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De la continuité écologique des corridors rivulaires

K. van Looy

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K. van Looy. De la continuité écologique des corridors rivulaires. Sciences de l'environnement. HDR, Université de Lyon I, 2015. tel-02601734

HAL Id: tel-02601734

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MEMOIRE

D'HABILITATION A DIRIGER DES RECHERCHES
DE LA CONTINUITE ECOLOGIQUE DES CORRIDORS
RIVULAIRES



Mémoire présenté devant l'Université Lyon I
Soutenu à Irstea Lyon le 10/3/2015 | par Kris Van Looy

MEMOIRE

présenté devant
L'UNIVERSITE Lyon I

par
Kris Van Looy

pour obtenir
L'HABILITATION A DIRIGER DES RECHERCHES

DE LA CONTINUITÉ ECOLOGIQUE DES CORRIDORS RIVULAIRES

Soutenu le 10/3/2015 devant la commission d'examen :

Eric Tabacchi, Laboratoire d'écologie fonctionnelle et environnement, Université Paul Sabatier,
Toulouse

Gudrun Bornette, Laboratoire Chronoenvironnements, Université de Franche-Comté, Besançon

Pierre Marmonier, Laboratoire d'Ecologie des Hydrosystèmes Naturels et Anthropisés, Université
Lyon I

David Gilvear, Research Group River Science, School of Geography, Earth and Environmental
Sciences, University Plymouth, Great Britain

Patrick Meire, Research Group Ecosystem Management, University of Antwerp, Belgium

**Direction de la recherche
et des études doctorales (D.R.E.D.)
Service des Etudes Doctorales**
Bâtiment Atrium
43, Bd du 11 Novembre 1918
69622 VILLEURBANNE cedex

Affaire suivie par : Angélique CLEMENTE
Tél. : 04 72 43 27 45
Courriel : angelique.clemente@univ-lyon1.fr

Villeurbanne, le 26 février 2015

Monsieur Kris VAN LOOY
La Croix Blanche
69770 Chambost-Longessaigne

Monsieur,

Conformément à l'article 5 de l'arrêté du 23 novembre 1988 modifié relatif à l'Habilitation à Diriger des Recherches et après avoir pris connaissance des rapports établis par

- **Madame Gudrun BORNETTE**
- **Monsieur Pierre MARMONIER**
- **Monsieur Eric TABACCHI**

J'ai l'honneur de vous faire connaître que je vous autorise à présenter l'Habilitation à Diriger des Recherches devant le jury suivant :

- **Madame Gudrun BORNETTE**, Directeur de Recherche, UFR des Sciences et Techniques, Université de Franche-Comté
- **Monsieur David GILVEAR**, Professeur, School of Geography-Earth and Environmental Sciences, University Plymouth, Angleterre
- **Monsieur Pierre MARMONIER**, Professeur des Universités, CNRS – UMR 5023- LEHNA, Université Claude Bernard Lyon 1
- **Monsieur Patrick MEIRE**, Professor at Ecosystem, Management Research Group, University of Antwerp, Belgique
- **Monsieur Eric TABACCHI**, Professeur des Universités, Laboratoire d'écologie fonctionnelle et environnement, Université Paul Sabatier, Toulouse

.../...

Je vous rappelle que vous devez adresser à chaque membre du jury le dossier que vous jugez utile.

Je vous prie de croire, Monsieur, à l'assurance de mes sentiments distingués.

Le Président de l'Université Claude Bernard Lyon 1,

Pour le Président ex par Délégation
Le Vice Président du Conseil d'Administration

François-Noël GILLY

Hamda BEN HADID



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Avant-propos et remerciements

La première partie de ce mémoire est consacré à la présentation de mes activités d'encadrement et d'organisation des recherches, avec les listes des projets, encadrements, publications et un résumé en Français des orientations et approches des travaux effectués depuis ma thèse doctorale. Après, dans une deuxième partie, les raisonnements et orientations de mes travaux jusqu'à présent et les pistes pour le futur seront présentés dans quelques chapitres rédigés en Anglais. Chaque chapitre présente les conclusions et perspectives sur un de mes thèmes de recherche. Pour la troisième partie, j'ai choisi d'intégrer mes articles les plus significatifs dans cette synthèse, permettant de présenter le panorama de mes recherches.

Je tiens à remercier tous ceux qui m'ont inspiré et orienté dans cette piste de recherche : tous mes anciens collègues de l'Inbo (institut de recherche de nature et forêts) ; tous ces gens autour du projet de restauration sur la Meuse ; et surtout mes collègues du Laboratoire d'Hydroécologie Quantitative, une équipe exceptionnelle, avec laquelle j'aimerais bien poursuivre les travaux entamés. Bien sûr l'Irstea, institut national de recherche en sciences et technologies pour l'environnement et l'agriculture. Centre d'excellence qui est focalisé sur 3 défis sociétaux : la gestion durable des eaux et des territoires, les risques naturels et la qualité environnementale. Défis et domaines de recherche auxquels je me suis inscrit depuis longtemps. Bien inséré dans le paysage de la recherche française et européenne, l'Irstea m'a offert des opportunités inédites de mener des recherches en appui aux politiques publiques et en partenariat avec des experts mondiaux. Il me reste bien évidemment à remercier la personne qui à elle seul porte la plus grande stimulation et part de ces travaux ; je veux dédier cet ouvrage à Anouck.

Partie 1. Parcours de recherche et d'encadrement

1. Parcours de direction de recherches et d'encadrement

Après ma thèse (06/2006), je suis resté sur mon poste de Chargé de Recherche à l'Inbo, Institut de recherche pour la conservation de la nature et des forêts. J'ai poursuivi ma tâche de coordinateur du projet de recherche sur le projet de restauration écologique sur la Meuse mitoyenne entre la Belgique et les Pays-Bas, pour lequel j'ai surtout contribué à l'élaboration des projets de suivis intégrées (sédiments, hydrologie, milieux aquatiques, milieux terrestres lit majeur) entre 2006 et 2010.

En plus, plusieurs travaux d'implémentation de la Directive Cadre Eau demandaient une coordination au sein de notre institut (j'ai pris la coordination sur les sujets des DCE et Directive Habitats pour les Cours d'eau et Vallées alluviales au niveau de l'Inbo entre 2007-2010), et du groupe de travail Ecologie de la Commission Internationale de la Meuse que je présidais. Sur ces différents niveaux, j'ai réussi à construire et encadrer des projets de définition des objectifs pour la Meuse Mitoyenne et ses projets de restauration (encadrement A. Van Braeckel 2006-2010, E. Lommelen 2009-2010), pour les lacs et bras morts dans la plaine alluviale (K. Lock 2006-2007, G. Louette 2008-2009), pour les cours d'eau en région Flamande (A. Leyssen 2006-2009), pour la restauration écologique au niveau du bassin de la Meuse (inventaire restauration écologique (2008) et plan de gestion des grands migrateurs (2010) et les suivis long-terme de la qualité biologique de la Meuse (Usseglio-Polatera & Beisel 2008). Quelques stagiaires sont encadrés sur les suivis écologiques des développements de forêts alluviales (M. Van Hellemont 2007-2008, K. Kenzeler 2008-2009) et des recolonisations des Carabidae (E. Lommelen 2008), et quelques thèses sur ces projets (co-encadrement et stimulation des recherches de K. Lambeets sur les arthropodes et de R. Pasmans pour les suivis de poissons). Pour illustrer ces travaux, en grande partie résultant dans des rapports scientifiques pour les administrations contractants, le cadre ci-dessous reprend les titres principaux.

Leyssen, A.; Denys, L.; Schneiders, A.; Van Looy, K.; Packet, J.; Vanhecke, L. (2006). Reference conditions and evaluation methods for biotic quality elements and development of monitoring strategy for the WFD. Reports Inbo 2006(9). Brussel. 127 pp.

Lock, K.; Van Wichelen, J.; Packet, J.; Simoens, I.; Van Looy, K.; Louette, G.; Warmoes, T.; Denys, L.; Leyssen, A. (2007). Defining ecological objectives for water bodies: Lakes. Reports Inbo, 2007(51). Brussel. 192 pp.

