivore defences (Crawley 1989). On the contrary, pioneer species such as *B. pendula* are characterized by low investment in constitutive plant defences (Coley et al. 1985). Mäntylä et al. (2008) also showed that leaves of *Betula pubescens* can release volatile organic compounds and have lower light reflectance as result of insect damage. These olfactory and visual cues are used by insectivorous birds and may explain why they prefer foraging on highly damaged plants. Last, birch seedlings are taller than the two oak species, with longer and less dense branches. This crown architecture may have provided insectivorous birds with easier access to insect prey since avian foraging intensity is highly dependent on foliage structure (Robinson and Holmes 1984; Marquis and Whelan 1996; Whelan 2001).

Bird exclusion clearly increased defoliation on *B. pendula* seedlings when all the herbivory assessments were pooled. However, when the five assessments were analyzed separately, it appeared that bird exclusion effect showed an important temporal variation. For both years, significant bird exclusion effect was mainly observed during early- and mid-season of vegetation (July 2007 and May 2008). Again this might be a density-dependent response since during this period, the abundance peak of insect larvae matched with bird breeding season when food demand for fledglings is the highest (Holmes 1990). On the other hand, *Betula pendula* leaves are known to be subjected to early leaf abscission when severely damaged (Giertych et al. 2006) which suggests a lack of accuracy in damage assessment in autumn. Our study is one of the first providing experimental evidence of associational resistance to insect herbivory in tree seedlings. It gives support to both the natural enemies hypothesis, since bird predation was more effective in the more diverse association of seedling and canopy species (broadleaved seedlings under conifers), and the resource concentration hypothesis, since the lowest insect herbivory level was observed in seedling species planted under non-congeneric canopy species. Furthermore, our results underline the importance of considering both the identity of focal plant species and the composition of habitats as determinants of the occurrence of trophic cascades.

References

Atlegrim O (1989) Exclusion of birds from bilberry stands - impact on insect larval density and damage to the bilberry. Oecologia 79:136-139

Barbaro L, Pontcharraud L, Vetillard F, Guyon D, Jactel H (2005) Comparative responses of bird, carabid, and spider assemblages to stand and landscape diversity in maritime pine plantation forests. Ecoscience 12:110-121

Barbaro L, van Halder I (2009) Linking bird, carabid beetle and butterfly life-history traits to habitat fragmentation in mosaic landscapes. Ecography 32:321-333

Barber NA, Marquis RJ (2009) Spatial variation in top-down direct and indirect effects on white oak (Quercus alba L.). Am Midl Nat 162:169-179

Barbosa P, Hines J, Kaplan I, Martinson H, Szczepaniec A, Szendrei Z (2009) Associational resistance and associational susceptibility: having right or wrong neighbors. Annu Rev Ecol Evol Syst 40:1-20

Batzer HO, Benzie JW, Popp MP (1987) Spruce budworm damage in aspen/balsam fir stands affected by cutting methods. North J Appl For 4:73-75

Björkman M, Hambäck PA, Hopkins RJ, Rämert B (2010) Evaluating the enemies hypothesis in a clover-cabbage intercrop: effects of generalist and specialist natural enemies on the turnip root fly (Delia floralis). Agric For Entomol 12:123-132

Bock CE, Bock JH, Grant MC (1992) Effects of bird predation on grasshopper densities in an Arizona grassland. Ecology 73:1706-1717

Borenstein M, Hedges LV, Higgins JPT, Rothstein HR (2009) Introduction to meta-analysis, 1st edn, John Wiley & Sons Ltd, Chichester, UK

Bridgeland WT, Beier P, Kolb T, Whitham TG (2010) A conditional trophic cascade: birds benefit faster growing trees with strong links between predators and plants. Ecology 91:73-84

Brockerhoff EG, Jactel H, Parrota JA, Quine CP, Sayer J (2008) Plantation forests and biodiversity: oxymoron or opportunity? Biodivers Conserv 17:925-951

Coley PD, Bryant JP, Chapin FS III (1985) Resource availability and plant antiherbivore defense. Science 230:895-899

Crawley MJ (1989) Insect herbivores and plant-population dynamics. Ann Rev Entomol 34:531-564

Dial R, Roughgarden J (1995) Experimental removal of insectivores from rain forest canopy: direct and indirect effects. Ecology 76:1821-1834

Finch S, Collier RH (2000) Host-plant selection by insects - a theory based on 'appropriate/inappropriate landings' by pest insects of cruciferous plants. Entomol Exp Appl 96:91-102

Forkner RE, Hunter MD (2000) What goes up must come down? Nutrient addition and predation pressure on oak herbivores. Ecology 81:1588-1600

Giertych MJ, Karolewski P, Zytkowiak R, Oleksyn J (2006) Differences in defence strategies against herbivores between two pioneer tree species: Alnus glutinosa (L.) Gaertn. and Betula pendula Roth. Pol J Ecol 54:181-187

Glen DM (2004) Birds as predators of lepidopterous larvae. In: Van Emden HF, Rothschild M (eds) Insect and Bird Interactions. Intercept, Andover (UK), pp 89ï 108

González-Gómez P, Estades CF, Simonetti JA (2006) Strengthened insectivory in a temperate fragmented forest. Oecologia 148:137-143

Greenberg R, Bichier P, Angon AC, MacVean C, Perez R, Cano E (2000) The impact of avian insectivory on arthropods and leaf damage in some Guatemalan coffee plantations. Ecology 81:1750-1755

Greenberg R, Bichier P, Angon AC, Reitsma R (1997) Bird populations in shade and sun coffee plantations in Central Guatemala. Conserv Biol 11:448-459

Hedges LV, Olkin I (1985) Statistical methods for meta-analysis, Academic Press, New York

Holmes RT (1990) Ecological and evolutionary impacts of bird predation on forest insects: an overview. Stud Avian Biol 13:6-13

Holmes RT, Schultz JC, Nothnagle P (1979) Bird predation on forest insects: an exclosure experiment. Science 206:462-463

Jactel H, Brockerhoff EG (2007) Tree diversity reduces herbivory by forest insects. Ecol Lett 10:835-848

Kaitaniemi P, Riihimaki J, Koricheva J, Vehvilainen H (2007) Experimental evidence for associational resistance against the European pine sawfly in mixed tree stands. Silva Fenn 41:259-268

Kalka MB, Smith AR, Kalko EKV (2008) Bats limit arthropods and herbivory in a tropical forest. Science 320:71-71

Karban R (2010) Neighbors affect resistance to herbivory ï a new mechanism. New Phytol 186:564-566

Keenan R, Lamb D, Sexton G (1995) Experience with mixed species rainforest plantations in North Queensland. Commonwealth For Rev 74:315-321

Lemen C (1981) Elm trees and elm leaf beetles - Patterns of herbivory. Oikos 36:65-67

Low C, Connor EF (2003) Birds have no impact on folivorous insect guilds on a montane willow. Oikos 103:579-589

Maetô K, Fukuyama K (1997) Mature tree effect of Acer mono on seedling mortality due to insect herbivory. Ecol Res 12:337-343

Mäntylä E, Alessio GA, Blande JD, Heijari J, Holopainen JK, Laaksonen T, Piirtola P, Klemola T (2008) From plants to birds: higher avian predation rates in trees responding to insect herbivory. Plos ONE 3:e2832

Mäntylä E, Klemola T, Laaksonen T (2011) Birds help plants: a meta-analysis of top-down trophic cascades caused by avian predators. Oecologia 165:143-151

Marquis RJ, Whelan CJ (1994) Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. Ecology 75:2007-2014

Marquis RJ, Whelan CJ (1996) Plant morphology and recruitment of the third trophic level: subtle and little-recognized defenses? Oikos 75: 330-334

Mazía CN, Thomas K, Enrique JC (2004) Interannual changes in folivory and bird insectivory along a natural productivity gradient in northern Patagonian forests. Ecography 27:29-40

Mooney KA, Gruner DS, Barber NA, Van Bael SA, Philpott SM, Greenberg R (2010) Interactions among predators and the cascading effects of vertebrate insectivores on arthropod communities and plants. Proc Natl Acad Sci USA 107:7335-7340

Nakagawa S, Cuthill IC (2007) Effect size, confidence interval and statistical significance: a practical guide for biologists. Biol Rev 82:591-605

Norghauer JM, Grogan J, Malcolm JR, Felfili JM (2010) Long-distance dispersal helps germinating mahogany seedlings escape defoliation by a specialist caterpillar. Oecologia 162:405-412

Pace ML, Cole JJ, Carpenter SR, Kitchell JF (1999) Trophic cascades revealed in diverse ecosystems. Trends Ecol Evol 14:483-488

Perfecto I, Vandermeer JH, Bautista GL, Nuñez GI, Greenberg R, Bichier P, Langridge S (2004) Greater predation in shaded coffee farms: the role of resident neotropical birds. Ecology 85:2677-2681

Philpott SM, Soong O, Lowenstein JH, Pulido AL, Lopez DT, Flynn DFB, DeClerck F (2009) Functional richness and ecosystem services: bird predation on arthropods in tropical agroecosystems. Ecol Appl 19:1858-1867

Pigot AL, Leather SR (2008) Invertebrate predators drive distance-dependent patterns of seedling mortality in a temperate tree Acer pseudoplatanus. Oikos 117:521-530

Pinheiro J, Bates D (2004) Mixed-effects models in S and S-PLUS. Springer, New York

Price PW, Bouton CE, Gross P, McPheron BA, Thompson JN, Weis AE (1980) Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. Ann Rev Ecol Syst 11:41-65

R Development Core Team (2008). R: A language and environment for statistical computing. R Foundation for Statistical Computing V, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Riihimäki J, Kaitaniemi P, Koricheva J, Vehviläinen H (2005) Testing the enemies hypothesis in forest stands: the important role of tree species composition. Oecologia 142:90-97

Robinson SK, Holmes RT (1984) Effects of plant-species and foliage structure on the foraging behavior of forest birds. Auk 101:672-684

Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (Brassica oleracea). Ecol Monogr 43:95-124

Rosenberg MS AD, Gurevitch J. 2000. Metawin: statistical software for meta-analysis, version 2.0. Sunderland, MA, USA: Sinauer Associates.

Russell EP (1989) Enemies hypothesis: a review of the effect of vegetational diversity on predatory insects and parasitoids. Environ Entomol 18:590ï 599

Schuldt A, Baruffol M, Böhnke M, Bruelheide H, Härdtle W, Lang AC, Nadrowski K, Von Oheimb G, Voigt W, Zhou H, Assmann T (2010) Tree diversity promotes insect herbivory in subtropical forests of south-east China. J Ecol 98:917-926

Sipura M (1999) Tritrophic interactions: willows, herbivorous insects and insectivorous birds. Oecologia 121:537-545

Sobek S, Scherber C, Steffan-Dewenter I, Tscharntke T (2009) Sapling herbivory, invertebrate herbivores and predators across a natural tree diversity gradient in Germanyôs largest connected deciduous forest. Oecologia 160:279-288

Van Bael SA, Philpott SM, Greenberg R, Bichier P, Barber NA, Mooney KA, Gruner DS (2008) Birds as predators in tropical agroforestery systems. Ecology 89:928-934

van Halder I, Barbaro L, Corcket E, Jactel H (2008) Importance of semi-natural habitats for the conservation of butterfly communities in landscapes dominated by pine plantations. Biodivers Conserv 17:1149-1169

Vásquez PA, Grez AA, Bustamante RO, Simonetti JA (2007) Herbivory, foliar survival and shoot growth in fragmented populations of Aristotelia chilensis. Acta Oecol 31:48-53

Vehviläinen H, Koricheva J, Ruohomäki K (2007) Tree species diversity influences herbivore abundance and damage: meta-analysis of long-term forest experiments. Oecologia 152:287-298

Vehviläinen H, Koricheva J, Ruohomäki K (2008) Effects of stand tree species composition and diversity on abundance of predatory arthropods. Oikos 117:935-943

Vehviläinen H, Koricheva J, Ruohomäki K, Johansson T, Valkonen S (2006) Effects of tree stand species composition on insect herbivory of silver birch in boreal forests. Basic Appl Ecol 7:1-11

Whelan CJ (2001) Foliage structure influences foraging of insectivorous forest birds: an experimental study. Ecology 82:219-231

Whelan CJ, Wenny DG, Marquis RJ (2008) Ecosystem services provided by birds. Ann NY Acad Sci 1134:25-60

White JA, Whitham TG (2000) Associational susceptibility of cottonwood to a box elder herbivore. Ecology 81:1795-1803

3ème partie :

Discussion générale et perspectives

Contentons-nous de lôhypothèse selon laquelle tous les détails importent en définitive,
dôune manière aussi vitale quôinconnue.

Edward O. Wilson. - Biophilie

La discussion générale sôorganise selon trois parties correspondant aux trois principaux axes de mes perspectives de recherche. Dôabord, les **réponses multi-échelles des communautés dôoiseaux et de lépidoptères dans les paysages hétérogènes et fragmentés** sont replacées dans un contexte finalisé, celui du rôle de la sylviculture pour la gestion conservatoire de ces communautés dans les forêts de plantation. Pour aller plus loin dans lôanalyse macro-écologique des communautés dôoiseaux forestiers, nous proposons comme première perspective de recherche dôétudier les préférences climatiques des communautés et les patrons de coexistence dôoiseaux natifs et exotiques sur des gradients de structure et de composition forestière en France et en Nouvelle Zélande, en collaboration avec un groupe de chercheurs sôintéressant à ces questions.

Ensuite, nous revenons sur la relation existant entre **diversité fonctionnelle des communautés et magnitude des interactions trophiques** oiseaux-lépidoptères en forêt. Nous proposons des expérimentations complémentaires, notamment pour explorer le lien entre métriques de diversité fonctionnelle et intensité dôinsectivorie dans les paysages forestiers fragmentés en France et en Nouvelle-Zélande, afin de tester la généralité des résultats obtenus précédemment. Nous insistons également sur lôimportance des mécanismes régissant lôaccessibilité et de la détectabilité des insectes-proies pour les oiseaux insectivores et ses conséquences en terme de réponses numériques et fonctionnelles à la densité des proies.

Enfin, dans une troisième partie nous développons lôaspect finalisé de ces recherches en explicitant le rôle de la **complémentarité fonctionnelle des traits de vie des vertébrés prédateurs dans le contrôle biologique** des insectes ravageurs forestiers. En prenant lôexemple dôun défoliateur majeur des pinèdes, la processionnaire du pin, nous montrons lôintérêt de conserver la guilde complète de ces prédateurs vertébrés comme une óassurance biotiqueô dans la régulation dôun lépidoptère défoliateur en pleine expansion géographique sous lôeffet des changements globaux. Les perspectives de recherche dans ce domaine concernent en particulier lôanalyse des réponses numériques et fonctionnelles des chauves-souris généralistes et spécialistes à la densité de ce lépidoptère défoliateur. Nous proposons également une future extension de ces travaux à des paysages mixtes viticoles et forestiers, en collaboration avec des chercheurs travaillant sur ces agro-systèmes.