Van Braeckel, A.; Van Looy, K. (2007). Ecological effects of restoration measures along the Common Meuse. Reports Inbo, 2007(52). Brussel. 106 pp.

Van Braeckel, A.; Van Looy, K. (2007). River restoration Common Meuse : evaluation of management and restoration measures in a model. *Water: Journal of Integrated Water management* 30

Van Looy, K.; Martens, K.; Huybrechts, W.; Decler, K.; Meire, P.; Van den Bergh, E.; Schneiders, A. (2007). Ecological restoration of running waters in Flanders; Where are we now ? *Water: Journal of Integrated Water management* 30.

Van Looy, K. (2007). Dynamic prediction of river restoration. *Water: Journal of Integrated Water Management* 30.

Leyssen, A.; Adriaens, P.; Denys, L.; Packet, J.; Schneiders, A.; Van Looy, K.; Vanhecke, L. (2008). Application of biotic assessment methods for Flemish intercalibration sites according to the EU WFD: partim macrophytes. Conservation status of the Natura 2000 habitats and species. Reports Inbo, 2008(28)

Leyssen, A.; Van Looy, K.; Vandevoorde, B.; Van Landuyt, W.; Paelinckx, D. (2008). Conservation status of the Natura 2000 freshwater habitats for the Belgian Atlantic region, in: Paelinckx, D. et al. (Ed.) (2008). Conservation status of the Natura 2000 habitats and species. Reports Inbo, 2008(15): pp. 22

Leyssen, A.; Van Looy, K.; Vandevoorde, B.; Van Landuyt, W.; Paelinckx, D. (2008). Conservation status of the Natura 2000 habitat 3260 (Water courses of plain to montane levels with the Ranunculion fluitantis and Callitriche-Batrachion vegetation), habitat 3270 (Rivers with muddy banks with Chenopodium rubri p.p. and Bidens p.p. vegetation), habitat 3150 (Natural eutrophic lakes with Magnopotamion or Hydrocharition-type vegetation), habitat 3160 (Natural dystrophic lakes and ponds), habitat 3110 (Oligotrophic waters containing very few minerals of sandy plains (Littorelletalia uniflorae), habitat 3140 (Hard oligo-mesotrophic waters with benthic vegetation of Chara spp.) for the Belgian Atlantic region, in: Paelinckx, D. et al. (Ed.) (2008). Conservation status of the Natura 2000 habitats and species. Reports Inbo, 2008(15)

Demolder, H.; Van Landuyt, W.; Wouters, J.; Van Looy, K.; Paelinckx, D. (2008). Conservation status of the Natura 2000 habitat 6510 (Lowland hay meadows (Alopecurus pratensis, Sanguisorba officinalis)) for the Belgian Atlantic region, in: Paelinckx, D. et al. (Ed.) (2008). Conservation status of the Natura 2000 habitats and species. Reports Inbo, 2008(15)

Demolder, H.; Delescaille, L.M.; Van Landuyt, W.; Wouters, J.; Van Looy, K.; Paelinckx, D. (2008). Conservation status of the Natura 2000 natural and semi-natural grassland habitats for the Belgian Atlantic region, in: Paelinckx, D. et al. (Ed.) (2008). Conservation status of the Natura 2000 habitats and species. Reports Inbo, 2008(15): pp. 20

Van Looy, K.; Wouters, J.; Schneiders, A.; Denys, L.; Packet, J.; Decler, K.; Adriaens, P.; Van Hoydonk, G. (2008). Objectives for Integrated water management (DIW-KRW) and Natura2000 : ecological criteria protected habitat types and species. Reports Inbo, 2008(42). Brussel. 53 pp.

Van Looy, K.; Denys, L.; Schneiders, A. (2008). Methods for objective definition Maximum and Good Ecological Potential (MEP-GEP) for modified water bodies. Reports Inbo, R.2008.12. INBO: [s.l.]. 20 pp.

Van Looy, K. (2008). Nature restoration measure evaluation Common Meuse phase 2. Reports Inbo, 2008(19). Brussel. 31 pp.

Van Looy, K.; Lommelen, E. (2008). Defragmentation at the border : development of a management vision for Kempen-Broek. *Natuur.Focus* 7(3): 93-99

Van Looy, K.; Van Braeckel, A. (2008). Nature restoration measure evaluation Common Meuse phase 3. Reports Inbo, 2008(6). Brussel. 58 pp.

Van Looy, K.; Kurstjens, G.; Peters, B. (2009). Maas in view : results of 15 years of ecological restoration. 150 pp.

Van Looy, K.; Van Braeckel, A. (2009). Nature restoration measure evaluation Common Meuse phase 4. Reports Inbo, 2009(6). Instituut voor Natuur- en Bosonderzoek: Brussel. 57 pp.

Van Looy, K. (2009). Conservation of habitats in the Common Meuse valley. Reports Inbo, 2009(14). Instituut voor Natuur- en Bosonderzoek: Brussel. 89 pp.

Van Looy, K. (2009). Sediment management plan Common Meuse. Reports inbo, 2009(15). Instituut voor Natuur- en Bosonderzoek: Brussel. 44 pp.

Van Looy, K. (2010). Investigation of pioneer conditions in the Meuse valley: Creating optimal recruitment and restoration situations for floodplain grasslands. Reports Inbo, 2010(20). Brussel. 66 pp.

Pour approfondir les connaissances sur les potentiels de restauration des populations d'espèces menacées ou fragmentées, nous avons construit un projet de recherche partenarial avec l'université de Louvain (Olivier Honnay) de 2006 à 2010 (fondées par le FWO, le ANR Belge), avec notre labo d'analyse génétique (Peter Breyne).

Ce projet a contribué à l'encadrement de trois thèses également (K. Nackaerts, K. Helsen et K. Vandepitte). Kris Nackaerts a essayé avec des techniques méta-analytiques de révéler les patterns généraux de la diversité génétique des plantes le long des cours d'eau, Kenny Helsen a regardé plus sur les aspects de restauration écologique pour les populations (et leur génétique), en particulier sur *Origanum vulgare* encore. Katrien Vandepitte a continué les recherches sur la diversité génétique de l'espèce de vocation invasive *Sisymbrium austriacum*, jusqu'aux analyses des 'genomics' et adaptations génétiques.

Jacquemyn, H., Honnay, O., Van Looy, K. & Breyne, P. 2006. Spatio-temporal structure of genetic variation of a spreading plant metapopulation on dynamic riverbanks along the Meuse River. *Heredity*, 96: 471-478.

Van Looy, K., Jacquemyn, H., Breyne, P. & Honnay, O. 2009. Effects of flood events on the genetic structure of riparian populations of the grassland plant *Origanum vulgare*. *Biological Conservation*, 142: 870-878.

Honnay, O., Jacquemyn, H., Van Looy, K., Vandepitte, K., Breyne, P. (2009). Temporal and spatial genetic variation in a metapopulation of the annual *Erysimum cheiranthoides* on stony river banks. *Journal of Ecology*, 97 (1), 131-141.

Jacquemyn H., Van Looy, K., Breyne, P. & Honnay O. 2009. The Meuse River as a corridor for range expansion of the plant species *Sisymbrium austriacum*: evidence for long-distance seed dispersal. *Biological Invasions*, 12: 553-561.

Honnay Olivier; Jacquemyn Hans; Nackaerts Kris; Van Looy Kris 2010. Patterns of population genetic diversity in riparian and aquatic plant species along rivers. *Journal of Biogeography* 37: 1730-1739.

Van Looy Kris; Honnay Olivier; Breyne Peter 2011. Adaptive strategy of a spreading gynodioecious plant species (*Origanum vulgare*, Labiatae) in a riparian corridor. *Plant Ecology and Evolution* 144: 138-147.

Vandepitte, K., Honnay, O., Breyne, P., Mergeay, J., Roldan-Ruiz, I., De Meyer, T. (2013). SNP discovery using Paired End RAD-tag sequencing on pooled genomic DNA of *Sisymbrium austriacum* (Brassicaceae). *Molecular ecology resources*, 13 (2), 269-75.

Helsen, K., Jacquemyn, H., Hermy, M., Vandepitte, K., Honnay, O. (2013). Rapid buildup of genetic diversity in founder populations of the gynodioecious plant species *Origanum vulgare* after semi-natural grassland restoration. *PLoS One*, 8 (6), e67255.

De Kort, H., Vandepitte, K., Honnay, O. (2013). A meta-analysis of the effects of plant traits and geographical scale on the magnitude of adaptive differentiation as measured by the difference between QST and FST. *Evolutionary Ecology*, 27, 1081-1097.

Vandepitte, K., Gristina, A., Meekers, T., De Hert, M., Roldan-Ruiz, I., Honnay, O. (2012). Restoration facilitated recolonization decreased population genetic variation of a terrestrial orchid species. *Molecular Ecology*, 21 (17), 4206-4215.

Vandepitte, K., De Meyer, T., Helsen, K., Van Acker, K., Roldan-Ruiz, I., Mergeay, J., Honnay, O. (2014). Rapid genetic adaptation precedes the spread of an exotic plant species. *Molecular Ecology*, 23, 2157-2164.

Début 2010, j'ai fait une réponse positive à l'invitation d'Yves Souchon de postuler pour le poste d'Accueil de Haut Niveau à l'Irstea de Lyon. Question d'élargir mes horizons et retrouver les possibilités et défis de la recherche. L'Inbo en restructuration vers un service d'appui, ne pouvait plus m'offrir l'opportunité de poursuivre les recherches sur la Meuse, ni d'autres perspectives de recherche.

En intégrant l'équipe du Laboratoire d'Hydroécologie Quantitative (LHQ) j'ai trouvé un groupe de chercheurs bien munis pour répondre à des questions de fonctionnement et gestion des écosystèmes, épaulé par un staff d'ingénierie gérant de grosses bases de données nationales et construisant des couches renseignant les pressions multiples des échelles bassins versants aux échelles plus locales du tronçon. Le groupe était prêt à entamer des recherches intégrant des disciplines de l'hydromorphologie, chimie, analyse spatiale et modélisation.

Avec deux thésards en fin de trajet et début de poste permanent dans l'équipe (Thierry Tormos & Jérémy Piffady), et l'ensemble de l'équipe qui voulait progresser vers des recherches et une valorisation scientifique des travaux réalisés, j'ai toute de suite intégré et participé à l'animation scientifique de ce collectif. Dans une très bonne interaction intellectuelle, j'ai pris un rôle moteur de chercheur publiant et à instiller une culture de publications scientifiques. Avec Thierry, j'ai continué les recherches sur les continuités écologiques, en élargissant vers des thématiques des espèces cibles et des réseaux écologiques (lien vers la trame verte et bleu). Avec Jérémy, on a construit le projet pluridisciplinaire d'approche risque (avec des modélisations et réseaux Bayésiens à la base) pour les écosystèmes de cours d'eau, à travers les altérations hydromorphologiques (projet Syrah_CE), les pesticides (projet Arpèges), et récemment l'eutrophisation (Euridyce).

Depuis 2011, j'ai enthousiasmé Marta Prieto-Montes dans son travail d'harmonisation des séries temporelles des chroniques long-termes de macro-invertébrés, et j'ai dirigé ses analyses afin d'identifier les mécanismes des changements des communautés au niveau de la France pour les dernières décennies. Les résultats j'ai intégrés dans quelques manuscrits soumis à 'Oikos' et 'Climatic Change'. Pour faire la suite de ces analyses, nous avons eu l'occasion d'embaucher Mathieu Floury, qui venait de finir sa thèse sur des chroniques biotiques de la Loire. Maintenant, j'encadre les analyses de Mathieu dans cette démarche d'identification des tendances régionales et des hypothèses sur la résilience expliqué plus loin dans ce dossier. Pour l'avenir, nous estimons d'arriver à une analyse encore beaucoup plus poussée sur ces questions avec des méthodes de macro-écologie et méta-communautés. Nouveaux projets et collaborations internationaux sont proposés pour analyser ces aspects de résilience des communautés biotiques des cours d'eau (CESAB, ANR, ISRS, BIODIVERSA). Depuis 2014 je suis membre du 'board of directors' de la International Society of River Science, qui nous a permis d'intensifier les contacts avec des collègues mondiales sur ces thématiques.

Nouvelle thématique qu'on a abordé avec l'équipe depuis deux ans, c'est la thématique de restauration des cours d'eau de plaine à partir du rôle protecteur du corridor. Avec un réseau de mesures de températures dans 3 petits bassins versants et une étude plus profonde des relations hydromorphologiques sur un bassin versant, nous allons approfondir nos connaissances sur les forçages environnementaux et le rôle du corridor pour le milieu aquatique. Avec les travaux de quelques stagiaires (H. Roche, M. Poulain), et la nouvelle thèse (M-L. Merg), nous avons construit un

projet de recherche assez conséquent pour identifier des relations significatives entre gestion, contexte bassin versant et environnement local et la biologie.

Les nouvelles orientations de mes recherches à court terme portent sur les capacités d'adaptation et de résilience des cours d'eau et de leurs communautés biologiques (principalement macro-invertébrés et poissons) face aux pressions anthropiques locales (altérations hydro-morphologiques, interactions avec le risque chimique) et globales. Des approches plus dynamiques (intégration de la composante temporelle) et fonctionnelles des écosystèmes (réseaux trophiques) sont proposés afin d'intégrer les contraintes liées aux changements globaux en cours (climatiques et anthropiques). Un effort de recherche appliquée sur les aspects de restauration des écosystèmes est prévu en intégrant la notion de services écosystémiques, qui doit entraîner le développement d'approches plus interdisciplinaires (sciences sociales) avec une prise en compte explicite des demandes, perceptions et usages.

En plus nous envisageons une collaboration internationale intensifiée (contacts au sein de ISRS, Horizon 2020, EPA Scotland, ...) et un approfondissement des recherches et thèmes abordés par l'équipe LHQ, l'esprit sera ouvert envers des collaborations et contacts scientifiques. Mais surtout j'appuierai à mettre en valeur la force de l'équipe LHQ qui est construite avec vision pour aborder des recherches novatrices multidisciplinaires et de haute qualité (grâce à ses qualifications de traiter des 'big data' avec des techniques statistiques innovantes). Mon rôle sera surtout d'identifier les hypothèses et analyses pour construire des projets de l'équipe, assurer les liens avec les gestionnaires et leurs questions pour rester sur notre position privilégiée de centre d'excellence en appui pour la gestion des cours d'eau.

2. Résumé

Dans mes activités de direction de recherche sur la continuité écologique des corridors rivulaires, j'ai exploré au fil du temps plusieurs pistes et orientations nouvelles : j'ai questionné la pertinence des échelles, et décrit les processus de flux et d'échanges, la connectivité et ses obstacles, la résilience et les changements climatiques, avec des prolongements relatifs au potentiel de restauration des espaces aquatiques continentaux.

D'une façon générale, un corridor représente une emprise spatiale garante de la connectivité dans un réseau écologique. Pour les cours d'eau, cette notion est non seulement liée à une zone spatialement identifiée comme riparienne, ou corridor rivulaire, qui se définit comme une bande de végétation naturelle située le long d'un cours d'eau, Mais, c'est également un milieu où se cumulent de nombreuses fonctionnalités écosystémiques : zone tampon, filtre d'épuration, zone de provision et de rétention de nutriments, habitat, écotone et couloir de connexion, de contact et d'échange. L'étude du corridor rivulaire est par conséquent indissociable de celle de la rivière, de son paysage et de son bassin versant.

Quelles sont les échelles pertinentes à considérer pour appréhender la continuité écologique des corridors rivulaires? Comment construire une approche qui tienne compte de l'échelle de réalisation des processus d'échange et de contact ?