3.1. Réponses multi-échelles des communautés dans les paysages hétérogènes

3.1.1. Les communautés dôoiseaux et de lépidoptères en forêt de plantation

Les travaux menés sur les communautés dôoiseaux et de papillons dans des paysages forestiers hétérogènes dominés par les plantations de conifères à croissance rapide soulignent lôinfluence multi-échelles de la composition et de la fragmentation des habitats (**chapitre 2.1**, voir aussi Barbaro et al. 2005, van Halder et al. 2008, Deconchat et al. 2009). Les communautés dôoiseaux et de lépidoptères forestiers répondent à une série de filtres environnementaux constitués par ces facteurs spatialement hiérarchisés en fonction de leurs traits de vie ou leur appartenance à certaines guildes trophiques (**chapitre 2.2**). Cette intercorrélation entre prédicteurs multi-échelles est certainement une des difficultés majeures de lôanalyse des données en écologie du paysage (Burel & Baudry 1999, Cushman & McGarigal 2002, Ewers & Didham 2006, Fletcher et al. 2007, Smith et al. 2011, Pasher et al. 2013). On peut cependant sôinterroger sur lôexistence dôun équilibre entre habitats temporaires et permanents dans ces paysages forestiers hétérogènes à forte dynamique spatiale et temporelle, et notamment sur le rôle respectif de la rotation sylvicole des parcelles de plantations et du maintien de fragments d’habitats semi-naturels pour y conserver la biodiversité (Fischer et al. 2007, Brockerhoff et al. 2008, Najera & Simonetti 2009, Pawson et al. 2013).

En forêt de plantation, un des principaux facteurs pilotant la réponse des communautés d’oiseaux est en effet la succession des stades de rotation sylviculturale suivant les coupes rases (Donald et al. 1998, Paquet et al. 2006, Brockerhoff et al. 2008). Par exemple, en forêt des Landes de Gascogne, un assemblage d’oiseaux nicheurs spécialistes des premiers stades successionnels apparaît en quelques années après la coupe rase, dont plusieurs espèces à enjeu de conservation comme l’alouette lulu *Lullula arborea*, le pipit rousseline *Anthus campestris* ou la fauvette pitchou *Sylvia undata* (Lopez & Moro 1997, Diaz et al. 1998, Moreira et al. 2003, Barbaro et al. 2005, **chap. 2.1.1**). La coupe rase permet de maintenir la diversité β des communautés d’oiseaux à l’échelle du paysage en remplaçant continuellement les plantations matures par des nouvelles (Costello et al. 2000, Shochat et al. 2001, Paquet et al. 2006). La colonisation des habitats de coupes rases par les espèces de milieu ouvert est sans doute le processus-clé permettant d’augmenter la richesse spécifique des plantations équiennes au niveau du paysage (du Bus de Warnaffe & Lebrun 2004). En l’absence d’espèces spécialistes des forêts anciennes éliminées de longue date par l’histoire de la fragmentation forestière dans les plantations, il est peu probable qu’allonger les durées de rotation permettrait une re-colonisation par des spécialistes forestières, à l’exception peut-être du pic noir *Dryocopus martius* qui est en pleine expansion démographique (Gil-Tena et al. 2013). Cela diminuerait au contraire l’abondance des espèces patrimoniales de milieux ouverts dépendant des grandes coupes rases qui ne sont pas immédiatement replantées (Diaz et al. 1998, Costello et al. 2000). De même, l’importance de parefeux à végétation herbacée permanente pour les communautés de papillons, incluant des espèces menacées comme *Melitaea cinxia* ou *Euphydryas aurinia*, est à souligner (Wahlberg et al. 2002, van Halder et al. 2008).

Le deuxième facteur important pour les communautés d’oiseaux et de papillons est la distribution spatiale des fragments de boisements feuillus dans le paysage, ceux-ci étant plus riches en espèces et hébergeant des espèces absentes de la matrice paysagère dominée par les plantations de pins (Barbaro et al. 2005, van Halder et al. 2008, **chap. 2.1**). Les boisements feuillus et mixtes pins-feuillus sont généralement plus riches en espèces en raison d’une plus grande hétérogénéité structurale intra-parcelle, générant plus de sites de reproduction, moins de prédation et plus de ressources alimentaires que dans les peuplements de pins adjacents (Bibby et al. 1989, Donald et al. 1998, Herrando & Brotons 2002, Najera & Simonetti 2009). D’une manière générale, l’introduction d’essences feuillues dans les plantations de conifères permet d’augmenter la biodiversité à l’échelle du paysage (Bibby et al. 1989, Hobson & Bayne 2000, Brockerhoff et al. 2008), en favorisant à la fois les espèces spécialistes des feuillus natifs et celles qui ont besoin d’une complémentation de ressources entre habitats (Jansson & Angelstam 1999, Lindenmayer et al. 2003, Barbaro et al. 2005, Deconchat et al. 2009). En effet, même des fragments de petite taille ont une importance en terme de conservation, en agissant comme des refuges et des habitats sources pour les oiseaux insectivores ou les papillons, pour tout ou partie de leur cycle de vie (Estades & Temple 1999, Griffis-Kyle & Beier 2003, González-Gómez et al. 2006, **chap. 2.3.1**).

3.1.2. Fragmentation du paysage ou hétérogénéité spatiale ?

L’effet négatif de la fragmentation peut être en effet accentué ou compensé par des effets de lisières entre forêts et milieux ouverts dans les paysages hétérogènes (Fahrig 2003, Ewers et al. 2013), incluant des processus de supplémentation et de complémentation de ressources entre fragments d'habitats (Dunning et al. 1992, Burel & Baudry 1999, Ouin et al. 2004). La composition de la matrice environnante peut alors devenir plus importante pour expliquer la réponse des espèces que les caractéristiques propres du fragment d'habitat occupé (Wiens 1995, Estades & Temple 1999, Norton et al. 2000, Brotons et al. 2003). Les effets de lisière et l'indentation des lisières forestières peuvent favoriser par exemple certaines espèces caractéristiques des feuillus au sein des plantations de pin maritime, comme le tircis *Pararge aegeria*, le tabac d'Espagne *Argynnis paphia* ou le thécla du chêne *Neozephyrus quercus* pour les papillons, la huppe fasciée *Upupa epops*, le torcol fourmilier *Jynx torquilla* ou le rougequeue à front blanc *Phoenicurus phoenicurus* pour les oiseaux (Barbaro et al. 2005, van Halder et al. 2008). En effet, la diversité avifaunistique augmente avec des formes de fragment irrégulières (ratio périmètre/surface), sans doute car les lisières forestières représentent des micro-habitats favorables pour les oiseaux ou les papillons (McCollin 1998, Herrando & Brotons 2002, **chap. 2.1.2**). En effet, les ressources alimentaires peuvent augmenter en lisière et dans les petits fragments forestiers, provoquant ainsi une concentration accrue d'oiseaux insectivores (van Wilgenburg et al. 2001, Ries et al. 2004, Gonzalez-Gomez et al. 2006, **chap. 2.4.1**).

Les traits de vie et l'appartenance à certaines guildes trophiques vont filtrer les probabilités de persistance des espèces dans les paysages fragmentés (Estades & Temple 1999, Boulinier et al. 2001, Fischer et al. 2007, Newbold et al. 2013). Dans les paysages tempérés, les espèces de milieux ouverts sont plus sensibles aux effets négatifs des lisières et de la fragmentation de leur habitat que les espèces forestières (Shochat et al. 2001, Fahrig 2003, Rodewald & Vitz 2005, Reino et al. 2009, Fonderflick et al. 2013, **chap. 2.1.1**). Une matrice paysagère dominée par des habitats plus ou moins favorables comme les forêts cultivées va donc favoriser ou non la dispersion des espèces en fonction de leurs traits (Brotons et al. 2005, Baguette & Van Dyck 2007, Sirami et al. 2008, **chap. 2.2.2**). Il existe en effet une relation directe entre hétérogénéité du paysage et diversité spécifique pour les groupes taxonomiques ayant une bonne capacité de dispersion comme les oiseaux (Balent & Courtiade 1992, Burel et al. 1998, Atauri & de Lucio 2001, Barbaro et al. 2005). De plus, le processus de fragmentation implique non seulement un isolement croissant de l'habitat initialement fragmenté dans la matrice paysagère mais également un processus inverse dans lequel les fragments du nouvel habitat se connectent de manière de plus en plus continue (Shochat et al. 2001). L'hétérogénéité spatiale peut donc favoriser un groupe taxonomique aux dépens d'un autre, tandis qu'au-delà d'un certain seuil l'hétérogenéité intra-habitat devient de la fragmentation et ne favorise plus que des espèces généralistes (Burel et al. 1998, Tews et al. 2004). La prise en compte de l'histoire du paysage permet alors de mieux comprendre la distribution actuelle des communautés et ce rôle pilote joué par l'hétérogénéité spatiale (Burel & Baudry 1999, Knick & Rotenberry 2000, Ernoult et al. 2006, Sirami et al. 2010, Bonthoux et al. 2013).

3.1.3. Fragmentation, niche climatique et coexistence des oiseaux forestiers

A échelle large (macro-échelle), la distribution spatiale des espèces et la composition des communautés qui en résultent sont le résultat d'une interaction complexe entre les préférences climatiques et les préférences d'habitat des espèces (Svenning et al. 2011). Ces préférences dépendent elles-mêmes de leur origine biogéographique, et singulièrement de leur caractère natif ou exotique, ainsi que de leur degré de spécialisation à l'habitat ou à la ressource alimentaire (MacKinney & Lockwood 1999, Devictor et al. 2008, Clavero &

Brotons 2010, Barnagaud et al. 2012, Maitner et al. 2012). Les recherches que je souhaite développer dans ce cadre général de la macro-écologie des oiseaux forestiers feront l'objet de collaborations avec un groupe de chercheurs intéressés par ces questions, comprenant entre autres Jean-Yves Barnagaud, Ecki Brockerhoff, Marc Deconchat, Arndt Hampe ou Frédéric Archaux. On s'intéressera d'une part à la manière dont les préférences thermiques des communautés d'oiseaux représentent une composante importante de leurs réponses à la fragmentation forestière, d'autre part à la manière dont l'habitat interagit avec les interactions biotiques pour filtrer les espèces d'oiseaux forestiers en fonction de leur origine native ou exotique, à différentes échelles.

Pour répondre à la première question, nous chercherons à analyser le lien existant entre la niche climatique moyenne des communautés d'oiseaux (mesurée par l'indice thermique de communauté ou CTI, cf par exemple Devictor et al. 2012) et la structure de l'habitat forestier à plusieurs échelles. Nous examinerons plus précisément les patrons de variation du CTI, donc de la “préférence climatique moyenne” des communautés d'oiseaux, sur des gradients de configuration et de couverture forestière à l'échelle du paysage pour un large jeu de données issu du programme STOC de monitoring des oiseaux nicheurs en France (Jiguet et al. 2012). En utilisant un cadre d'inférence multi-modèles, nous testerons ensuite la variation du CTI sur des gradients locaux de structure et de composition forestière pour des communautés d'oiseaux de massifs de forêts domaniales du nord-ouest de la France. Il est attendu que le lien entre préférence d'habitat et niche climatique des oiseaux sur des gradients d'habitat forestier soit à la fois une conséquence de la variation microclimatique inter-habitats et des corrélations macro-échelles entre préférences thermiques et d'habitat des espèces.

Pour répondre à la deuxième question, nous étudierons les patrons de coexistence des espèces d'oiseaux natifs et exotiques introduits par l'homme dans les paysages hétérogènes de Nouvelle-Zélande, où la forêt native est fragmentée par des habitats exotiques, plantations de pins ou prairies intensives (Brockerhoff et al. 2003, Berndt et al. 2008, Deconchat et al. 2009). Nous avons déjà montré que les oiseaux natifs dépendaient étroitement de la distribution des fragments de forêt native dans le paysage tandis que les oiseaux introduits étaient plutôt favorisés par les effets de lisières entre forêts et milieux ouverts (Deconchat et al. 2009, **chap. 2.4.1**). Pour aller plus loin dans la comparaison des réponses des espèces natives et exotiques aux paysages forestiers en mosaïque, nous utiliserons des modèles hiérarchiques bayésiens pour analyser les patrons de co-occurrence, en tenant compte des probabilités de détection, d'une dizaine d'espèces d'oiseaux natifs et d'une dizaine d'oiseaux exotiques dans un jeu de 501 points d'écoute distribués dans 25 paysages néo-zélandais, variant en fonction du niveau de fragmentation forestière (Deconchat et al. 2009, Fig. 1a). Nous testerons en particulier l'hypothèse selon laquelle les passereaux exotiques seraient plus abondants dans les paysages mixant plantations de conifères exotiques et habitats agricoles tandis que les oiseaux endémiques et natifs devraient être plus abondants en forêt native continue. De plus, les analyses préliminaires montrent que les espèces natives et exotiques introduites se chevauchent très peu dans une ordination multidimensionnelle des espèces en fonction de 10 traits de vie, seuls le merle noir *Turdus merula* et la grive musicienne *T. philomelos* présentant un certain degré de “chevauchement fonctionnel” avec les oiseaux natifs (cf **chap. 2.4.1**, Fig. 1b). Les patrons de ségrégation de niche que l'on s'attend à observer seraient donc probablement plus liés à un filtre des traits de vie des espèces par la composition et la structure de l'habitat à différentes échelles qu'à des interactions marquées de compétition interspécifique entre espèces natives et exotiques (Maitner et al. 2012).

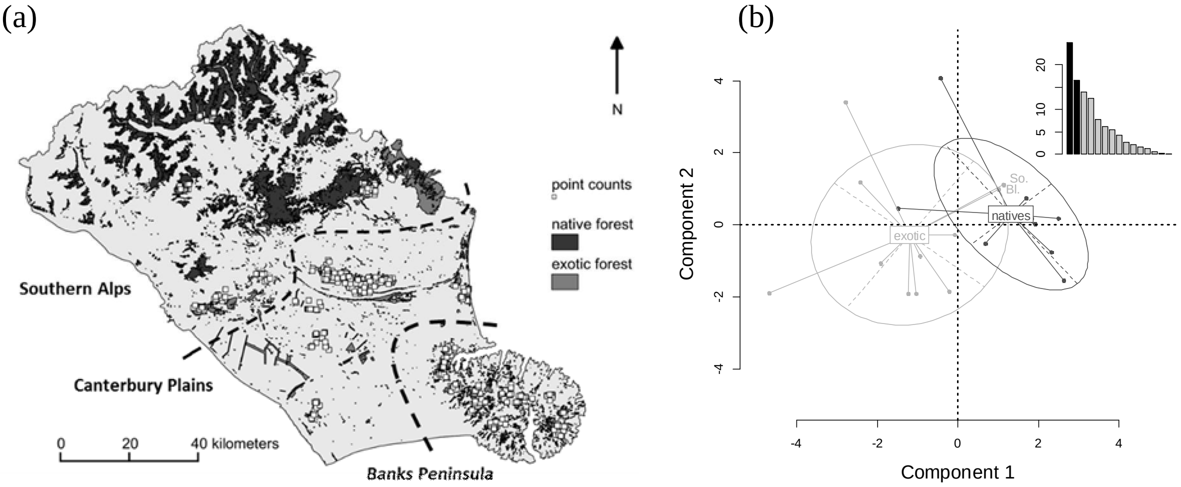


Fig. 1. (a) Carte de localisation des 501 points dôécoute, Ile du Sud de Nouvelle-Zélande. (b) Biplot de distribution des 21 espèces dôoiseaux natifs (ellipse noire) et exotiques (ellipse grise) dans une analyse de Hill & Smith basée sur lôordination des espèces par 8 traits de vie liés à lôutilisation de lôhabitat et des ressources. Les positions du merle noir *Turdus merula* (Bl.) et de la grive musicienne *T. philomelos* (So.) sont indiquées.

3.2. Diversité et fonction des communautés dôoiseaux et de lépidoptères

3.2.1. Réponses des guildes dôarthropodes à lôinsectivorie avienne

Lôétat de conservation des communautés dôoiseaux incluant des espèces dôinsectivores fonctionnels dans les paysages forestiers en mosaïque a sans doute un effet direct sur la fonction de prédation dôinsectes exercée par ces espèces-clés (Jones et al. 2005, Fischer et al. 2007, Whelan et al. 2008, Philpott et al. 2009, Jedlicka et al. 2011, Mäntylä et al. 2011, Sekercioglu 2012, voir aussi Barbaro & Battisti 2011 et **chap. 2.3** pour le cas particulier dôun lépidoptère défoliateur). Dans le **chapitre 2.4.2**, nous avons mis en évidence lôexistence de cascades trophiques entre oiseaux insectivores, lépidoptères herbivores et plantes du sous-bois à lôéchelle de la parcelle forestière dans les paysages hétérogènes et fragmentés dominés par les plantations de pins. Cette expérimentation menée en collaboration avec Brice Giffard, doctorant co-encadré avec Emmanuel Corcket et Hervé Jactel, a notamment montré que la magnitude de lôeffet indirect lié à lôexclusion des oiseaux prédateurs dépendait à la fois du type dôhabitat forestier et de lôessence de la plantule-cible sur laquelle lôherbivorie était mesurée. Pour aller plus loin, nous avons expérimentalement manipulé la végétation du sous-bois environnant les plantules-cibles afin de quantifier comment celle-ci peut modifier la détectabilité et lôaccessibilité des insectes-proies pour les prédateurs (Almenar et al. 2013).

Nous avons trouvé que non seulement lôeffet de lôexclusion des oiseaux insectivores variait en présence ou en absence de végétation environnant les plantules, mais quôen plus cet effet variait selon la guilde trophique des arthropodes-proies (Giffard et al. in press). La prédation par les oiseaux a réduit les densités de larves dôhyménoptères symphytes (tenthrèdes) avec ou sans végétation environnante, celles des lépidoptères défoliateurs externes et des larves mineuses de feuilles seulement quand la végétation est éclaircie, et celles des araignées seulement quand la végétation est conservée (Fig. 2). De plus, lôexclusion des oiseaux insectivores augmente significativement la densité totale dôarthropodes avec ou sans voisins (Giffard et al. in press). Nos résultats corroborent ceux des travaux précédents ayant expérimentalement exclus les vertébrés insectivores, se traduisant généralement par une augmentation significative de lôabondance des arthropodes (Whelan et al. 2008, Mooney et al. 2010, Mäntylä et al. 2011). Cependant, nous montrons ici que cette augmentation nôest pas systématique mais dépend de la suppression ou non de la vegetation environnante et de la guilde dôarthropodes considérée. La détectabilité et lôaccessibilité des proies pour les oiseaux est certainement le facteur expliquant ces réponses contrastées, ces éléments étant souvent plus importants que lôabondance des proies elle-même dans la réponse des prédateurs à leurs proies (Whelan 2001, Moorman et al. 2007, Almenar et al. 2013, **chap. 2.3.1**).

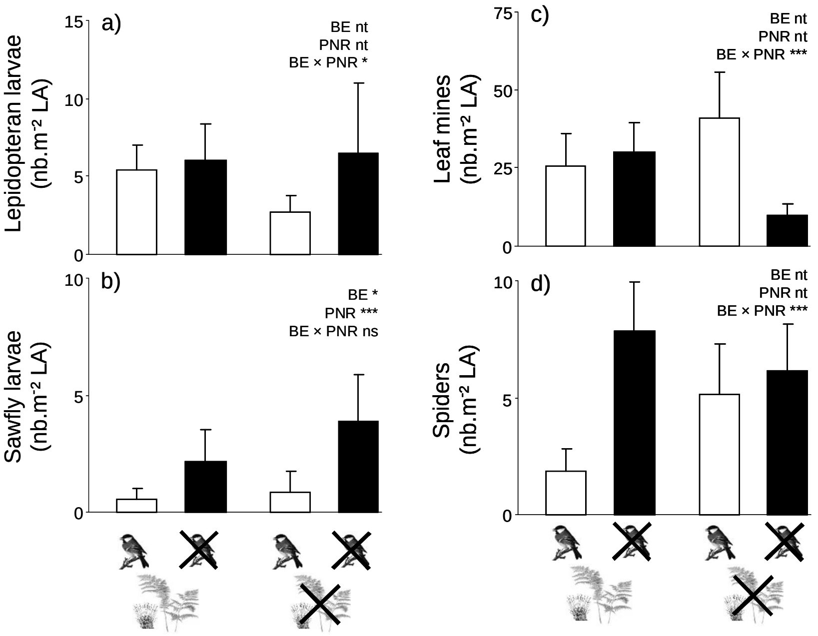


Fig. 2. Effets croisés de lôexclusion des oiseaux et de suppression de la végétation environnante sur les densités moyennes par unité de surface de feuille des plantules-cibles pour a) les lépidoptères défoliateurs externes, b) les larves de tenthrèdes, c) les larves mineuses de feuilles et d) les araignées (tiré de Giffard et al. in press). La significativité des effets et de leurs interactions est indiquée (ns : non significatif, nt : non testé).

En effet, quand la végétation avoisinante est plus haute que les plantules-cibles, elle peut gêner la prospection alimentaire de chenilles de lépidoptères par les oiseaux en réduisant la détectabilité et lôaccessibilité des proies, surtout pour les oiseaux à stratégie de ófoliage-gleaningô (Mac Nally 1994, Moorman et al. 2007). Inversement les óunderstorey gleanersô typiques comme le troglodyte mignon *Troglodytes troglodytes* préfèrent prospecter les arachnides dans des zones de végétation dense (Kristin & Patocka 1997, Artman 2003, Camprodon & Brotons 2006), ce qui pourrait expliquer pourquoi les araignées nôont été affectées par la prédation quôen présence de végétation avoisinante dans notre expérimentation. Une hypothèse alternative serait une diminution de la prédation intra-guilde par augmentation de la prédation des araignées sur les lépidoptères dans les cages dôexclusion des oiseaux (Mooney et al. 2010). Cependant, nous nôavons pas trouvé de corrélation entre densités dôaraignées et de chenilles de lépidoptères qui corroborerait cette hypothèse. Par contre, la diminution observée de lôherbivorie par les défoliateurs externes en présence dôoiseaux insectivores est en accord avec lôhypothèse de meilleure accessibilité des proies dans les sous-bois dont la végétation a été éclaircie (Whelan 2001, Camprodon & Brotons

2006, Moorman et al. 2007). De plus, cette accessibilité est sans doute accrue dans une végétation moins dense par une augmentation de la probabilité de détection des proies grâce à la vision ultra-violet des passereaux insectivores, notamment via des variations dans la réflectance des feuilles (Mäntylä et al. 2004, Rowland et al. 2008).

3.2.2. Insectivorie et diversité fonctionnelle des communautés d’oiseaux

Les résultats obtenus en mesurant expérimentalement l’insectivorie avienne par les taux de prédation *in situ* de chenilles-leurres dans les lisières forestières (**chap. 2.3.1**) nous ont conduit à envisager d’étendre ce travail, en testant plus formellement l’hypothèse d’un lien entre cette insectivorie et la diversité fonctionnelle des communautés d’oiseaux. Pour cela, en collaboration avec Ecki Brockerhoff, Brice Giffard, Yohan Charbonnier, Inge van Halder et Marc Deconchat, nous dupliquerons cette expérimentation, d’abord réalisée dans 12 fragments de forêt native en Nouvelle Zélande, dans les lisières et les intérieurs de 12 plantations de pin adjacentes à des milieux ouverts herbacés en Aquitaine. Nous pourrons ainsi comparer les réponses des communautés d’oiseaux sur la base de la diversité fonctionnelle plutôt que taxonomique pour s’affranchir des variations importantes dans la densité et la composition du pool d’espèces d’oiseaux présent sur chaque site d’étude, soumis par ailleurs à des histoires de fragmentation forestière très différentes (cf **chap. 2.1.1 et 2.4.1**). La diversité fonctionnelle sera calculée par une série d’indices mesurant la composition en traits de vie pondérés par l’abondance des différents traits dans les communautés d’oiseaux (Mason et al. 2005, Laliberté & Legendre 2010), échantillonnées par points d’écoute en Nouvelle-Zélande et par transects linéaires en France. Nous compilerons pour cela 7 traits biologiques et écologiques caractérisant l’origine biogéographique, la masse du corps, la mobilité, la méthode de prospection alimentaire, le régime alimentaire adulte, la localisation du nid et la taille des pontes séparément pour les espèces d’oiseaux contactées en France et en Nouvelle Zélande (cf **chap. 2.2.2 et 2.4.1**). Nous comparerons les patrons de richesse, d’équitabilité, de divergence et de dispersion fonctionnelles des communautés d’oiseaux en lisières et en intérieurs forestiers en Nouvelle-Zélande et en France. En effet, on peut s’attendre à ce que les effets de lisière forestière dépendent à la fois de la composante de la diversité fonctionnelle considérée et du contexte biogéographique régional, en accord avec l’hypothèse de “landscape-divergence” (Laurance et al. 2007).

De plus, les espèces répondent aux effets de lisière et de fragmentation forestière en fonction de leurs traits de vie (Rodewald & Vitz 2005, Villard et al. 2007, Clough et al. 2009, Fonderflick et al. 2013, Newbold et al. 2013, **chap. 2.2.2**). Aussi, la préférence des espèces d’oiseaux exotiques pour les lisières en Nouvelle-Zélande (**chap. 2.4.1**) se traduira peut être sur la richesse fonctionnelle des communautés, celle-ci répondant souvent de la même manière que la richesse taxonomique aux facteurs environnementaux. Au contraire, l’équitabilité fonctionnelle, qui mesure l’équidistribution d’abondance des traits de vie dans les communautés, peut être considérée comme une vraie mesure de diversité fonctionnelle, variant indépendamment de la richesse en types fonctionnels (Mason et al. 2005, Petchey & Gaston 2006, Fischer et al. 2007, Flynn et al. 2009, Laliberté & Legendre 2010). Une augmentation en parallèle de l’équitabilité fonctionnelle et de l’insectivorie en lisière pourrait par exemple indiquer une fonction écologique accrue via une utilisation plus efficiente de la ressource alimentaire par les oiseaux insectivores en lisière. Cette hypothèse est en accord avec la prédiction théorique que les processus écosystémiques dépendent plus de l’équidistribution d’abondance des espèces ou des traits de vie que de la richesse taxonomique ou fonctionnelle des communautés (Mason et al. 2005, Petchey & Gaston 2006, Hillebrand et al. 2008). Ainsi, la complémentarité entre traits de vie au sein des assemblages de prédateurs pourrait être le mécanisme-clé pilotant une prédation efficace des vertébrés insectivores à lôéchelle de lôécosystème et structurant fortement les réseaux trophiques (Philpott et al. 2009, Crowder et al. 2010, Hagen et al. 2012). Nous testerons donc ici lôhypothèse dôun effet multi-échelles de lôhétérogénéité de lôhabitat sur le rôle fonctionnel des communautés dôoiseaux dans les paysages forestiers fragmentés, avec dôabord un filtre exercé par la diversité du paysage sur le pool dôespèces disponible à une large échelle (Fischer et al. 2007, Clough et al. 2009, Newbold et al. 2013), puis un filtre exercé par les lisières entre habitats forestiers et non-forestiers sur lôintensité de prédation à une échelle plus fine (González-Gómez et al. 2006, Skoczylas et al. 2007, **chap. 2.4.1**).

3.3. Contrôle biologique par conservation dans les paysages forestiers

3.3.1. Lutte biologique et complémentarité fonctionnelle entre prédateurs

Les oiseaux sont des prédateurs efficaces capables de suivre les fluctuations de leurs proies et de sôaggréger de manière densité-dépendante dans les sites de plus grande abondance de leurs proies (Barber et al. 2008). En particulier, les passereaux insectivores des forêts tempérées de lôhémisphère nord peuvent se concentrer dans les secteurs dôimportantes défoliations des arbres, provoquées par le comportement collectif dôalimentation de lépidoptères hétérocères sociaux (et souvent urticants) comme *Choristoneura fumiferana, C. occidentalis, Ennomos subsignarius, Epirrita autumnata, Operophtera brumata, Lymantria dispar* ou *T. pityocampa* (Crawford & Jennings 1989, Patten & Burger 1998, Haney 1999, Hogstad 2005, Pimentel & Nilsson 2007, Barber et al. 2008, Barbaro & Battisti 2011). Une telle aggrégation de prédateurs dans les zones de forte densité des proies se trouve à la fois chez des espèces insectivores spécialistes et généralistes, comme les coulicous nord-américains du genre *Coccyzus* (Barber et al. 2008), les parulines (Parulinae) ou les mésanges (Paridae) en Europe et Amérique du Nord (Crawford & Jennings 1989, Patten & Burger 1998, Haney 1999, Brotons & Herrando 2003, Kaunisto et al. 2012). La prédation des chrysalides et chenilles de *Choristoneura fumiferana* peut par exemple représenter jusquôà 84% quand les populations sont à faible densité, et jusquôà 22% à plus forte densité (Crawford & Jennings 1989), tandis que la huppe fasciée peut prédater jusquôà 70% des chrysalides de processionnaires enfouies sous terre pour la nymphose printanière (Battisti et al. 2000). En Europe, dôautres passereaux forestiers, comme le pinson du Nord *Fringilla montifringilla*, peuvent montrer une réponse numérique aux pullulations de chenilles de géomètres (Hogstad 2005). Côest également le cas des mésanges (Paridae), qui sont des ócanopy gleanersô sédentaires pouvant exploiter rapidement une ressource alimentaire nouvelle et localisée, y compris en dehors de la saison de reproduction (Brotons 1997, Brotons & Herrando 2003, Pimentel & Nilsson 2007, Kaunisto et al. 2012, **chap. 2.3.2**).