Le focus de mes travaux au laboratoire d'hydroécologie quantitative repose sur les cours d'eau à l'échelle large de la France avec une attention particulière portée à leur structure et leur fonctionnement hydromorphologique. Les altérations physiques, la fragmentation des habitats, mais aussi la pollution se présentent comme des pressions embêtées à différentes échelles, qui peuvent se cumuler au sein des réseaux hydrographiques. Pour correctement identifier leurs impacts et pouvoir y remédier, il fallait mobiliser de nouveaux concepts et bâtir un programme de recherche à moyen terme pour développer de nouvelles méthodes d'analyse hiérarchique, notamment pour caractériser la notion de connectivité. Le travail repose sur une sélection de variables spatiales d'intérêt, concrétisée ensuite par leur extraction géomatique à partir de bases de données couplées à des systèmes d'informations géographiques ou à partir de documents cartographiques, incluant par exemple l'imagerie à très haute résolution spatiale. Ces caractéristiques, résumées par des indicateurs spatiaux qui renseignent les ruptures de continuité, sont ensuite utilisées pour explorer avec un nouveau regard et une ouverture du champ spatial (réseaux hydrographiques, effets amont aval) des relations fonctionnelles entre corridor et différents processus ou réponses écologiques.

Cette construction d'indicateurs homogènes sur tout le réseau hydrographique métropolitain a déjà permis de rechercher des relations spécifiques et quantitatives aussi bien avec des réponses physico-chimiques (qualité de l'eau), des communautés aquatiques de poissons ou de macroinvertébrés, qu'avec des potentiels de répartition de mammifères (loutre et castor). Cette approche nous a entre autres permis de proposer une méthode innovante de modélisation intégrée de la connectivité fonctionnelle et structurelle.

Une autre question qui a été adressée est celle des métapopulations végétales, partant du principe que la dynamique de leurs communautés est intimement liée aux processus hydromorphologiques et gouvernée par la structuration des habitats dans les réseaux dendritiques. C'est pourquoi, nous avons eu recours à des analyses de la génétique des populations rivulaires. Nous avons été les

premiers à identifier les échanges entre populations le long les corridors avec des 'assignment tests', la structuration génétique des populations rivulaires hiérarchisée par l'intensité des crues et les dispersions sur longues distances, et parmi les premiers à mettre en évidence des métapopulations vraies chez des plantes, en révélant les mécanismes de dispersion et de survie responsables de la structuration des populations dans le corridor rivulaire.

Cette théorie de métapopulation étendue à celle de méta communautés incluant de nouveaux groupes, notamment les macroinvertébrés, va constituer une de nos recherches futures. Nous projetons d'analyser les forçages environnementaux des pressions multiples dans les réseaux hydrographiques, , au moyen d'analyses sur de grands territoires et en mobilisant des séries de données temporelles et spatiales conséquentes.

Enfin, les changements globaux et leurs conséquences interrogent à plus d'un titre la communauté scientifique : les connaissances sont encore insuffisantes pour expliquer et prédire correctement les tendances et les processus de dégradation de la biodiversité dans ce contexte changeant. Une première étape est de comprendre les changements intervenus au cours des décennies passées, qui ont déjà subi des effets climatiques. Nous avons identifié des évolutions significatives des communautés de macroinvertébrés sur l'ensemble du territoire français, induits par des mécanismes régionaux et locaux qui ne sont pas jusqu'à présent pris en compte dans les prédictions.

Enfin, pour intégrer l'ensemble de ces démarches, nous proposons un cadre conceptuel reposant sur différentes propriétés de la résilience : comment le contexte spatial, l'agencement des paysages et la résilience du milieu régissent-ils la résilience des écosystèmes et de leur biodiversité? Ce concept sera testé dans différentes situations écologiques contrastées, par des interprétations d'analyses temporelles ou par des comparaisons de situations dégradées et restaurées.

3. Encadrement, Enseignement, Contrats de recherché

ENCADREMENT DE TRAVAUX DE RECHERCHE

Nom	Période	Durée	Niveau	Taux	Projet et contractant/titre thèse
Inbo					
Jan Butaye	1996-1997	1 an	Chercheur	100%	étude hydro-écologique lit majeur Meuse, Ministère écologie, partenaire Université Anvers
Stijn Vanacker	1998-2005	7 ans	Chercheur	100%	etude potentiel restauration Meuse mitoyenne, Ministère écologie, De Scheepvaart
Hans Jochems	2000-2003	3 ans	Chercheur	100%	Projet Interreg Intermeuse
Veerle VandenBussche	2001-2002	18 mois	Chercheur	60%	etude objectives écologiques des cours d'eau navigables, De Scheepvaart
Joep Fourneau	2002-2003	16 mois	Chercheur	80%	étude hydro-écologique lit majeur Meuse, Ministère écologie, partenaire Université Anvers
Alexander Van Braeckel	2004-2010	6 ans	Chercheur	100%	Convention gestion/restauration Meuse mitoyenne, De Scheepvaart
Margot Vanhellemont	2004	6 mois	Thèse Master 2	100%	étude des influences de dynamique rivulaire et gestion sur le développement des forêts alluviales de la Meuse. Ghent University
Koen Lock	2006	1 an	Chercheur	40%	étude objectives DCE plans d'eau alluviales, VMM
An Leysen	2007-2009	2 ans	Chercheur	33%	études objectives DCE cours d'eau, VMM, ministère écologie
Gerald Louette	2008-2009	18 mois	Chercheur	33%	étude objectives DCE plans d'eau alluviales, VMM
Kevin Lambeets	2007-2009	3 ans	thèse PhD	10%	The effects of flooding disturbance on the distribution and behaviour of riparian arthropods along a lowland gravel river
Robin Pasmans	2008-2010	3 ans	thèse PhD	10%	suivi des populations piscicoles par télémétrie dans la Meuse Mitoyenne
Kris Kenzeler	2008-2009	6 mois	Thèse Master 2	100%	structure et développement d'un forêt alluviale de la Meuse Mitoyenne, MSc thesis, Uhaselt
Els Lommelen	2008-2009	6 mois	Thèse Master 2	50%	dynamique des peuplement et relation avec la dynamique de rivière pour les Carabidae des berges de la Meuse Mitoyenne, Msc thesis, KULeuven
Els Lommelen	2010	1 an	Chercheur	80%	étude plan de cohésion paysagère, région Limbourg
Kris Nackaerts	2008-2010	3 ans	thèse PhD	10%	Patterns of population genetic diversity in plant species along rivers
Katrien Vandepitte	2009-2011	3 ans	thèse PhD + postdoc	10%	Population genetics of invasive plant species along rivers
Kenny Helsen	2009-2011	3 ans	thèse PhD	10%	Population genetics in restoration context for threatened plant species
Irstea					
Thierry Tormos	2010-2011	2 ans	thèse PhD	10%	Analyse à l'échelle régionale de l'impact de l'occupation du sol dans les corridors rivulaires sur l'état écologique des cours d'eau
Thierry Tormos	2011-2012	2 ans	Chercheur	50%	Pôle Onema-Irstea d'hydroécologie des cours d'eau
Jérémy Piffady	2011-2012	2 ans	Chercheur (IPEF)	50%	Pôle Onema-Irstea d'hydroécologie des cours d'eau
Cyril Cavillon	2011	7 mois	Thèse Master 2	50%	Qualité et fragmentation du réseau d'habitats du corridor rivulaire des bassins versants de la Loire et du Rhône. Ingénierie en écologie et gestion de la biodiversité, Montpellier 2
Laurent Lafuente	2011	6 mois	Thèse Master 2	50%	Développement d'une méthodologie de caractérisation des zones rivulaires par télédétection, Université Toulouse III
Marta Prieto-Montes	2012-2014	2,5 ans	Chercheur	50%	Pôle Onema-Irstea d'hydroécologie des cours d'eau
Louis-Patrick Diallo	2012	6 mois	Thèse Master 2	50%	Développement d'une méthodologie de caractérisation de l'état des formations végétales rivulaires par télédétection, SILAT Toulouse
Cyrille Gouat	2012	6 mois	Thèse Master 2	33%	Spatial and temporal variability of indices, metrics and traits used for biomonitoring of French rivers, biosciences, ENS Lyon
Marion Poulain	2013	6 mois	Thèse Master 2	50%	Développement d'une méthodologie de caractérisation des ripisylves sur de grands territoires par télédétection, géographie EDMR, Paris
Honorine Roche	2013	5 mois	Thèse Master 1	50%	Caractérisation de cours d'eau de plaine dans le but d'une étude sur la relation entre le réchauffement de l'eau et la ripisylve
Mathieu Flourey	2014-	1 an	Chercheur	50%	Pôle Onema-Irstea d'hydroécologie des cours d'eau
Marie-Line Merg	2015-	4 mois	thèse PhD	33%	Irstea - AgroParisTech
Paul Cavallé	2014-2015	1 an	Jury thèse PhD	10%	Irstea Grenoble, Biodiversité spécifique et fonctionnelle des berges de cours d'eau : caractérisation diachronique des protections de berges