Cette efficacité des mésanges comme prédateurs, reconnue en lutte biologique, est liée à la rapidité de leurs réponses aux fluctuations spatiales et temporelles de leurs proies, à leur plasticité adaptative et leur comportement dôapprentissage social leur permettant dôexploiter très vite de nouvelles ressources (Brotons 1997, Mols & Visser 2002, Bouvier et al. 2005, Charmantier et al. 2008, Silva et al. 2012). Cet apprentissage comportemental est en effet bien connu par les éthologistes depuis la célèbre affaire des bouteilles de lait trouées en Angleterre dans les années 20 (Lefebvre 1995). Ces prédateurs généralistes peuvent ainsi en partie répondre à la densité dôun défoliateur forestier comme la processionnaire du pin, dont lôexpansion vers le Nord sôaccélère avec le réchauffement climatique (Battisti et al. 2005,

chap. 2.3.2). Bien que les prédateurs généralistes puissent à eux seuls réguler efficacement leurs proies en lutte biologique (Symondson et al. 2002), côest bien lôoccurrence dôune guilde complète de prédateurs vertébrés qui présente la meilleure assurance contre les pullulations de ravageurs en permettant une importante complémentarité fonctionnelle entre prédateurs se succédant au cours du cycle de vie des lépidoptères défoliateurs (Philpott et al. 2009, Nixon & Roland 2012, Tscharntke et al. 2012, Barbaro et al. in press, cf Annexe 3). Il est donc essentiel de promouvoir des pratiques sylvicoles permettant la plus grande coexistence possible entre prédateurs spécialistes et généralistes en forêt, à la fois aux échelles locale et paysagère. Par exemple, dans le cas de la processionnaire du pin, cela signifierait garder une structure de sous-bois forestier compatible avec le óforagingô aérien nocturne des engoulevents et des chiroptères (Sierro et al. 2001, Jung et al. 2012), favoriser la diversité de la végétation arbustive en lisière des plantations de pins pour favoriser les passereaux insectivores migrateurs prédateurs en automne (Rodewald & Brittingham 2004, Moorman et al. 2007), et maintenir des structures herbacées rases en lisière des plantations de pins pour les insectivores se nourrissant au sol comme la huppe fasciée (Tagmann-Ioset et al. 2012, **chap. 2.3.1**). Ainsi, les insectes ravageurs forestiers peuvent-ils être considérés aussi dôun point de vue de la gestion conservatoire des forêts comme des espèces-clés permettant de conserver une dynamique de perturbation naturelle très favorable, voire indispensable, à la conservation de la biodiversité forestière (Müller et al. 2008).

3.3.2. Réponses numériques et fonctionnelles de chauves-souris insectivores

Lôefficacité du contrôle biologique des insectes herbivores par leurs prédateurs est directement fonction de la forme et de la magnitude de leurs réponses fonctionnelles (Abrams and Ginzburg 2000), en particulier pour les lépidoptères défoliateurs forestiers sujets à des pullulations périodiques (Klemola et al. 2002, Klapwijk et al. 2012). Parmi les prédateurs de ces lépidoptères défoliateurs forestiers, il est conu de longue date que les oiseaux et les petits mammifères montrent des réponses numériques et fonctionnelles à la densité de leurs proies (Buckner 1967, Dempster 1983, Glen 2004). La prédation par les vertébrés insectivores permet de maintenir les populations dôinsectes à des niveaux de densité faibles mais elle cesse dôavoir un effet significatif lors des pullulations à cause dôune prédominance de réponse fonctionnelle óen clocheô de type II (Crawford & Jennings 1989, Glen 2004). Cependant, la reconnaissance du rôle fonctionnel et des services écosystémiques de prédation dôinsectes rendus par les oiseaux, et plus encore par les chauves-souris, est relativement récent (Whelan et al. 2008, Kunz et al. 2011, Müller et al. 2012). Les expérimentations ócross-taxaô ont pourtant montré que les chiroptères insectivores forestiers avaient un impact encore plus important que les oiseaux sur les populations dôinsectes-proies (Kalka et al. 2008, Williams-Guillén et al. 2008). De plus, le rôle de lôécholocation des chauves-souris sur les réponses évolutives des lépidoptères hétérocères tympanés pour échapper à leur prédation est bien connu (Waters 2003, Windmill et al. 2006). Certaines espèces spécialistes des lépidoptères hétérocères comme la barbastelle *Barbastella barbastellus* peuvent même utiliser deux fréquences dôultra-sons en alternance afin de leurrer le papillon-proie en faussant son estimation acoustique de la proximité du prédateur (Sierro & Arlettaz 1997, Barataud & Tupinier 2012). Dôautres espèces généralistes de chiroptères, comme les oreillards *Plecotus* spp, les *rhinolophes* Rhinolophus spp, la sérotine commune *Eptesicus serotinus* et la pipistrelle de Kuhl *Pipistrellus kuhlii*, peuvent consommer des quantités importantes de lépidoptères (Goiti et al. 2003, Kervyn & Libois 2008, Barbaro et al. in press, Annexe 3).

Une importante perspective de mes travaux de recherche sera donc dôétudier, en collaboration avec Yohan Charbonnier, Pierre Gauzère, Andrea Battisti et Hervé Jactel, les réponses numériques et fonctionnelles des chiroptères insectivores à la densité dôun défoliateur forestier majeur, la processionnaire du pin. Pour cela, nous utiliserons un dispositif expérimental dans lequel seront appariés des pièges à phéromone de processionnaire et des enregistreurs automatiques dôultrasons en lisières de plantations de pins. Nous quantifierons lôabondance des chauves-souris par le nombre de signaux dôécholocation enregistrés par espèce, et lôactivité de prédation par le nombre de signaux de óbuzzsô indiquant une tentative effective de capture de proies par une accélération et une augmentation de la fréquence du signal dôécholocation (Barataud & Tupinier 2012). Les pièges à phéromone seront utilisés pour simuler des aggrégations de papillons mâles de processionnaires après leur émergence en été, en lisière de plantations de pins utilisées par les chauves-souris en chasse. Nous analyserons en parallèle les réponses numériques et fonctionnelles des espèces généralistes et spécialistes (cf Annexe 3) à la densité de processionnaires mesurée par les captures dans les pièges à phéromone. En effet, les premiers résultats montrent que trois espèces généralistes, la pipistrelle commune, la pipistrelle de Kuhl et la sérotine commune, et trois espèces spécialistes des lépidoptères, la barbastelle et les deux oreillards, sont assez abondantes en forêt de plantation dans les Landes de Gascogne, sur un gradient de mixité pins-feuillus des peuplements forestiers (Gauzère 2012). La réponse de la pipistrelle de Kuhl sera particulièrement intéressante à suivre puisque cette chauve-souris dôorigine méditerranéo-atlantique est en expansion vers le Nord avec le réchauffement climatique comme la processionnaire du pin (Battisti et al. 2005, Sachanowicz et al. 2006, Rebelo et al. 2010). Dans le cadre de la thèse de Yohan Charbonnier, nous étudierons également la réponse des guildes de chiroptères à la structure et à la composition des habitats à lôéchelle locale et à celle du paysage (Frey-Ehrenbold et al. 2013), dans un réseau de paysages forestiers répartis sur un gradient latitudinal en Europe. Enfin, nous mènerons aussi dans le futur, en collaboration avec Jean-Charles Bouvier et Adrien Rusch, des expérimentations sur le contrôle biologique par les vertébrés insectivores dans les paysages viticoles.

Conclusion : conservation et fonction de la biodiversité dans les paysages hétérogènes

Lôincertitude sur lôévolution des relations prédateurs-proies sous lôeffet du changement climatique est encore considérable (Berggren et al. 2009, Bretagnolle & Gillis 2010), en particulier dans les forêts de plantation (Pawson et al. 2013). Par exemple, des décalages spatiaux et temporels entre un prédateur et ses proies pourrait diminuer lôefficacité du contrôle biologique dans les paysages dédiés à la production (Thomson et al. 2010). Prédateurs généralistes et spécialistes nôont pas la même efficacité en lutte biologique, notamment en raison des différentes formes et magnitudes de leurs courbes de réponse à la densité des proies (Klemola et al. 2002, Symondson et al. 2002). Il y a donc une nécessité à maintenir une grande diversité fonctionnelle de vertébrés insectivores à lôéchelle du paysage, incluant à la fois des prédateurs généralistes et spécialistes pour permettre une lutte biologique efficace sur le long terme (Tscharntke et al. 2007, Philpott et al. 2009). Ainsi, les discontinuités multi-échelles dans la structure et la composition des habitats sont créatrices dôune hétérogénéité spatiale cruciale pour la conservation de la diversité tant taxonomique que fonctionnelle dans les paysages de production en mosaïque (Tews et al. 2004, Najera & Simonetti 2009, Fahrig et al. 2011). Les discontinuités spatiales créées par les lisières entre forêts et milieux ouverts, ou entre habitats semi-naturels et parcelles de production, peuvent en effet être vues comme des óstructures-clésô permettant une complémentation ou une supplémentation des ressources à lôéchelle du paysage pour des espèces partageant certains traits de vie (Tews et al. 2004, **chap. 2.2.2**). Lõimportance du degré de fragmentation des forêts natives, ou de la distance aux fragments de forêts naturelles, pour la conservation de certaines guildes et de certains groupes fonctionnels de vertébrés insectivores au sein de paysages agro-forestiers fragmentés doit aussi être soulignée (Tscharntke et al. 2008, Clough et al. 2009).

Maintenir des fragments dõhabitats semi-naturels dans les mosaïques paysagères à vocation de production agricole ou forestière permet de relier conservation et fonction de la biodiversité dans ces paysages hétérogènes (Fischer et al. 2007, Flynn et al. 2009, Sekercioglu 2012). Ces fragments jouent en effet un rôle majeur dans la persistance des populations ódõinsectivores fonctionnelsô à lõéchelle du paysage, dont la présence dépend souvent de la complémentation entre habitats semi-naturels et parcelles de production adjacentes (Jones et al. 2005, Jedlicka et al. 2011, **chap. 2.3.1**). De fait, il existe sans doute une relation quantitative entre métriques de diversité fonctionnelle et intensité du service écosystémique de prédation rempli par les vertébrés insectivores dans les agro-écosystèmes et les forêts de plantation. Lõexploration de cette relation nécessite de nouvelles recherches liant la composition des communautés et leur fonction par la mise en place de dispositifs simultanés dõexpérimentations et dõobservations (González-Gómez et al. 2006, Philpott et al. 2009, **chap. 2.4**). Le rôle de lõéquitabilité fonctionnelle pourrait être particulièrement essentiel, en raison dõune équirépartition des traits de vie des prédateurs dans les communautés dõennemis naturels, assurant ainsi un contrôle biologique plus efficace que celui produit par des communautés dominées par un petit nombre de types fonctionnels de prédateurs (Hillebrand et al. 2008, Crowder et al. 2010). Les mosaïques dõhabitats semi-naturels et de parcelles de production permettent sans doute de conserver à la fois la diversité et la fonction des oiseaux insectivores dans les paysages hétérogènes et fragmentés (Fahrig et al. 2011, Hagen et al. 2012, Sekercioglu 2012, Tscharntke et al. 2012). Le maintien dõune diversité ou dõune équitabilité fonctionnelle élevée fournit vraisemblablement une óassurance biotiqueô pour la durabilité des services écosystémiques assurés par les vertébrés prédateurs dans ces paysages, en permettant de stabiliser leur rôle fonctionnel au sein de réseaux écologiques à la fois complexes et changeants.

Photo 6. Fragment de forêt native et zostérops à dos gris *Zosterops lateralis*, péninsule de Banks, Ile du sud de Nouvelle-Zélande, février 2011 (Luc Barbaro).

Références

Abrams, P.A., Ginzburg L.R. 2000. The nature of predation: prey dependent, ratio dependent or neither? Trends in Ecology & Evolution 15: 337ï 341.

Albrecht, J., Neuschulz, E.L., Farwig, N., 2012. Impact of habitat structure and fruit abundance on avian seed dispersal and fruit predation. Basic and Applied Ecology 13, 347ï 354.

Alldredge, M.W., Simons, T.R., Pollock, K.H., 2007. Factors affecting aural detections of songbirds. Ecological Applications 17, 948ï 955.

Allen, T.F.H., Starr, T.B. 1982 Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago.

Allen, C.R., Nemec, K.T., Wardwell, D.A., Hoffman, J.D., Brust, M., Decker, K.L., Fogell, D., Hogue, J., Lotz, A., Miller, T., Pummill, M., Ramirez-Yañez, L.E., Uden, D.R., 2013. Predictors of regional establishment success and spread of introduced non-indigenous vertebrates. Global Ecology and Biogeography, in press.

Almenar, D., Aihartza, J., Goiti, U., Salsamendi, E., Garin, I., 2013. Hierarchical patch choice by an insectivorous bat through prey availability components. Behavioral Ecology and Sociobiology 67, 311ï 320.

Anderson, S.H., Kelly, D., Ladley, J.J., Molloy, S., Terry, J., 2011. Cascading effects of bird functional extinction reduce pollination and plant density. Science 331, 1068ï 1071.

Aragón, P., Sánchez-Fernández, D., 2013. Can we disentangle predator-prey interactions from species distributions at a macro-scale? A case study with a raptor species. Oikos 122, 64ï 72.

Archaux, F., Henry, P.Y., Gimenez, O., 2012. When can we ignore the problem of imperfect detection in comparative studies? Methods in Ecology and Evolution 3, 188ï 194.

Artman, V.L., 2003. Effects of commercial thinning on breeding bird populations in western hemlock forests. The American Midland Naturalist 149, 225ï 232.

Atauri, J.A., de Lucio, J.V. 2001. The role of landscape structure in species richness distribution of birds, amphibians, reptiles and lepidopterans in Mediterranean landscapes. Landscape Ecology, 16: 147-159.

Auer, S.K., Martin, T.E., 2013. Climate change has indirect effects on resource use and overlap among coexisting bird species with negative consequences for their reproductive success. Global Change Biology 19, 411ï 419.

Aviron, S., Burel, F., Baudry, J., Schermann, N. 2005 Carabid assemblages in agricultural landscapes: impacts of habitat features, landscape context at different spatial scales and farming intensity. Agriculture, Ecosystems and Environment, 108, 205-217.

Baguette, M., Van Dyck, H. 2007. Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. Landscape Ecol. 22: 1117-1129.

Balent, G., Courtiade, B. 1992 Modelling bird communities/landscape patterns relationships in a rural area of south-western France. Landscape Ecology, 6, 195-211.

Barataud, M., Tupinier, Y. 2012 Écologie acoustique des chiroptères dŒurope identification des espèces, étude de leurs habitats et comportements de chasse. Biotope, Muséum national dôhistoire naturelle, Paris.

Barbaro L., Pontcharraud L., Vetillard F., Guyon D., Jactel H. 2005. Comparative responses of bird, carabid, and spider assemblages to stand and landscape diversity in maritime pine plantation forests. Ecoscience 12: 110-121.

Barbaro L., Battisti A. 2011 Birds as predators of the pine processionary moth (Lepidoptera: Notodontidae). Biological Control 56: 107-114.

Barbaro L., Charbonnier Y., Vetillard F., Blache S., Battisti A. in press Numerical and functional responses of predatory vertebrates to the pine processionary moth. In: Roques A. (coord.). Processionary moths and global change: an update. Springer Verlag.

Barber, N.A., Marquis, R.J., Tori, W.P., 2008. Invasive prey impacts the abundance and distribution of native predators. Ecology 89, 2678ï 2683.

Barnagaud, J.Y., Devictor, Vincent, Jiguet, Frédéric, Barbet-Massin, M., Le Viol, I., Archaux, F., 2012. Relating Habitat and Climatic Niches in Birds. PLoS One 7, e32819.

Battisti, A., Bernardi, M., Ghiraldo, C., 2000. Predation by the hoopoe (Upupa epops) on pupae of Thaumetopoea pityocampa and the likelyinfluence on other natural enemies. Biocontrol 45, 311ï 323.

Battisti, A., Stastny, M., Netherer, S., Robinet, C., Schopf, A., Roques, A., Larsson, S. 2005 Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. Ecol. Appl. 15, 2084ï 2096.

Baudry, J., Burel, F., Aviron, S., Martin, M., Ouin, A., Pain, G., Thenail, C., 2003. Temporal variability of connectivity in agricultural landscapes: do farming activities help? Landscape Ecology 18, 303ï 314.

Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends in Ecology & Evolution 18, 182ï 188.

Berggren, Å., Björkman, C., Bylund, H., Ayres, M.P., 2009. The distribution and abundance of animal populations in a climate of uncertainty. Oikos 118, 1121ï 1126.

Berndt, L.A., Brockerhoff, Eckehard G., Jactel, H., 2008. Relevance of exotic pine plantations as a surrogate habitat for ground beetles (Carabidae) where native forest is rare. Biodiversity and Conservation 17, 1171ï 1185.

Bibby, C.J., Aston, N. Bellamy, P.E. 1989. Effects of broadleaved trees on birds of upland conifer plantations in North Wales. Biological Conservation, 49: 17-29.

Bibby, C.J., Burgess, N.D., Hill, D.A., Mustoe, S. 2000. Bird census techniques. Academic Press, London.

Blackburn, T.M., Gaston, K.J., Parnell, M., 2010. Changes in non-randomness in the expanding introduced avifauna of the world. Ecography 33, 168ï 174.

Blondel, J., Ferry, C. Frochot, B. 1981. Point counts with unlimited distance. Studies in Avian Biology, 6: 414-420.

Blumstein, D.T., Mennill, D.J., Clemins, P., Girod, L., Yao, K., Patricelli, G., Deppe, J.L., Krakauer, A.H., Clark, C., Cortopassi, K.A., Hanser, S.F., McCowan, B., Ali, A.M., Kirschel, A.N.G., 2011. Acoustic monitoring in terrestrial environments using microphone arrays: applications, technological considerations and prospectus. Journal of Applied Ecology 48, 758ï 767.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.-S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24, 127ï 135.

Bonter, D.N., Cooper, C.B., 2012. Data validation in citizen science: a case study from Project FeederWatch. Frontiers in Ecology and the Environment 10, 305ï 307.

Bonthoux, S., Balent, G., 2012. Point count duration: five minutes are usually sufficient to model the distribution of bird species and to study the structure of communities for a French landscape. Journal of Ornithology 153, 491ï 504.

Bonthoux, S., Barnagaud, J.-Y., Goulard, M., Balent, G., 2013. Contrasting spatial and temporal responses of bird communities to landscape changes. Oecologia, in press.

Bossenbroek, J.M., Wagner, H.H., Wiens, J.A. 2005 Taxon-dependent scaling: beetles, birds and vegetation at four North American grassland sites. Landscape Ecology, 20, 675-688.

Both, C., Van Turnhout, C.A.M., Bijlsma, R.G., Siepel, H., Van Strien, A.J., Foppen, R.P.B., 2010. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. Proceedings of the Royal Society B: Biological Sciences 277, 1259ï 1266.

Boulinier, T., Nichols, J.D., Hines, J.E., Sauer, J.R., Flather, C.H., Pollock, K.H., 2001. Forest fragmentation and bird community dynamics: inference at regional scales. Ecology 82, 1159ï 1169.

Bouvier, J.C., Toubon, J.F., Boivin, T., Sauphanor, B., 2005. Effects of apple orchard management strategies on the great tit (Parus major) in southeastern France. Environmental Toxicology and Chemistry 24, 2846ï 2852.

Bretagnolle V., Gillis H. 2010. Predatorï prey interactions and climate change. In: Moller A.P., Fiedler W., Berthold P. (eds) Effects of climate change on birds. Oxford Univ Press, New York: 227-248.

Brockerhoff, E.G, Ecroyd, C.E., Leckie, A.C., Kimberley, M.O., 2003. Diversity and succession of adventive and indigenous vascular understorey plants in Pinus radiata plantation forests in New Zealand. Forest Ecology and Management 185, 307ï 326.

Brockerhoff, E.G., Barratt, B.I., Beggs, J.R., Fagan, L.L., Malcolm, K., Phillips, C.B., Vink, C.J., 2010. Impacts of exotic invertebrates on New Zealandôs indigenous species and ecosystems. New Zealand Journal of Ecology 34, 158ï 174.

Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Quine, C.P., Sayer, J., 2008. Plantation forests and biodiversity: oxymoron or opportunity? Biodiversity and Conservation 17, 925ï 951.

Brooks, D.R., Storkey, J., Clark, S.J., Firbank, L.G., Petit, S., Woiwod, I.P., 2012. Trophic links between functional groups of arable plants and beetles are stable at a national scale. Journal of Animal Ecology 81, 4ï 13.

Brotons, L., 1997. Changes in foraging behaviour of the Coal Tit Parus ater due to snow cover. Ardea 85, 249ï 258.

Brotons, L., Herrando, S., 2003. Effect of increased food abundance near forest edges on flocking patterns of Coal Tit Parus ater winter groups in mountain coniferous forests. Bird Study 50, 106ï 111.

Brotons, L., Mönkkönen, M., Martin, J.L., 2003. Are Fragments Islands? Landscape Context and Density-Area Relationships in Boreal Forest Birds. The American Naturalist 162, 343ï 357.

Brotons, L., Pons, P., Herrando, S. 2005 Colonization of dynamic Mediterranean landscapes: where do birds come from after fire? Journal of Biogeography, 32, 789-798.

Brotons, L., De Cáceres, M., Fall, A., Fortin, M.-J., 2012. Modeling bird species distribution change in fire prone Mediterranean landscapes: incorporating species dispersal and landscape dynamics. Ecography 35, 458ï 467.

Brown, J.H., 1999. The legacy of Robert MacArthur: from geographical ecology to macroecology. Journal of Mammalogy 333ï 344.

Buckland, S.T., 2006. Point-transect surveys for songbirds: robust methodologies. The Auk 123, 345ï 357.

Buckner C.H. 1967 Avian and mammalian predators of forest insects. Entomophaga 12: 491-501.

Burel, F., Baudry, J. 1999 Ecologie du paysage: concepts, méthodes et applications. Editions Tec & Doc, Paris.

Burel, F., Baudry, J., Butet, A., Clergeau, P., Delettre, Y., Le Coeur, D., Dubs, F., Morvan, N., Paillat, G., Petit, S. 1998. Comparative biodiversity along a gradient of agricultural landscapes. Acta Oecologica 19, 47ï 60.

Burnham, K.P., Anderson, D.R. 2002. Model selection and inference: a practical information-theoretic approach. Springer.

Butterfield, B.J., Suding, K.N., 2013. Single-trait functional indices outperform multi-trait indices in linking environmental gradients and ecosystem services in a complex landscape. Journal of Ecology 101, 9ï 17.

Calenge, C., 2006. The package ñadehabitatò for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modelling 197, 516ï 519.

Cameron, E.K., Bayne, E.M., 2012. Invasion by a non-native ecosystem engineer alters distribution of a native predator. Diversity and Distributions 18, 1190ï 1198.

Camprodon, J., Brotons, L., 2006. Effects of undergrowth clearing on the bird communities of the Northwestern Mediterranean Coppice Holm oak forests. Forest Ecology and Management 221, 72ï 82.

Carnicer, J., Brotons, Lluís, Stefanescu, Constantí, Peñuelas, J., 2012. Biogeography of species richness gradients: linking adaptive traits, demography and diversification. Biological Reviews 87, 457ï 479.

Charmantier, A., McCleery, R.H., Cole, L.R., Perrins, C., Kruuk, L.E.B., Sheldon, B.C., 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. Science 320, 800ï 803.

Chollet, S., Martin, J.-L., 2013. Declining woodland birds in North America: should we blame Bambi? Diversity and Distributions 19, 481ï 483.

Clavel, J., Julliard, Romain, Devictor, Vincent, 2011. Worldwide decline of specialist species: toward a global functional homogenization? Frontiers in Ecology and the Environment 9, 222ï 228.

Clavero, M., Brotons, Lluís, 2010. Functional homogenization of bird communities along habitat gradients: accounting for niche multidimensionality. Global Ecology and Biogeography.

Clavero, M., Villero, D., Brotons, Lluís, 2011. Climate Change or Land Use Dynamics: Do We Know What Climate Change Indicators Indicate? PLoS ONE 6, e18581.

Clergeau, P., Burel, F., 1997. The role of spatio-temporal patch connectivity at the landscape level: an example in a bird distribution. Landscape and Urban Planning 38, 37ï 43.

Clergeau, P., Croci, S., Jokimäki, J., Kaisanlahti-Jokimäki, M.-L., Dinetti, M., 2006. Avifauna homogenisation by urbanisation: Analysis at different European latitudes. Biological Conservation 127, 336ï 344.

Clough, Y., Dwi Putra, D., Pitopang, R., Tscharntke, T., 2009. Local and landscape factors determine functional bird diversity in Indonesian cacao agroforestry. Biological Conservation 142, 1032ï 1041.

Cooper, J.K., Li, J., Montagnes, D.J.S., 2012. Intermediate fragmentation per se provides stable predator-prey metapopulation dynamics. Ecology Letters 15, 856ï 863.

Coreau, A., Martin, J.-L., 2007. Multi-scale study of bird species distribution and of their response to vegetation change: a Mediterranean example. Landscape Ecology 22, 747ï 764.

Costello, C.A., Yamasaki, M., Pekins, P.J., Leak, W.B., Neefus, C.D. 2000. Songbird response to group selection harvests and clearcuts in a New Hampshire northern hardwood forest. Forest Ecology and Management, 127: 41-54.

Crawford H.S., Jennings D.T. 1989. Predation by birds on spruce budworm Choristoneura fumiferana: functional, numerical, and total responses. Ecology 70: 152-163.

Crowder, D.W., Northfield, T.D., Strand, M.R., Snyder, W.E., 2010. Organic agriculture promotes evenness and natural pest control. Nature 466, 109ï 112.

Cumming, G.S., Child, M.F., 2009. Contrasting spatial patterns of taxonomic and functional richness offer insights into potential loss of ecosystem services. Philosophical Transactions of the Royal Society B: Biological Sciences 364, 1683ï 1692.

Cushman, S.A., McGarigal, K., 2002. Hierarchical, multi-scale decomposition of species-environment relationships. Landscape Ecology 17, 637ï 646.

Deconchat, M., Balent, G. 1996. Biodiversité et forêt dans un paysage agricole: étude bibliographique. Etudes et Recherches sur les Systèmes Agraires et le Développement 29: 15-36

Deconchat, M., Brockerhoff E., Barbaro L. 2009. Effects of surrounding landscape composition on the conservation value of native and exotic habitats for native forest birds. Forest Ecology and Management 258S: S196-S204.

Dempster, J.P. 1983. The natural control of butterflies and moths. Biological Reviews, 58, 461-481.

Devictor, V., Julliard, R., Clavel, J., Jiguet, F., Lee, A., Couvet, D., 2008. Functional biotic homogenization of bird communities in disturbed landscapes. Global Ecology and Biogeography 17, 252ï 261.

Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W., Mouquet, N., 2010. Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. Ecology Letters noï no.

Devictor, V., van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliölä, J., Herrando, S., Julliard, R., Kuussaari, M., Lindström, Å., Reif, J., Roy, D.B., Schweiger, O., Settele, J., Stefanescu, C., Van Strien, A., Van Turnhout, C., Vermouzek, Z., WallisDeVries, M., Wynhoff, I., Jiguet, F. 2012. Differences in the climatic debts of birds and butterflies at a continental scale. Nature Climate Change 2, 121ï 124.

Diaz, M., Carbonell R., Santos T., Telleria, J.L. 1998. Breeding bird communities in pine plantations of the Spanish plateaux: biogeography, landscape and vegetation effects. Journal of Applied Ecology, 35: 562-574.

Didham, R., Tylianakis, J., Gemmell, N., Rand, T., Ewers, R., 2007. Interactive effects of habitat modification and species invasion on native species decline. Trends in Ecology & Evolution 22, 489-496.

Donald, P.F., Fuller R.J., Evans A.D., Gough, S.J. 1998. Effects of forest management and grazing on breeding bird communities in plantations of broadleaved and coniferous trees in western England. Biological Conservation, 85: 183-197.

Dormann, C.F., M. McPherson, J., B. Araújo, M., Bivand, R., Bolliger, J., Carl, G., G. Davies, R., Hirzel, A., Jetz, W., Daniel Kissling, W., Kühn, I., Ohlemüller, R., R. Peres-Neto, P., Reineking, B., Schröder, B., M. Schurr, F., Wilson, R., 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30, 609ï 628.

Dray, S., Royer-Carenzi, M., Calenge, C., 2010. The exploratory analysis of autocorrelation in animal-movement studies. Ecological Research 25, 673ï 681.

du Bus de Warnaffe, G., Lebrun, P. 2004. Effects of forest management on carabid beetles in Belgium: implications for biodiversity conservation. Biological Conservation, 118: 219-234.

Dunning, J.B., Danielson, B.J., Pulliam, H.R. 1992 Ecological processes that affect populations in complex landscapes. Oikos, 65, 169-175.

Dupuy, G., Giraudoux, P., Delattre, P., 2009. Numerical and dietary responses of a predator community in a temperate zone of Europe. Ecography 32, 277ï 290.

Eisenberg, C., Seager, S.T., Hibbs, D.E., 2013. Wolf, elk, and aspen food web relationships: Context and complexity. Forest Ecology and Management.

Ernoult, A., Freiré-Diaz, S., Langlois, E., Alard, D., 2006. Are similar landscapes the result of similar histories? Landscape Ecology 21, 631ï 639.

Estades, C.F., Temple, S.A. 1999 Deciduous-forest bird communities in a fragmented landscape dominated by exotic pine plantations. Ecological Applications, 9, 573-585.

Ethier, K., Fahrig, L., 2011. Positive effects of forest fragmentation, independent of forest amount, on bat abundance in eastern Ontario, Canada. Landscape Ecology 26, 865ï 876.

Ewers, R.M., Didham, R.K. 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biological Review 81, 117-142.

Ewers, R.M., Bartlam, S., Didham, R.K., 2013. Altered species interactions at forest edges: contrasting edge effects on bumble bees and their phoretic mite loads in temperate forest remnants. Insect Conservation and Diversity in press.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34, 487ï 515.

Fahrig, L., Baudry, J., Brotons, L., Burel, F., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M., Martin, J.L., 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecology Letters 14, 101ï 112.

Fischer, J., Lindenmayer, D.B., Blomberg, S.P., Montague-Drake, R., Felton, A., Stein, J.A., 2007. Functional Richness and Relative Resilience of Bird Communities in Regions with Different Land Use Intensities. Ecosystems 10, 964ï 974.

Fletcher, Jr., R.J., Ries, L., Battin, J., Chalfoun, A.D., 2007. The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined? Canadian Journal of Zoology 85, 1017ï 1030.

Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B., Simpson, N., Mayfield, M.M., DeClerck, F., 2009. Loss of functional diversity under land use intensification across multiple taxa. Ecology Letters 12, 22ï 33.