PRINCIPALES ACTIVITES D'ENSEIGNEMENT

Je n'étais jamais attaché à une université ou autre structure d'enseignement. En Belgique j'avais des contacts étroits avec des amis dans les départements de biologie des universités d'Anvers, Gand et Louvain ; pour lesquelles j'ai organisé des stages de terrain annuels sur la thématique de restauration écologique, pour Dries Bonte (rédacteur en chef Oikos) les étudiants en master 2 Biologie de Gand, pour Patrick Meire et Rudy Van Diggelen (éditeur Wetlands) les étudiants en master 2 Biologie d'Anvers, pour Olivier Honnay les étudiants en master 2 Biologie de Louvain. J'ai donné un cours théorique de 4h (2008-2010) sur la restauration écologique pour les étudiants du département de biologie de Gand en master de Maurice Hoffman.

- Université Anvers, Master 2 Biologie, excursion grand project de restauration écologique sur la Meuse : 8h, 1998-2010
- Université Gand, Master 2 Biologie, stages de terrain annuels grand projets de restauration : projets parc national Hautes Campines et Rivière Meuse : 2x 4h, 2002-2010
- Université Louvain, Master 2 Biologie : stages de terrain annuels grand projets de restauration : projets parc national Hautes Campines et Rivière Meuse. 8h, 2000-2010.
- Cours de restauration écologique, Master 1-2 biologie Université Gand, 4h, 2008-2010.
- Organisation, comités scientifiques et présentation des conférences scientifiques sur la protection de la Meuse (CIM) ; Maastricht 2000, Liège 2004, Sedan 2008.
- Van Looy, K., Tormos, T., (2013) La continuité écologique des cours d'eau : caractérisation et liens avec la biologie. Ecole thématique « Approche interdisciplinaire de la Trame verte et bleue » - Trames bleues, des concepts à la gestion. Saint-Malo 16 au 18 Septembre 2013.
- Organisation, comité scientifique et organisation d'une session 'Resilience' à l'International Society for River Science ISRS conference 2015; 23-28 august La Crosse, USA.
- Special session Ecohydraulics conference, Melbourne February 2016: Scale-hierarchic analyses of biotic community responses to changing environments and multiple stressors; Kris Van Looy & Jérémy Piffady
- expertises d'articles pour revues internationales depuis 2010: Ecography (3), Ecological Indicators (3), Aquatic Ecology (6), Environmental Management (2), River Research & Applications (4), Environmental Reviews (2), Hystrix (2), PlosOne (2), Freshwater Biology (2).

CONTRATS DE RECHERCHE

1. Projet d'étude hydro-écologique du lit majeur de la Meuse, Ministère écologie, partenaire Université Anvers, « C », durée 1996-2003.
2. Projet d'étude de potentiel de restauration pour la Meuse mitoyenne, Ministère écologie, De Scheepvaart, « C », durée 1998-2005.
3. Projet Européen Interreg, IRMA, de recherche : « The Meuse Reconnected » 2000-2004 « P » ; Alterra, Delft Hydraulics, Inbo, Universités Liège, Namur et Metz. Publications 1, 3 et 4.

4. Projet d'étude objectives écologiques des cours d'eau navigables, De Scheepvaart, « C », durée 18 mois.
5. Convention d'appui pour la gestion et étude de potentiel de restauration et conception des mesures pour la Meuse mitoyenne, De Scheepvaart, « C », durée 2004-2010.
6. Projet d'étude objectives DCE plans d'eau alluviales, Flemish Environment Agency VMM, « C », durée 2006-2009
7. Projet d'étude objectives DCE cours d'eau, Flemish Environment Agency VMM, « C », durée 2006-2009
8. Projet Populations rivulaires et leur génétique « C »; fonds de recherche scientifique Belge (2007-2010), Inbo, Université Louvain. Publications 10, 15-16, 18-19.
9. Projet INDECO 2014 IRSTEA – ICEEL – MINES : IBBHIS : Indicateurs de Biodiversité en Bayésien Hiérarchique Spatialisé. « C » Irstea Lyon et Irstea Nogent (F. Gosselin & C. Bouget). 2015-2016, Durée 2 ans.
10. Projet CETACE: adaptation aux changements climatiques pour les bassins sensibles du Rhône. « C » Irstea Lyon, Agence de l'Eau Rhône Méditerranée Corse. 2015-2016, Durée 2 ans.
11. Castor, CARTographie Socio-écologique des Territoires d'Occurrences potentielles de la Loutre et du Castor en Région NPdC, « P »; UMR CNRS 8198 (GEPV) Université des Sciences et Technologies de Lille - Lille 1: Nina Hautekèete, Yves Piquot (Maîtres de conférences en écologie), UMR7533/CNRS/LADYSS Université Paris, Laboratoire Dynamique Sociale et Recomposition des espaces : Richard Raymond (CR CNRS), Laboratoire Territoires, Villes, Environnement et Société (TVES), Université des Sciences et Technologies de Lille - Lille 1 : Magalie Franchomme (Maître de Conférences en Géographie-Aménagement), IRSTEA Lyon - UR Maly - Pôle hydroécologie des cours d'eau : Kris Van Looy (Chargé de Recherche en Hydrobiologie), Laboratoire Génie Civil et géo-Environnement, Université des Sciences et Technologies de Lille - Lille 1 : Alain Leprêtre (Professeur en Ecologie). Projet de recherche « Biodiversité » Région Nord-Pas-de-Calais, FRB, 2014-2017. Durée 2,5 ans.

Projets soumises:

12. APPEL ANR 2015: INTERNATIONAL COLLABORATIVE PROJECT WITH GERMANY: **RIFFLE:** Restoration of Inland Freshwater Functional Linkages over Europe, « C » Irstea Lyon (Kris Van Looy coordinator France, Jérémy Piffady, Mathieu Floury), Irstea Antony (Jérôme Belliard), CNRS Toulouse (Gaël Grenouillet), Senckenberg biodiversity and climate research center, river research department (Peter Haase (Coordinator Germany), Stefan Stoll & Jonathan Tonkin), Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), University Berlin, Department of Ecosystem Research (Simone Langhans, Sonja Jähnig & Christian Wolter). 2015-2017, durée 2 ans.
13. Projet **EURIDYCE** : Eutrophisation : Risques de Dystrophie dans les Cours d'Eau. Méthode d'évaluation du risque d'eutrophisation des cours d'eau : approche intégrée et multi-scalaire applicable en France métropolitaine. Proposé au sein de l'ESCO Eutrophisation des ministères en charge de l'agriculture et de l'écologie.

4. Publications

PUBLICATIONS DANS DES REVUES INTERNATIONALES A COMITE DE LECTURE

1. Pedroli, B., De Blust, G., **Van Looy, K.** & S. van Rooij 2002. Setting targets in strategies for river restoration. *Landscape ecology* 17: 5-18. IP 3.061
2. **Van Looy, K.**, Honnay, O., Bossuyt, B. & Hermy, M. 2003. The effects of river embankment and forest fragmentation on the plant species richness and composition of floodplain forests in the Meuse valley, Belgium. *Belg. Journ. Bot.* 136 (2): 97-108. IP 1.104
3. Geilen, N., H. Jochems, H., Krebs, L., Muller, S., Pedroli, B., Van der Sluis, T., **Van Looy, K.** & Van Rooij, S. 2004. Integration of ecological aspects in flood protection strategies: defining an ecological minimum. *River Research and Applications* 20: 269-283. IP 2.425
4. **Van Looy, K.**, Vanacker, S., Jochems, H., De Blust, G. & Dufrêne, M. 2005. Ground beetle habitat templates and riverbank integrity. *River Research & Applications* vol. 21(10): 1-14. IP 2.425
5. Lambeets K., **Van Looy K.**, Hendrickx F., Maelfait J.-P. & Bonte D. 2005. Synecology of spiders (Araneae) of gravel banks and environmental constraints along a lowland river system, the Intermeuse (Belgium, the Netherlands). *Acta Zoologica Bulgarica*: 137-149. IP 1.013
6. **Van Looy K.**, Severyns J., Jochems H. and De Smedt F. 2005. Predicting patterns of riparian forest restoration. *Large Rivers* Vol. 15, No. 1-4, Arch. Hydrolbiol. Suppl. 155/1-4, p. 373-390. IP 1.401
7. **Van Looy, K.**, Honnay, O., Pedroli, B., Muller, S 2006. Order and disorder in the river continuum: the contribution of continuity and connectivity to floodplain meadow biodiversity. *Journal of Biogeography* 33: 1615-1627 IP 4.863
8. Jacquemyn, H., Honnay, O., **Van Looy, K.** & Breyne, P. 2006. Spatio-temporal structure of genetic variation of a spreading plant metapopulation on dynamic riverbanks along the Meuse River. *Heredity*, 96: 471-478. IP 4.110
9. **Van Looy, K.**, Jochems, H., Vanacker, S. & Lommelen, E. 2007. Hydropeaking impact on a riparian ground beetle community. *River Research & Applications* vol. 23: 223-233. IP 2.425
10. Lambeets K., Hendrickx F., Vanacker S., **Van Looy K.**, Maelfait J.-P. & Bonte D. 2008. Assemblage structure and conservation value of spiders and carabid beetles from restored lowland river banks. *Biodiversity and Conservation* 17: 3133-3148. IP 2.264.
11. **Van Looy, K.**, Meire, P. & Wasson, J.-G. 2008. Including riparian vegetation in the definition of morphologic reference conditions for large rivers: a case study for Europe's Western Plains. *Environmental Management* 41: 625-639.
12. Honnay, O., Jacquemyn, H., **Van Looy, K.**, Vandepitte, K. & Breyne, P. 2009. Temporal and spatial genetic variation in a metapopulation of the annual *Erysimum cheiranthoides* on stony river banks. *Journal of Ecology* 97, 131-141. IP 5.431
13. **Van Looy, K.**, Jacquemyn, H., Breyne, P & Honnay, O. 2009. Effects of flood events on the genetic structure of riparian populations of the grassland plant *Origanum vulgare*. *Biological Conservation*, 142: 870-878. IP 3.794
14. **Van Looy, K.** & Meire, P. 2009. A conservation paradox for riparian habitats and river corridor species. *Journal for Nature Conservation* 17: 33-46. IP 1.843
15. Jacquemyn H., **Van Looy, K.**, Breyne, P. & Honnay O. 2009. The Meuse River as a corridor for range expansion of the plant species *Sisymbrium austriacum*: evidence for long-distance seed dispersal. *Biological Invasions*, 12: 553-561. IP 2.509.

16. Honnay Olivier; Jacquemyn Hans; Nackaerts Kris; **Van Looy Kris** 2010. Patterns of population genetic diversity in riparian and aquatic plant species along rivers. *Journal of Biogeography* 37: 1730-1739. IP 4.863
17. **Van Looy Kris** 2011. Restoring river grasslands: Influence of soil, isolation and restoration technique. *Basic and Applied Ecology* 12: 342-349. IP 2.696.
18. **Van Looy Kris**; Honnay Olivier; Breyne Peter 2011. Adaptive strategy of a spreading gynodioecious plant species (*Origanum vulgare*, Labiatae) in a riparian corridor. *Plant Ecology and Evolution* 144: 138-147. IP 1.192.
19. **Van Looy K.**, Cavillon C., Tormos T., Piffady J., Landry P., Souchon Y. 2013. Are generalist and specialist species influenced differently by anthropogenic stressors and physical environment of riparian corridors? *Riparian Ecology and Conservation* 1: 25-35.
20. **Van Looy K.**, Tormos T., Ferréol M., Villeneuve B., Valette L., Chandesris A., Bougon N., Oraison F. & Souchon Y. 2013. Benefits of riparian forest for the aquatic ecosystem assessed at a large geographic scale. *Knowledge and Management of Aquatic Ecosystems* 408,06. IP 0.467
21. **Van Looy, K.**, Cavillon, C., Tormos, T., Piffady, J., Landry, P., Souchon, Y. 2013. A scale-sensitive connectivity analysis to identify ecological networks and conservation value in river networks. *Landscape Ecology*, **28**, 1239-1249. IP 3.574
22. Tormos, T., **Van Looy, K.**, Kosuth, P., Villeneuve, B. & Souchon, Y. 2013. Catchment scale analysis of the influence of riparian vegetation on the river ecological integrity using earth observation data. In: *Earth observation of ecosystem services*. Eds. D. Alcaraz-Segura, C.M. Di Bela, J.V. Straschnoy. CRC Press, Taylor & Francis Group, Boca Raton 469p.
23. **Van Looy, K.**, Tormos, T. & Souchon, Y. 2014. Disentangling dam impacts in river networks. *Ecological Indicators*, **37**, 10-20. IP 2.890
24. **Van Looy, K.**, Piffady, J., Cavillon, C., Tormos, T., Landry, P. & Souchon, Y. 2014. Integrated modelling of functional and structural connectivity of river corridors for European otter recovery. *Ecological Modelling*, **273**, 228-235. IP 2.069
25. Tormos, T., **Van Looy, K.**, Villeneuve, B., Kosuth, P. & Souchon, Y. 2014. Higher spatial resolution land cover data improves understanding of mechanistic linkages with stream integrity. *Freshwater Biology* 59 (8), 1721-1734. IP 3.725

PUBLICATIONS RANG B

Oraison, F., Souchon, Y., Van Looy K. 2010. Les nutriments dans les cours d'eau, processus d'autoépuration et fonctionnement hydromorphologique. Synthèse bibliographique. Pôle Hydroécologie des cours d'eau Cemagref-Onema, partenariat 2010- restauration des milieux aquatiques.

Oraison, F., Souchon, Y., Van Looy, K. 2011. Restaurer l'hydromorphologie des cours d'eau et mieux maîtriser les nutriments : une voie commune ? 41p.

Tormos T., Van Looy, K., Souchon, Y. 2011. Effets des ouvrages transversaux sur la biologie des cours d'eau en France : étude de faisabilité et analyse régionale exploratoire. Rapport Pôle Hydroécologie des cours d'eau Onema-Cemagref Lyon MAEP-LHQ, 18p.

Van Looy, K., T. Tormos, Souchon, Y. 2011. Rapport d'avancement : corridor rivulaire et état écologique. Rapport Pôle Hydroécologie des cours d'eau Onema-Cemagref Lyon MAEPLHQ, 39 p.

Nicolas V., Oraison F., Souchon Y., Van Looy K., 2012. Restaurer l'hydromorphologie des cours d'eau et mieux maîtriser les nutriments, une voie commune ? Comprendre pour agir, Onema, 8 p.

Tormos, T., Van Looy, K. 2012. Étude de faisabilité sur l'impact des ouvrages transversaux sur la biologie des cours d'eau en France à partir du référentiel des obstacles à l'écoulement (ROE). Rapport Pôle Hydroécologie des cours d'eau Onema-Irstea, Lyon MAEPLHQ, 69 p

Van Looy, K. ; Tormos, T. Souchon, Y. 2012. Ripisylves: caractérisation et indicateurs en lien avec l'état écologique des cours d'eau - Rapport Pôle Hydroécologie des cours d'eau Onema-Irstea, MALY-LHQ, Lyon, 20 p.