Fonderflick, J., Besnard, A., Martin, J.-L., 2013. Species traits and the response of open-habitat species to forest edge in landscape mosaics. Oikos 122, 42ï 51.

Forsman, J.T., Hjernquist, M.B., Gustafsson, L., 2009. Experimental evidence for the use of density based interspecific social information in forest birds. Ecography 32, 539ï 545.

Frey-Ehrenbold, A., Bontadina, F., Arlettaz, R., Obrist, M.K., 2013. Landscape connectivity, habitat structure and activity of bat guilds in farmland-dominated matrices. Journal of Applied Ecology 50, 252ï 261.

Gasc, A., Sueur, J., Jiguet, F., Devictor, V., Grandcolas, P., Burrow, C., Depraetere, M., Pavoine, S., 2013. Assessing biodiversity with sound: Do acoustic diversity indices reflect phylogenetic and functional diversities of bird communities? Ecological Indicators 25, 279ï 287.

Gaston, K.J., Blackburn, T.M., 1997. How many birds are there? Biodiversity & Conservation 6, 615ï 625.

Gaston, K.J., Chown, S.L., Evans, K.L., 2008. Ecogeographical rules: elements of a synthesis. Journal of Biogeography 35, 483ï 500.

Gauzère P. 2012. Effects of forest composition on activity and structure of bat communities. Mémoire de Master, Univ. de Perpignan.

Giffard B., Barbaro L., Jactel H., Corcket E. 2013. Plant neighbours mediate bird predation effects on arthropod abundance and herbivory. Ecological Entomology, in press.

Gil-Tena, A., Brotons, L., Fortin, M.J., Burel, F., Saura, S., 2013. Assessing the role of landscape connectivity in recent woodpecker range expansion in Mediterranean Europe: forest management implications. European Journal of Forest Research 132, 181ï 194.

Glen D.M. 2004. Birds as predators of lepidopterous larvae. In, van Hemden H, Rothschild M (eds) Insect and bird interactions. Intercept, Andover.

Goiti U., Vecin P., Garin I., Saloña M., Aihartza J.R. 2003. Diet and prey selection in Kuhl's pipistrelle Pipistrellus kuhlii (Chiroptera, Vespertilionidae) in south-western Europe. Acta Theriologica 48, 457-468

González-Gómez, P.L., Estades, C.F., Simonetti, J.A., 2006. Strengthened insectivory in a temperate fragmented forest. Oecologia 148, 137ï 143.

Gordo, O., Brotons, L., Ferrer, X., Comas, P., 2005. Do changes in climate patterns in wintering areas affect the timing of the spring arrival of trans-Saharan migrant birds? Global Change Biology 11, 12ï 21.

Gotelli, N.J., Graves, G.R., Rahbek, C., 2010. Macroecological signals of species interactions in the Danish avifauna. Proceedings of the National Academy of Sciences 107, 5030ï 5035.

Griffis-Kyle, K.L., Beier, P. 2003. Small isolated aspen stands enrich bird communities in southwestern ponderosa pine forests. Biological Conservation, 110, 375-385.

Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. Journal of Evolutionary Biology 24, 699ï 711.

Hagen, M., Kissling, W.D., Rasmussen, C., De Aguiar, M.A.M., Brown, L.E., Carstensen, D.W., Alves-Dos-Santos, I., Dupont, Y.L., Edwards, F.K., Genini, J., Guimarães, P.R., Jenkins, G.B., Jordano, P., Kaiser-Bunbury, C.N., Ledger, M.E., Maia, K.P., Marquitti, F.M.D., Mclaughlin, Ó., Morellato, L.P.C., OôGorman, E.J., Trøjelsgaard, K., Tylianakis, J.M., Vidal, M.M., Woodward, G., Olesen, J.M., 2012. Biodiversity, species interactions and ecological networks in a fragmented world. Advances in Ecological Research, 46, 89ï 210.

Hampe, A., Petit, R.J., 2005. Conserving biodiversity under climate change: the rear edge matters. Ecology Letters 8, 461ï 467.

Haney, J.C., 1999. Numerical response of birds to an irruption of elm spanworm (Ennomos subsignarius, Geometridae: Lepidoptera) in old-growth forest of the Appalachian Plateau, USA. Forest Ecology and Management 120, 203ï 217.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press.

Hargrove, L., Rotenberry, J.T., 2011. Spatial structure and dynamics of breeding bird populations at a distribution margin, southern California. Journal of Biogeography 38, 1708ï 1716.

Haslem A., Bennett A.F. 2011. Countryside vegetation provides supplementary habitat at the landscape scale for woodland birds in farm mosaics. Biodiversity and Conservation 20, 2225ï 2242.

Hausner, V. H. et al. 2003. Selecting indicator traits for monitoring land use impacts, birds in northern coastal birch forests. Ecol. Appl. 13, 999-1012.

Heikkinen, R.K., Luoto, M., Virkkala, R., Rainio, K. 2004 Effects of habitat cover, landscape structure and spatial variables on the abundance of birds in an agricultural-forest mosaic. Journal of Applied Ecology, 41, 824-835.

Henle, K., Davies K.L., Kleyer M., Margules C., Settele J. 2004. Predictors of species sensitivity to fragmentation. Biodivers. Conserv. 13, 207-251.

Hermy, M., Verheyen, K., 2007. Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. Ecological Research 22, 361ï 371.

Herrando, S., Brotons, L. 2002 Forest bird diversity in Mediterranean areas affected by wildfires, a multi-scale approach. Ecography, 25, 161-172.

Hillebrand, H., Bennett, D.M., Cadotte, M.W. 2008. Consequences of dominance, a review of evenness effects on local and regional ecosystem processes. Ecology, 89, 1510ï 1520.

Hobson, K.A., Bayne, E. 2000. Breeding bird communities in boreal forest of Western Canada, consequences of "unmixing" the mixedwoods. The Condor, 102, 759-769.

Hogstad, O., 2005. Numerical and functional responses of breeding passerine species to mass occurrence of geometrid caterpillars in a subalpine birch forest: a 30-year study. Ibis 147, 77ï 91.

Holmes R.T. 1990. Ecological and evolutionary impacts of bird predation on forest insects, an overview. Stud Avian Biol 13, 6-13.

Holt, R.D., 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. Proceedings of the National Academy of Sciences 106, 19659ï 19665.

Huntley, B., Collingham, Y.C., Willis, S.G., Green, R.E. 2008. Potential impacts of climatic change on European breeding birds. PLoS One, 3, 1-11.

Jansson, G., Angelstam, P. 1999. Threshold levels of habitat composition for the presence of the long-tailed tit (Aegithalos caudatus) in a boreal landscape. Landscape Ecology, 14, 283-290.

Jax, K., 2005. Function and ñfunctioningò in ecology: what does it mean? Oikos 111, 641ï 648.

Jedlicka, J.A., Greenberg, R., Letourneau, D.K., 2011. Avian conservation practices strengthen ecosystem services in California vineyards. PLoS One 6, e27347.

Jenerette, G.D., Shen, W., 2012. Experimental landscape ecology. Landscape Ecology 27, 1237ï 1248.

Jenkins, D.G., Ricklefs, R.E., 2011. Biogeography and ecology: two views of one world. Philosophical Transactions of the Royal Society B: Biological Sciences 366, 2331ï 2335.

Jiguet, Frédéric, Devictor, Vincent, Julliard, Romain, Couvet, Denis, 2012. French citizens monitoring ordinary birds provide tools for conservation and ecological sciences. Acta Oecologica 44, 58ï 66.

Jones, G.A., Sieving, K.E., Jacobson, S.K., 2005. Avian diversity and functional insectivory on North-Central Florida farmlands. Conservation Biology 19, 1234ï 1245.

Jongsomjit, D., Stralberg, D., Gardali, T., Salas, L., Wiens, J., 2013. Between a rock and a hard place: the impacts of climate change and housing development on breeding birds in California. Landscape Ecology 28, 187ï 200.

Jonsson, M., Englund, G., Wardle, D.A., 2011. Direct and indirect effects of area, energy and habitat heterogeneity on breeding bird communities. Journal of Biogeography 38, 1186ï 1196.

Jung, K., Kaiser, S., Böhm, S., Nieschulze, J., Kalko, Elisabeth K. V., 2012. Moving in three dimensions: effects of structural complexity on occurrence and activity of insectivorous bats in managed forest stands. Journal of Applied Ecology 49, 523ï 531.

Kalka, M.B., Smith, A.R., Kalko, E. K. V., 2008. Bats Limit Arthropods and Herbivory in a Tropical Forest. Science 320, 71ï 71.

Kaunisto, S, Valimaki, P, Kortet, R, Koskimaki, J, Harkonen, S, Kaitala, A, Laaksonen, S, Harkonen, L, Ylonen, H 2012 Avian predation on a parasitic fly of cervids during winter, can host-related cues increase the predation risk? Biological Journal of the Linnean Society 106, 275ï 286.

Keil, P., Schweiger, Oliver, Kühn, I., Kunin, W.E., Kuussaari, M., Settele, J., Henle, K., Brotons, Lluís, Peôer, G., Lengyel, S., Moustakas, A., Steinicke, H., Storch, D., 2012. Patterns of beta diversity in Europe: the role of climate, land cover and distance across scales. Journal of Biogeography 39, 1473ï 1486.

Kervyn, T., Libois, R., 2008. The diet of the serotine bat: A Comparison between rural and urban environments. Belgian Journal of Zoology 138.

Kéry, M., 2010. Introduction to WinBUGS for ecologists: A Bayesian approach to regression, ANOVA, mixed models and related analyses.

Kissling, W.D., Field, R., Böhning-Gaese, K., 2008. Spatial patterns of woody plant and bird diversity: functional relationships or environmental effects? Global Ecology and Biogeography 17, 327ï 339.

Kissling, W.D., Dormann, C.F., Groeneveld, J., Hickler, T., Kühn, I., McInerny, G.J., Montoya, J.M., Römermann, C., Schiffers, K., Schurr, F.M., Singer, A., Svenning, J.-C., Zimmermann, N.E., OôHara, R.B., 2012. Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. Journal of Biogeography 39, 2163ï 2178.

Klapwijk, M.J., Ayres, M.P., Battisti, A., Larsson, S., 2012. Assessing the impact of climate change on outbreak potential. Insect outbreaks revisited, 2nd edn. Blackwell Publishing Ltd, Oxford 429ï 450.

Klemola, T., Tanhuanpia, M., Korpimaki, E., Ruohomaki, K. 2002. Specialist and generalist natural enemies as an explanation for geographical gradients in population cycles of northern herbivores. Oikos 99, 83-94.

Knick, S.T., Rotenberry, J.T. 2000. Ghosts of habitats past, contribution of landscape change to current habitats used by shrubland birds. Ecology, 81, 220-227.

Knick, S.T., Rotenberry, J.T., Leu, M., 2008. Habitat, topographical, and geographical components structuring shrubsteppe bird communities. Ecography 31, 389ï 400.

Kristin, A., Patocka, J., 1997. Birds as predators of Lepidoptera, selected examples. Biologia 52, 319-326.

Kunz, T.H., Braun de Torrez, E., Bauer, D., Lobova, T., Fleming, T.H., 2011. Ecosystem services provided by bats. Annals of the New York Academy of Sciences 1223, 1ï 38.

Kupfer, J.A., Malanson, G.P., Franklin, S.B. 2006 Not seeing the ocean for the islands, the mediating influence of matrix-based processes on forest fragmentation effects. Global Ecology and Biogeography, 15, 8-20.

Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91, 299ï 305.

Laliberté, E., Tylianakis, J.M., 2012. Cascading effects of long-term land-use changes on plant traits and ecosystem functioning. Ecology 93, 145ï 155.

Larrère, C., Larrère R. 1997. Du bon usage de la nature, pour une philosophie de lôenvironnement. Aubier, Paris.

Laurance W.F. 2002. Hyperdynamism in fragmented habitats. J Veg Sci, 13, 595ï 602.

Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A., Ewers, R.M., Harms, K.E., Luizão, R.C.C., Ribeiro, J.E., 2007. Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. PLoS One 2, e1017.

Lavergne, S., Evans, M.E.K., Burfield, I.J., Jiguet, F., Thuiller, W., 2012. Are speciesô responses to global change predicted by past niche evolution? Philosophical Transactions of the Royal Society B: Biological Sciences 368, 20120091ï 20120091.

Lefebvre L. 1995. The opening of milk bottles by birds, evidence for accelerating learning rates, but against the wave-of-advance model of cultural transmission. Behavioural Processes 34, 43-54.

Legendre, P., Borcard, D., Peres-Neto, P.R. 2005. Analyzing beta diversity, partitioning the spatial variation of community composition data. Ecological Monographs, 75, 435-450.

Lindenmayer, D.B., Mc Intyre S., Fischer, J. 2003. Birds in eucalypt and pine forests, landscape alteration and its implications for research models of faunal habitat use. Biological Conservation, 110, 45-53.

Lopez, G., Moro, M.J. 1997. Birds of Aleppo pine plantations in south-east Spain in relation to vegetation composition and structure. Journal of Applied Ecology, 34, 1257-1272.

Lugo, A.E., Carlo, T.A., Wunderle, J.M., 2012. Natural mixing of species: novel plant-animal communities on Caribbean Islands. Animal Conservation 15, 233ï 241.

MacArthur R.H., Wilson E.O. 1967. The theory of island biogeography. Monographs in Population Biology, Princeton University Press.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A., Langtimm, C.A. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology, 83, 2248ï 2255.

MacNally, R., 1994. Habitat-specific guild structure of forest birds in south-eastern Australia: a regional scale perspective. Journal of Animal Ecology 988ï 1001.

MacNally, R., Horrocks, G., 2002. Relative influences of patch, landscape and historical factors on birds in an Australian fragmented landscape. Journal of Biogeography 29, 395ï 410.

MacNally, R., Fleishman, E., Bulluck, L.P., Betrus, C.J. 2004 Comparative influence of spatial scale on beta diversity within regional assemblages of birds and butterflies. Journal of Biogeography, 31, 917-929.

Maitner, B.S., Rudgers, J.A., Dunham, A.E., Whitney, K.D., 2012. Patterns of bird invasion are consistent with environmental filtering. Ecography 35, 614ï 623.

Manning A.D., Lindenmayer D.B., Nix H.A. 2004. Continua and Umwelt, novel perspectives on viewing landscapes. Oikos 104, 621-628.

Mäntylä, E., Alessio, G.A., Blande, J.D., Heijari, J., Holopainen, J.K., Laaksonen, T., Piirtola, P., Klemola, T., 2008. From plants to birds: higher avian predation rates in trees responding to insect herbivory. PLoS One 3, e2832.

Mäntylä, E., Klemola, T., Haukioja, E., 2004. Attraction of willow warblers to sawfly-damaged mountain birches: novel function of inducible plant defences? Ecology Letters 7, 915ï 918.

Mäntylä, E., Klemola, T., Laaksonen, T., 2011. Birds help plants: a meta-analysis of top-down trophic cascades caused by avian predators. Oecologia 165, 143ï 151.

Marquis R.J., Whelan C.J. 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. Ecology 75, 2007-2014.

Mason, N.W., Mouillot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111, 112ï 118.

McCollin, D., 1998. Forest edges and habitat selection in birds: a functional approach. Ecography 21, 247ï 260.

McGill, B.J., Nekola, J.C., 2010. Mechanisms in macroecology: AWOL or purloined letter? Towards a pragmatic view of mechanism. Oikos 119, 591ï 603.

McKinney, M.L., Lockwood, J.L., 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in ecology & evolution 14, 450ï 453.

Meynard, C.N., Devictor, Vincent, Mouillot, D., Thuiller, Wilfried, Jiguet, Frédéric, Mouquet, N., 2011. Beyond taxonomic diversity patterns: how do Ŭ, ɓ and ɔ components of bird functional and phylogenetic diversity respond to environmental gradients across France? Global Ecology and Biogeography 20, 893ï 903.

Mols, C.M., Visser, M.E., 2002. Great tits can reduce caterpillar damage in apple orchards. Journal of Applied Ecology 39, 888ï 899.

Mooney KA, Gruner DS, Barber NA, Van Bael SA, Philpott SM, Greenberg R 2010. Interactions among predators and the cascading effects of vertebrate insectivores on arthropod communities and plants. Proc Natl Acad Sci USA 107, 7335-7340.

Moorman, C.E., Bowen, L.T., Kilgo, J.C., Sorenson, C.E., Hanula, J.L., Horn, S., Ulyshen, M.D. 2007. Seasonal diets of insectivorous birds using canopy gaps in a bottomland forest. Journal of Field Ornithologist, 78, 11ï 20.

Moreira, F., Delgado A., Ferreira S., Borralho R., Oliveira N., Inacio M., Silva J.S., Rego, F.C. 2003. Effects of prescribed fire on vegetation structure and breeding birds in young Pinus pinaster stands of northern Portugal. Forest Ecology and Management, 184, 225-237.

Morris, D.W., 2003. Toward an ecological synthesis: a case for habitat selection. Oecologia 136, 1ï 13.

Müller, J., Bußler, H., Goßner, M., Rettelbach, T., Duelli, P., 2008. The European spruce bark beetle Ips typographus in a national park: from pest to keystone species. Biodiversity and Conservation 17, 2979ï 3001.

Müller, J., Mehr, M., Bässler, C., Fenton, M.B., Hothorn, T., Pretzsch, H., Klemmt, H.-J., Brandl, R., 2012. Aggregative response in bats: prey abundance versus habitat. Oecologia 169, 673ï 684.

Najera, A., Simonetti, J.A., 2010. Enhancing Avifauna in Commercial Plantations. Conservation Biology 24, 319ï 324.

Newbold, T., Scharlemann, J.P.W., Butchart, S.H.M., Sekercioglu, C. H., Alkemade, R., Booth, H., Purves, D.W., 2013. Ecological traits affect the response of tropical forest bird species to land-use intensity. Proceedings of the Royal Society B: Biological Sciences 280, 20122131ï 20122131.

Nixon, A.E., Roland, J., 2012. Generalist predation on forest tent caterpillar varies with forest stand composition: an experimental study across multiple life stages. Ecological Entomology 37, 13ï 23.

Norton, M.R., Hannon, S.J., Schmiegelow, F.K.A. 2000 Fragments are not islands, patch vs landscape perspectives on songbird presence and abundance in a harvested boreal forest. Ecography, 23, 209-223.

Nuttle, T., Yerger, E.H., Stoleson, S.H., Ristau, T.E., 2011. Legacy of top-down herbivore pressure ricochets back up multiple trophic levels in forest canopies over 30 years. Ecosphere 2, art4.

Ohlemuller, R., Anderson, B.J., Araujo, M.B., Butchart, S.H.., Kudrna, O., Ridgely, R.S., Thomas, C.D., 2008. The coincidence of climatic and species rarity: high risk to small-range species from climate change. Biology Letters 4, 568ï 572.

Ouin A., Aviron S., Dover J., Burel F. 2004. Complementation/supplementation of resources for butterflies in agricultural landscapes. Agr. Ecosyst. Environ. 103, 473-479.

Paquet J.Y., Vandevyvre X., Delahaye L., Rondeux J. 2006. Bird assemblages in a mixed woodland-farmland landscape, the conservation value of silviculture-dependant open areas in plantation forest. For Ecol Manag 227, 59-70.

Pasher, J., Mitchell, S.W., King, D.J., Fahrig, L., Smith, A.C., Lindsay, K.E., 2013. Optimizing landscape selection for estimating relative effects of landscape variables on ecological responses. Landscape Ecology 28, 371ï 383.

Patten, M.A., Burger, J.C., 1998. Spruce budworm outbreaks and the incidence of vagrancy in eastern North American wood-warblers. Canadian Journal of Zoology 76, 433ï 439.

Pautasso, M., Böhning-Gaese, Katrin, Clergeau, P., Cueto, V.R., Dinetti, M., Fernández-Juricic, E., Kaisanlahti-Jokimäki, M.-L., Jokimäki, J., McKinney, M.L., Sodhi, N.S., Storch, D., Tomialojc, L., Weisberg, P.J., Woinarski, J., Fuller, R.A., Cantarello, E., 2011. Global macroecology of bird assemblages in urbanized and semi-natural ecosystems. Global Ecology and Biogeography 20, 426ï 436.

Pawson, S.M., Brin, A., Brockerhoff, E.G., Lamb, D., Payn, T.W., Paquette, A., Parrotta, J. A., 2013. Plantation forests, climate change and biodiversity. Biodiversity and Conservation, in press.

Peôer, G., van Maanen, C., Turbé, A., Matsinos, Y.G., Kark, S., 2011. Butterfly diversity at the ecotone between agricultural and semi-natural habitats across a climatic gradient. Diversity and Distributions 17, 1186ï 1197.

Pellet, J., Bried, J.T., Parietti, D., Gander, A., Heer, P.O., Cherix, D., Arlettaz, R., 2012. Monitoring butterfly abundance: beyond Pollard walks. PLoS One 7, e41396.

Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. Ecology Letters 9, 741ï 758.

Petit, S., Burel, F., 1998. Effects of landscape dynamics on the metapopulation of a ground beetle (Coleoptera, Carabidae) in a hedgerow network. Agriculture, Ecosystems & environment 69, 243ï 252.

Philpott, S.M., Soong, O., Lowenstein, J.H., Pulido, A.L., Lopez, D.T., Flynn, D.F., DeClerck, F., 2009. Functional richness and ecosystem services: bird predation on arthropods in tropical agroecosystems. Ecological Applications 19, 1858ï 1867.

Pimentel, C., Nilsson, J., 2007. Response of Great Tits Parus major to an irruption of a Pine Processionary Moth Thaumetopoea pityocampa population with a shifted phenology. Ardea 95, 191ï 199.

Pollard E, Yates TJ 1993. Monitoring butterflies for Ecology and Conservation. Chapman & Hall, London

Preston, K.L., Rotenberry, J.T., Redak, R.A., Allen, M.F., 2008. Habitat shifts of endangered species under altered climate conditions: importance of biotic interactions. Global Change Biology 14, 2501ï 2515.

Prodon, R., Lebreton, J.D. 1981. Breeding avifauna of a mediterranean succession, the holm oak series in the Eastern Pyrénées. I-Analysis and modelling of the structure gradient. Oikos, 37, 21-38.

Rebelo, H., Tarroso, P., Jones, G., 2010. Predicted impact of climate change on European bats in relation to their biogeographic patterns. Global Change Biology 16, 561ï 576.

Reino, L., Beja, P., Osborne, P.E., Morgado, R., Fabião, A., Rotenberry, J.T., 2009. Distance to edges, edge contrast and landscape fragmentation: Interactions affecting farmland birds around forest plantations. Biological Conservation 142, 824ï 838.

Rempel, R.S., Francis, C.M., Robinson, J.N., Campbell, M., 2013. Comparison of audio recording system performance for detecting and monitoring songbirds. Journal of Field Ornithology 84, 86ï 97.

Ricklefs, R.E., 2013. Habitat-independent spatial structure in populations of some forest birds in eastern North America. Journal of Animal Ecology 82, 145ï 154.

Ries, L., Sisk, T.D., 2004. A predictive model of edge effects. Ecology 85, 2917ï 2926.

Rodewald PG, Brittingham MC 2004 Stopover habitats of landbirds during fall, use of edge-dominated and early-successional forests. Auk 121, 1040-1055

Rodewald, A.D., Vitz, A.C., 2005. Edge-and area-sensitivity of shrubland birds. Journal of Wildlife Management 69, 681ï 688.

Rowland, H.M., Cuthill, I.C., Harvey, I.F., Speed, M.P., Ruxton, G.D., 2008. Canôt tell the caterpillars from the trees: countershading enhances survival in a woodland. Proceedings of the Royal Society B: Biological Sciences 275, 2539ï 2545.

Sachanowicz K, Wower A, Bashta AT 2006 Further range extension of Pipistrellus kuhlii (Kuhl, 1817) in central and eastern Europe. Acta Chiropterologica, 8, 543ï 548.

Salido, L., Purse, B.V., Marrs, R., Chamberlain, D.E., Shultz, S., 2012. Flexibility in phenology and habitat use act as buffers to long-term population declines in UK passerines. Ecography 35, 604ï 613.

Samaġ P., Grim, T., Hauber, M.E., Cassey, P., Weidinger, K., Evans, K.L., 2013. Ecological predictors of reduced avian reproductive investment in the southern hemisphere. Ecography in press.

Samways, M.J., Lu, S.S. 2007. Key traits in a threatened butterfly and its common sibling, implications for conservation. Biodivers. Conserv. 16, 4095-4107.

Schweiger, O., Maelfait, J.P., Wingerden, W., Hendrickx, F., Billeter, R., Speelmans, M., Augenstein, I., Aukema, B., Aviron, S., Bailey, D., Bukacek, R., Burel, F., Diekötter, T., Dirksen, J., Frenzel, M., Herzog, F., Liira, J., Roubalova, M., Bugter, R., 2005. Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales. Journal of Applied Ecology 42, 1129ï 1139.

Schweiger, O., Settele, J., Kudrna, O., Klotz, S., Kühn, I., 2008. Climate change can cause spatial mismatch of trophically interacting species. Ecology 89, 3472ï 3479.

Sekercioglu, C.H., 2012. Bird functional diversity and ecosystem services in tropical forests, agroforests and agricultural areas. Journal of Ornithology 153, 153ï 161.

Settele, J., Kudrna, O., Harpke, A., Kühn, I., van Swaay, C., Verovnik, R.,Warren, M.,Wiemers, M., Hanspach, J., Hickler, T., Kühn, E., van Halder, I., Veling, K., Vleigenhart, A., Wynhoff, I. & Schweiger, O. 2008. Climatic risk atlas of European butterflies. BioRisk, 1, 1-710.

Shochat, E., Abramsky Z., Pinshow B., 2001. Breeding bird diversity in the Negev, effects of scrub fragmentation by planted forests. Journal of Applied Ecology, 38, 1135-1147.

Sierro, A., Arlettaz, R., 1997. Barbastelle bats (Barbastella spp.) specialize in the predation of moths: implications for foraging tactics and conservation. Acta Oecologica 18, 91ï 106.

Sierro, A., Arlettaz, R., Naef-Daenzer, B., Strebel, S., Zbinden, N., 2001. Habitat use and foraging ecology of the nightjar (Caprimulgus europaeus) in the Swiss Alps: towards a conservation scheme. Biological Conservation 98, 325ï 331.

Silva, L.P. da, Alves, J., Silva, A.A. da, Ramos, J.A., Fonseca, C., 2012. Variation in the Abundance and productive Characteristics of Great Tits Parus major in Forest and Monoculture Plantations. Acta Ornithologica 47, 147ï 155.

Simberloff, D., Martin, J.L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., 2013. Impacts of biological invasions: whatôs what and the way forward. Trends in Ecology & Evolution, in press.

Sinu, P.A., 2011. Avian pest control in tea plantations of sub-Himalayan plains of Northeast India: Mixed-species foraging flock matters. Biological Control 58, 362ï 366.

Sirami, C., Brotons, L., Martin, J.L., 2008. Spatial extent of bird species response to landscape changes: colonisation/extinction dynamics at the community-level in two contrasting habitats. Ecography 31, 509ï 518.

Sirami, C., Nespoulous, A., Cheylan, J.P., Marty, P., Hvenegaard, G.T., Geniez, P., Schatz, B., Martin, J.L., 2010. Long-term anthropogenic and ecological dynamics of a Mediterranean landscape: impacts on multiple taxa. Landscape and Urban Planning 96, 214ï 223.

Skoczylas, D.R., Muth, N.Z., Niesenbaum, R.A., 2007. Contribution of insectivorous avifauna to top down control of Lindera benzoin herbivores at forest edge and interior habitats. Acta Oecologica 32, 337ï 342.

Smith, A.C., Fahrig, L., Francis, C.M., 2011. Landscape size affects the relative importance of habitat amount, habitat fragmentation, and matrix quality on forest birds. Ecography 34, 103ï 113.

Snäll, T., Kindvall, O., Nilsson, J., Pärt, T., 2011. Evaluating citizen-based presence data for bird monitoring. Biological Conservation 144, 804ï 810.

Stevens, V.M., Trochet, A., Van Dyck, H., Clobert, J., Baguette, M., 2012. How is dispersal integrated in life histories: a quantitative analysis using butterflies. Ecology Letters 15, 74ï 86.

Strubbe, D., Broennimann, O., Chiron, F., Matthysen, E., 2013. Niche conservatism in non-native birds in Europe: niche unfilling rather than niche expansion. Global Ecology and Biogeography in press.

Suzuki, M., Miyashita, T., Kabaya, H., Ochiai, K., Asada, M., Kikvidze, Z., 2013. Deer herbivory as an important driver of divergence of ground vegetation communities in temperate forests. Oikos 122, 104ï 110.

Svenning, J.-C., Fløjgaard, C., Baselga, A., 2011. Climate, history and neutrality as drivers of mammal beta diversity in Europe: insights from multiscale deconstruction. Journal of Animal Ecology 80, 393ï 402.

Symondson, W.O.C., Sunderland, K.D., Greenstone, M.H., 2002. Can generalist predators be effective biocontrol agents? Annual Review of Entomology 47, 561ï 594.

Tagmann-Ioset, A, Schaub, M, Reichlin, TS, Weisshaupt, N, Arlettaz R 2012. Bare ground as a crucial habitat feature for a rare terrestrially foraging farmland bird of Central Europe. Acta Oecologica 39, 25-32.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., Jeltsch, F. 2004 Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography, 31, 79-92

Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L., Bishop, J.R.B., Marques, T.A., Burnham, K.P., 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47, 5ï 14.

Thomson, L.J., Macfadyen, S., Hoffmann, A.A., 2010. Predicting the effects of climate change on natural enemies of agricultural pests. Biological Control 52, 296ï 306.

Tscharntke, T., Bommarco, R., Clough, Y., Crist, T.O., Kleijn, D., Rand, T.A., Tylianakis, J.M., van Nouhuys, S., Vidal, S., 2007. Conservation biological control and enemy diversity on a landscape scale. Biological Control 43, 294ï 309.