Van Looy, K. ; Tormos, T. 2013. Indicateurs spatialisés du fonctionnement des corridors rivulaires. Rapport Pôle Hydroécologie des cours d'eau Onema-Irstea, Lyon MAEPLHQ, 54 p.

Prieto Montes, M. ; Ferréol, M. ; Van Looy, K. 2013. Chroniques à long terme : évolution des macroinvertébrés benthiques dans les cours d'eau de France métropolitaine. Suivi sur 112 sites (1986-2009).

Van Looy K Tormos T, Piffady J, Souchon Y. 2014. Le corridor fluvial : des trames déjà en place à renforcer et à protéger. *Sciences Eaux & Territoires, N° special Trame Verte et Bleue.*

Et plus : Titres co-écrits pour illustrer les activités : 89 publications à l'adresse <http://informatiecentrum.inbo.be>, 34 sur CEMADOC.

PROCEEDINGS

VAN LOOY K. 2006. River restoration & biodiversity conservation: a disorder approach "Water and the landscape: The Landscape Ecology of Freshwater Ecosystems" Proceedings of the IALE(UK) conference, Oxford Brookes University, 2006

VAN LOOY, K. 2008. Biodiversity of the Meuse floodplain in the context of the common Meuse restoration programme. *Symposium "Biodiversität von Gewässern, Auen und Grundwasser"* Bonn, Germany. http://www.bfn.de/fileadmin/MDB/documents/themen/wasser/teil02_14_vanLooy.pdf

VAN LOOY K. 2008. Hydromorphological aspects in the restoration of river habitats and species in the context of the common Meuse restoration programme. *Society for Ecological Restoration Conference "Towards a sustainable future for Ecosystems", SER 2008*, Ghent.

VAN LOOY, K. 2010. An experimental environmental flow implementation on the Common Meuse. *Proceedings of the EGU, Vienna conference, Austria.*

VAN LOOY, K. 2010. The River Meuse restoration project seen from the air. *Conference on Ecological Restoration "Ecological Restoration and Sustainable Development – Establishing Links Across Frontiers" SER2010*, Avignon, France.

IAVS Conference 2011 – Session "Biodiversity and functioning of riparian habitats: indicators of change" Chair: F. AGUIAR & K. VAN LOOY – 20-24 June 2011, Lyon, France.

THIERRY TORMOS, PASCAL KOSUTH, BERTRAND VILLENEUVE, KRIS VAN LOOY, YVES SOUCHON. 2011 Remote sensing and GIS techniques for assessing and prioritizing riparian corridor restoration. River Corridor Restoration Conference 2011 – Ascona (Suisse) – "Performance control of restoration projects" - Friday, March 18th

THIERRY TORMOS, PASCAL KOSUTH, KRIS VAN LOOY, YVES SOUCHON, BERTRAND VILLENEUVE. 2011 Remotely sensed riparian corridor indicators in relation to ecological status of rivers. Proceedings IAVS Conference 2011 – Lyon - Session "Biodiversity and functioning of riparian habitats: indicators of change" Chair: F. Aguiar & K. Van Looy – 20-24 juin.

THIERRY TORMOS, PASCAL KOSUTH, KRIS VAN LOOY, YVES SOUCHON, BERTRAND VILLENEUVE. 2011 Remote sensing and GIS techniques for large-scale assessment of the relative impacts of land cover pressures on macroinvertebrate communities. SEFS conference 2011- Gironne (Espagne) 27 juin.

VAN LOOY, K., TORMOS, T., FERREOL, M., VILLENEUVE, B., VALETTE, L., CHANDESRI, A., BOUGON, N., SOUCHON, Y. - 2012. Impact of fragmentation of riparian corridors and of dams to the aquatic environment assessed at large scale. *International Limnology Days, Biodiversity and functioning of aquatic ecosystems – Impacts of global change*. Clermont-Ferrand, France.

VAN LOOY, K. - 2012. Large River Restoration. *Europarcs Conference « Reconnecting society with biodiversity »*, 24/10/2012, Genk, Belgium.

TORMOS, T. ; DUPUY, S. ; VAN LOOY, K. ; BARBE, E. ; KOSUTH, P. 2012. An OBIA for fine-scale land cover spatial analysis over broad territories: demonstration through riparian corridor and artificial sprawl studies in France. Geobia Conference, Rio de Janeiro, Bresil.

VAN LOOY, K., GIELEN, H. - 2012. Images and experiences from the river Meuse restoration projet . *Seminar of programm Interreg IV A « Re-dynamisation of the Upper Rhine »*, 30/11/2012, Strasbourg, France.

CHANDESRI, A., VALETTE, L., MOY, J., BAUDOIN, J.M., PIFFADY, J., TORMOS, T., VAN LOOY, K., SOUCHON, Y. - 2012. Assessment of the hydromorphological impact. Hierarchical audit of hydromorphological pressures and alterations (France scale). Cis ecostat hydromorphology workshop, 12/06/2012 - 13/06/2012, Brussels, BEL. 26 p.

VAN LOOY, K., PIFFADY J., TORMOS T. & SOUCHON Y. 2013. A holistic integrated risk framework to river impairment. International Society for River Science, Biennial Conference 5-9/8 2013 Beijing.

PRIETO MONTES, M. ; FERREOL, M. ; VAN LOOY, K. 2013. Long-term trends of invertebrate communities in a changing environment. SEFS conference Munster, Germany.

VAN LOOY K., PIFFADY J., TORMOS T. & SOUCHON Y. 2014. Populations and river landscape resilience. SER 2014 conference Oulu, Finland.

TORMOS T., VAN LOOY K. 2014. Object-Based Image Analysis for Characterization of Riparian Areas over Broad Territories using Multisource Data. Geobia Conference, Grece.

VAN LOOY K., FERRÉOL M., PRIÉTO-MONTES M. & SOUCHON Y. 2014. Climate Change Challenges River Resilience. ISRS 2014 conference 'Are riverine landscapes resilient: can they survive increasing climate variability and human demands'.

Partie 2. Résumé des travaux en Anglais

5.1 River ecology, a matter of scale.



Scale-sensitivity of patterns is often overlooked!

QUESTIONING

Studying the ecological continuity of riparian corridors needs to emphasize elements of landscape dynamics and hydromorphology that intervene at different scale levels of basin, stretch and local reach. The way this scale-sensitivity impacts the corridor functioning and how these corridor functions are impaired by multiple and multi-scale stressors is hardly addressed up to now. Analyzing biotic community patterns and corridor functions might benefit from scale-hierarchic, network oriented approaches.

STATE OF THE ART

The European Water Framework Directive (WFD; EU, 2000) challenges scientists to analyse and model information and uncertainties from different scale levels of river ecosystem functioning (Page *et al.*, 2012; Ocampo-Duque *et al.*, 2013). During the last decade, scientific progress has been characterized by a tendency to use ever more complex models built on relationships observed locally, neglecting many important aspects of ecosystem functioning that occur at larger temporal and spatial scales (Allan, 2004; Wiens, 2002). The lack of scientific information gathered at accurate scales has prevented management actions from being effective (Palmer *et al.*, 2007). Thanks to technical and methodological improvements in data gathering, interpretation and extrapolation, new perspectives for holistic scale-hierarchic ecosystem analyses have recently been explored (Jones, 2006; Esselman and Allan, 2011; Fock, 2011). Evidence for the usefulness of these holistic approaches now exists for large scale models (Vörösmarty *et al.*, 2010) and for scale-hierarchic management-oriented approaches (Thoms *et al.*, 2007). However, even these advanced methods have limited diagnostic power to quantify environmental risks with multiple causalities, which is the prevailing situation in multiple stressor stream contexts. The effects of human-induced alterations in hydrological regime, water quality and physical structure on the functional attributes of riverine systems are multiple and complex (Ormerod *et al.*, 2010; Leigh *et al.*, 2012). Causal relationships between ecological integrity and the multitude of river system impairments and stressors in catchments are hard to evidence, and causalities are often difficult or even impossible to identify (Downes *et al.*, 2010; Norris *et al.*, 2012).