Tscharntke, T., Sekercioglu, Cagan H., Dietsch, T.V., Sodhi, N.S., Hoehn, P., Tylianakis, J.M., 2008. Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. Ecology 89, 944ï 951.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H., Westphal, C., 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biological Reviews 87, 661ï 685.

Tubelis D.P., Cowling A., Donnelly C. 2004. Landscape supplementation in adjacent savannas and its implications for the design of corridors for forest birds in the central Cerrado, Brazil. Biological Conservation 118, 353-364.

van Halder I., Barbaro L., Corcket E., Jactel H. 2008. Importance of semi-natural habitats for the conservation of butterfly communities in landscapes dominated by pine plantations. Biodiversity and Conservation 17, 1149-1169.

van Wilgenburg, S.L., Mazerolle D.F., Hobson, K.A. 2001. Patterns of arthropod abundance, vegetation and microclimate at boreal forest edge and interior in two landscapes: implications for forest birds. Écoscience 8, 454-461.

Villard, M.A., Schmiegelow, F.K.A., Trzcinski, M.K. 2007. Short-term response of forest birds to experimental clearcut edges. Auk 124, 828-840.

Visser, M.E., te Marvelde, L., Lof, M.E., 2012. Adaptive phenological mismatches of birds and their food in a warming world. Journal of Ornithology 153, 75ï 84.

Wahlberg N., Klemetti T., Hanski I. 2002. Dynamic populations in a dynamic landscape, the metapopulation structure of the marsh fritillary butterfly. Ecography 25, 224-232.

Warren, M.S. et al. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature 414, 65-69.

Waters, D.A., 2003. Bats and moths: what is there left to learn? Physiological Entomology 28, 237ï 250.

Wells, K., OôHara, R.B., Böhm, S.M., Gockel, S., Hemp, A., Renner, S.C., Pfeiffer, S., Böhning-Gaese, K., Kalko, E.K.V., 2012. Trait-dependent occupancy dynamics of birds in temperate forest landscapes: fine-scale observations in a hierarchical multi-species framework. Animal Conservation 15, 626ï 637.

Wenny, D.G., DeVault, T.L., Johnson, M.D., Kelly, Dave, H. Sekercioglu, C., Tomback, D.F., Whelan, C.J., 2011. The need to quantify ecosystem services provided by birds. The Auk 128, 1ï 14.

Whelan, C.J., 2001. Foliage structure influences foraging of insectivorous forest birds: an experimental study. Ecology 82, 219ï 231.

Whelan, C.J., Wenny, D.G., Marquis, R.J., 2008. Ecosystem services provided by birds. Annals of the New York Academy of Sciences 1134, 25ï 60.

Whittaker, R.J., Willis, K.J., Field, R. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. Journal of Biogeography, 28, 453-470.

Whittaker, R.J., Araújo, M.B., Paul, J., Ladle, R.J., Watson, J.E., Willis, K.J., 2005. Conservation biogeography: assessment and prospect. Diversity and Distributions 11, 3ï 23.

Wiens, J.A., 1995. Habitat fragmentation: island vs landscape perspectives on bird conservation. Ibis 137, S97ï S104.

Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V., Damschen, E.I., Jonathan Davies, T., Grytnes, J.A., Harrison, S.P., Hawkins, B.A., Holt, R.D., McCain, C.M., Stephens, P.R., 2010. Niche conservatism as an emerging principle in ecology and conservation biology. Ecology Letters 13, 1310ï 1324.

Williams-Guillen, K., Perfecto, I., Vandermeer, J., 2008. Bats Limit Insects in a Neotropical Agroforestry System. Science 320, 70.

Windmill, J.F.C., Jackson, J.C., Tuck, E.J., Robert, D., 2006. Keeping up with Bats: Dynamic Auditory Tuning in a Moth. Current Biology 16, 2418ï 2423.

Wu, J., 2013. Key concepts and research topics in landscape ecology revisited: 30 years after the Allerton Park workshop. Landscape Ecology 28, 1ï 11.

Yoccoz, N.G., Nichols, J.D., Boulinier, T., 2001. Monitoring of biological diversity in space and time. Trends in Ecology & Evolution 16, 446ï 453.

Zamora, R., Hódar, J.A., Matías, L., Mendoza, I., 2010. Positive adjacency effects mediated by seed disperser birds in pine plantations. Ecological Applications 20, 1053ï 1060.

Zuur, A.F., Ieno I.E., Walker, N.J., Saveliev, A.A. & Smith, G.M. 2009. Mixed effects models and extensions in ecology with R. Springer.

Annexe 1 Modalités des traits de vie utilisées pour les oiseaux (chap. 2.2.2)

Bird species traits	Categories	Code
National trend	1. Increasing or stable	T_increa
	2. Recently declining	T_recdec
	3. Long-term declining	T_londec
National rarity (% range)	1. > 95 %	NR_1
	2. 75-95 %	NR_2
	3. < 75 %	NR_3
Regional rarity (% range)	1. > 95 %	RR_1
	2. 75-95 %	RR_2
	3. < 75 %	RR_3
Biogeographic position	1. Mediterranean or atlantic	B_south
	2. Widespread	B_widesp
	3. Northern or central	B_north
Foraging technique	1. Ground prober	F_grprob
	2. Ground gleaner	F_grglean
	3. Understory gleaner	F_unglea
	4. Canopy foliage gleaner/hawker	F_caglea
	5. Bark forager	F_barfor
Diet	1. Insectivore	D_insect
	2. Mixed diet	D_mixed
	3. Granivore	D_graniv
Nest location	1. Cavity (tree or others)	N_cavity
	2. Open in tree	N_optree
	3. Open in shrub	N_opshru
	4. Open on ground	N_opgrou
Home-range size	1. Small (< 1 ha)	H_small
	2. Medium (1-4 ha)	H_mediu
	3. Large (> 4 ha)	H_large
Clutch size	1. Ò3 eggs	CS_1
	2. 4 eggs	CS_2
	3. 5-6 eggs	CS_3
	4. Ó7 eggs	CS_4
Body mass (g)	1. Ò14 g	BM_1
	2. 15-24 g	BM_2
	3. 25-49 g	BM_3
	4. Ó50 g	BM_4
Migration status	1. Resident	M_resid
	2. Temperate migrant	M_temmi
	3. Tropical migrant	M_tromig
Average laying date	1. March	L_march
	2. Early April	L_earapr
	3. Late April	L_latapr
	4. Early May	L_earmay
	5. Late May and June	L_latmay

Annexe 2 Modalités des traits de vie utilisées pour les papillons (chap. 2.2.2)

Butterfly species traits	Categories	Code
National trend	1. Stable	T_stable
	2. 1-10 % decline	T_dec1
	3. 10-25 % decline	T_dec2
	4. 25-55 % decline	T_dec3
National rarity (% range)	1. > 95 %	NR_1
	2. 75-95 %	NR_2
	3. < 75 %	NR_3
Regional rarity (% range)	1. 40-85 local districts	RR_1
	2. 20-40 local districts	RR_2
	3. 1-20 local districts	RR_3
Biogeographic position	1. Mediterranean or atlantic	B_south
	2. Widespread	B_widesp
	3. Northern or central	B_north
Polyphagy level	1. Monophagous	P_monoph
	2. Strongly oligophagous	P_oligo1
	3. Oligophagous	P_oligo2
	4. Polyphagous	P_polyph
Host plant type	1. Grasses	H_grass
	2. Herbaceous dicots	H_dicot
	3. Shrub or tree	H_shrub
Overwintering	1. Eggs or young caterpillar	O_eggs
	2. Mature caterpillar	O_caterp
	3. Chrysalis or imago	O_chrysa
Population density (ind.ha^{-1})	1. Low (< 4 ind.ha^{-1})	D_low
	2. Medium (4-16 ind.ha^{-1})	D_medium
	3. High (> 16 ind.ha^{-1})	D_high
Number of eggs	1. < 100 eggs	NE_1
	2. 100-200 eggs	NE _2
	3. 200-400 eggs	NE _3
	4. > 400 eggs	NE _4
Wing length (mm)	1. Ò14 mm	WL_1
	2. 15-19 mm	WL _2
	3. 20-24 mm	WL _3
	4. Ó25 mm	WL _4
Mobility	1. Sedentary	M_sedent
	2. Rather sedentary	M_ratsed
	3. Mobile	M_mobile
Flying period	1. 1 generation (spring)	F_1spring
	2. 1 generation (summer)	F_1summ
	3. 2 generations	F_2gener
	4. 3 generations	F_3gener

Annexe 3 Oiseaux et chiroptères insectivores prédateurs potentiels ou avérés de la processionnaire du pin *T. pityocampa* dans sa zone de distribution circum-mediterranéenne. Les périodes de prédation sont indiquées par mois (II = février, II = mars, etc..) ainsi que les stades du cycle prédatés, la taille et le poids du corps, la stratégie de ó foragingô et le degré de spécialisation alimentaires des espèces (modifié de Barbaro et al. in press).

Vertebrate species	**Body size (cm)**	**Predated stages**	**Period**	**Foraging methods**	**Diet specialization**
Birds					
Clamator glandarius	35-39 (130-192g)	Late-instar larvae	II-IV	Ground / canopy gleaning	Specialist (PPM is up to 100% of diet)
Cuculus canorus	32-34 (95-140g)	Late-instar larvae	III-IV	Ground / canopy gleaning	Specialist (hairy larvae are 75% of diet)
Caprimulgus europaeus	24-28 (51-101g)	Moths	VII-VIII	Aerial hawking	Specialist (moths are 80-90% of diet)
Caprimulgus ruficollis	28-32 (60-120g)	Moths	VII-VIII	Aerial hawking	Specialist (moths are a large part of diet)
Upupa epops	26-32 (47-87g)	Pupae, larvae	III-VI	Ground probing / gleaning	Specialist (PPM pupae are up to 70% of diet)
Parus major	14 (14-22g)	Eggs, larvae	IX-V	Canopy / ground gleaning	Generalist (PPM in up to 60-90% stomachs)
Periparus ater	11.5 (9.5-12.5g)	Eggs, larvae	X-IV	Canopy gleaning	Generalist (PPM in up to 66% stomachs)
Lophophanes cristatus	11.5 (10-13g)	Eggs, larvae	IX-IV	Canopy gleaning	Generalist (no data)
Bats					
Barbastella barbastellus	4.5-6 (6-14g)	Moths	VII-VIII	Aerial hawking	Specialist (moths are up to 90% of diet)
Plecotus austriacus	4.1-5.8 (6-14g)	Moths	VII-VIII	Aerial hawking or gleaning	Specialist (moths are up to 90% of diet)
Plecotus auritus	4.2-5.3 (6-14g)	Moths	VII-VIII	Canopy and ground gleaning	Generalist (moths are 20-100% of diet)
Pipistrellus kuhlii	3.9-5.5 (5-10g)	Moths	VII-VIII	Aerial hawking	Generalist (moths are 15-38% of diet)
Eptesicus serotinus	6.3-9 (18-35g)	Moths	VII-VIII	Aerial hawking	Generalist (moths are 10-15 % diet)

Résumé

Une question centrale en écologie du paysage et en biogéographie de la conservation est d’identifier les processus écologiques sous-tendant la distribution des assemblages d’espèces à différentes échelles spatiales. La première partie de ce travail cherche à comprendre les patrons de réponses multi-échelles des communautés d’oiseaux et de lépidoptères à la structure et à la composition de l’habitat dans les paysages forestiers fragmentés. La seconde partie porte sur le rôle structurant des interactions trophiques entre lépidoptères et oiseaux insectivores au sein de ces paysages hétérogènes, dans une perspective de service écosystémique de régulation de l’herbivorie par l’avifaune prédatrice. Les communautés d’oiseaux et de lépidoptères forestiers s’organisent de manière hiérarchisée selon plusieurs échelles spatiales emboîtées en fonction d’une combinaison de facteurs bioclimatiques, abiotiques et biotiques. A échelle large, l’hétérogénéité spatiale des habitats dans les mosaïques paysagères est le facteur-clé expliquant la composition taxonomique et fonctionnelle des communautés d’oiseaux et de papillons. A échelle plus fine, la structure et la qualité des habitats, ainsi que les effets de lisières entre forêts et milieux ouverts, affectent la réponse de l’avifaune et de la lépidofaune forestières par guildes trophiques et groupes fonctionnels. La seconde partie aborde la relation trophique existant entre lépidoptères herbivores et oiseaux insectivores comme un élément déterminant, mais souvent négligé, de leurs distributions spatiales et de leurs variations d’abondance à différentes échelles. L’analyse des réponses numériques et fonctionnelles d’un oiseau insectivore spécialiste et d’un généraliste à la densité d’un défoliateur forestier montre qu’elle est un prédicteur important de l’abondance de l’espèce spécialiste en période de reproduction et de l’espèce généraliste en hiver. L’intensité de prédation par les oiseaux insectivores est ensuite mesurée de manière directe et indirecte dans une série de dispositifs expérimentaux. Les effets de lisière entre forêts et milieux ouverts, la fragmentation forestière et la diversité du paysage favorisent l’insectivorie avienne et la diversité fonctionnelle des communautés d’oiseaux. Enfin, l’existence d’interactions tritrophiques significatives entre oiseaux insectivores, lépidoptères herbivores et plantules d’essences forestières est démontrée expérimentalement. Ce travail apporte ainsi une contribution à la mise en évidence d’un lien entre conservation des communautés d’oiseaux et rôle fonctionnel de l’insectivorie avienne, vue comme un important service écosystémique, dans les paysages forestiers fragmentés et hétérogènes.

Abstract

Focusing on the ecological processes underlying the distribution patterns of species assemblages at different spatial scales is a central question for landscape ecology and conservation biogeography. In the present work, we first aim at understanding the multi-scale response patterns of bird and lepidopteran communities to habitat structure and composition in fragmented forest landscapes. Second, we investigate the structuring role of trophic interactions between lepidopteran and insectivorous birds within these mosaic landscapes, in an ecosystem service perspective of herbivory control by avian predators. Bird and lepidopteran communities are hierarchically organized at several nested spatial scales according to a combination of bioclimatic, abiotic and biotic factors. At meso-scale, the key driver of taxonomical and functional composition of bird and butterfly communities is the spatial heterogeneity of habitat distribution in landscape mosaics. At smaller scale, trophic guilds and functional groups of forest avifauna and lepidofauna are affected by habitat quality and structure as well as edge effects between forests and open habitats. In the second part, we investigate the trophic interaction between herbivorous lepidoptera and insectivorous birds as a critical, albeit often neglected, factor underlying their spatial distributions and abundance levels at various spatial scales. Numerical and functional responses of specialist and generalist insectivorous birds to the density of a key forest-defoliating moth are significant predictors of the spatial distribution of specialist birds during the breeding season and the winter abundance of generalist birds. We further measure direct and indirect effets of avian insectivory through model predation rates and bird exclusion experiments at stand and landscape scales. Bird insectivory and functional diversity are both enhanced by forest edge effects, native forest fragmentation and landscape diversity. Finally, we demonstrate significant top-down tritrophic interactions between insectivorous birds, herbivorous lepidoptera and tree seedlings. The present work contributes to building a bridge between the conservation of diverse bird communities and the functional role of avian insectivory, seen as a major ecosystem service provided by birds, in fragmented and heterogeneous forest landscapes.