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These last years, we successfully answered several of these questions with our hydroecology Lab. We elaborated a scale-hierarchic risk-based framework to river ecosystem assessment for the French stream network integrating all potential intervening processes and functions. Secondly, we evidenced specific corridor functions at large scale in multiple stressor contexts in relationships between riparian forest cover and nutrient and biotic elements status, thanks to hierarchic inferences. Finally, we identified specific corridor functional linkages to determine biodiversity drivers in networks.

A holistic integrated risk framework to river impairment

The developed risk assessment approach considers the ecosystem functions and impairments in physico-chemistry, hydromorphology and ecology. Both within and in-between these components, functional relationships can be modelled with hierarchic Bayesian frameworks, by either quantitatively or qualitatively pointing out causal relationships. The modelling framework therefore relies on the identification of natural baselines and analysis of stressor influence on the processes and structures of the river system. The construction of this framework is present in the first publication of Part 3.

Few similar comprehensive assessment systems exist at such large scales using spatial hierarchic frameworks (Norris *et al.*, 2007; Davies *et al.*, 2010; Davies *et al.*, 2012; Wang *et al.*, 2011; Esselman *et al.*, 2013). These are habitat-oriented audit frameworks assembling relevant natural factors and human disturbances in order to assess remarkable biotopes. Still, it appears very difficult to bring all the relevant elements into the picture, both due to gaps in information and to the complexity of interactions. We believe the proposed risk approach provides a promising additional field for most comprehensive assessment systems, as it allows including all environmental insights and at the same time highlighting shortcomings to both information and understanding of relationships. This was successfully put to practice in the French national territory, for which the result was a highly

satisfactory, rigorous and global assessment of hydromorphology, a domain characterised by important lacks in knowledge and information.

The innovative elements in the proposed framework consist firstly in the extended comprehension of the risk concept to represent both uncertainty to information and to understanding of processes and causal relationships. Secondly, the integrative character of the BBN structure translates the complexity of the relationships studied. Risk approaches are advocated in the context of uncertainty and non-linearity of the response to stressors at large scale (Fock, 2011) and they prove to be very useful in terms of communicating the assumptions of any approach and reaching consensus in a decision-making process.

Evidenced corridor functioning

We assessed relationships between the forest cover in the riparian corridor and the anthropogenic pressures that were retrieved from several spatial scales (stretch, hydrologic unit and catchment) in order to assess the impact of the forest cover on physicochemical characteristics, and macroinvertebrate and fish metrics reflecting community structure and ecological condition over the French river network. The question underlying our research was: can we observe the claimed benefits of riparian forest cover for the aquatic environment from data at large geographic scale? If so, does the response vary with buffer width, with ecoregion and with pressure conditions, and can it even be identified in environments with multiple stressors? From the aggregated datasets of physicochemical and biotic monitoring networks, a selection of sites was extracted with the same stress conditions at the watershed and local riparian corridor scale and a gradient of riparian forest cover. The response of the biota was measured with data of the national biotic monitoring networks for macroinvertebrate and fish communities.

In literature, large scale inferences of a significant relationship of riparian forest cover with biotic integrity are weakly quantified or show loose correspondence (Allan 2004; Wasson *et al.* 2010; Arnaiz *et al.* 2011), often owing to the difficulty of retrieving accurate land cover data for the riparian corridor zone (Tormos *et al.*, 2011). We observed consistent responses to riparian forest cover in the selected datasets for nutrients and for biotic integrity indices (Van Looy *et al.* KMAE 2013). The results were consistent, as the same responses were observed over different selections, both over the chemical types and over the ecoregions. For the strongest responses of physicochemical parameters and biotic integrity indices, similar regression slopes were obtained and thus identical indications for ranges of riparian forest cover necessary for a good ecological functioning.

Single versus multi-stressor environments

In other parts of the world, much stronger relationships between the river's biotic integrity and the riparian corridor are found in strictly agricultural-forest landscapes, and are documented as consistent for single-pressure conditions. For smaller agricultural watersheds in North Carolina, 73% of the variance in fish and macroinvertebrate communities was explained by watershed and local riparian corridor characteristics (Stewart *et al.* 2001; Wilson *et al.* 2008; Arnaiz *et al.* 2011), whereas riparian forest as a single predictor explained 63% of the fish species assemblages in smaller headwater streams of agriculturally dominated catchments of a northern Great Plains ecoregion (Wilson *et al.*, 2008). In our multi-stressor context, only up to 22% of the variance for nutrients and 5% for biotic integrity metrics are explained by riparian forest cover. An indication of the gradual impact of the multiple stressors intervening in the biotic response to the riparian corridor is also present in our analysis, when we compare the responses in the different ecoregions. Biotic responses were lower or absent for regions with a strong presence of multiple stressors. Ecoregion HER10 showed a lower multi-stressor state than the HER9 and showed more significant responses to the

biological quality. Hence although certainly not a single-stressor environment, the HER10 is less influenced by multiple stressors.

How much riparian forest is required?

The detected relationship allows the determination of conditions for good ecological functioning of the riparian corridor. Not only were the responses consistent over the different selections and elements, they also showed similar response functions with respect to the different variables indicating the ecological status of the aquatic system. This enables the identification of boundary conditions for riparian forest cover to delineate good ecological status for the aquatic environment. The good and high status boundaries – the legal standards at national level according to the European Water Framework Directive – for the physicochemical variables and biotic integrity indices of the aquatic systems were consistently found to correspond to a narrow range of riparian forest cover values in all significant regressions. For the 10 m buffer, good status for physicochemical variables and biotic indices corresponded to 60% riparian forest cover, and high status to 70%. For the 30 m buffer these boundaries were at 45% cover for good and 55% for high status of riparian forest. The detected responses were comparable to recent recordings of 54% forest cover as a boundary for the biotic integrity based on the Plecoptera genera (Tornblom *et al.* 2011). Like these authors, we detected a 55% boundary for the biotic integrity based on the fish community with the additive quantile regression approach. These observed relationships give an indication that increasing riparian forest cover can significantly improve the rivers' purification potential and biotic integrity. Thus it can be classified as a 'no-regret' restoration measure (European Commission, 2007), easily and immediately applicable without conflicting with more exhaustive integrated management programmes.

Our resulting figure of 60% riparian forest cover necessary for a functional buffer, was already intuitively proposed in several management programs (fi. Chesapeake bay catchment plan, or Pennsylvania Code for Stream Management), and recently confirmed by other studies of catchments globally (or close value of 70% for Andes streams (Iñiguez–Armijos *et al.* 2014). General stream management recommendations concern the existing riparian buffer conversion to a riparian forest buffer. Riparian buffers that consist predominantly of native woody vegetation that do not satisfy the composition or the width requirements described, can be enhanced or widened, or both, by additional plantings in open spaces around existing native trees and shrubs that provide at least 60% uniform canopy cover (Pennsylvania Code § 102.14 for riparian buffer requirements). The Chesapeake Bay Riparian Forest Buffer Panel (Bay Area Regulatory Programs) strives for a minimum 50-foot forested buffer around all perennial streams, with a 60% crown cover.

Functional linkages

Questions whether upstream or downstream basin context and the network position prevails for nutrient retention, whether the configuration and specific rate of ruptures in riparian forest cover is crucial in the processes, and whether biotic response is predictable still remain unanswered. To answer these questions, a scale-sensitive fine-grained analysis to the configuration of ruptures was performed to infer physical and biotic responses (Tormos *et al.* 2014a) and associated ecosystem functions (Tormos *et al.* 2014b). For this purpose, remote sensing methods are deployed and investigated further to better characterize the riparian zones and especially the riparian forests

present. Furthermore, a set of spatial indicators is deployed all over the river network of France (250 000km) and a specific region (Bresse) instrumented with temperature loggers.

The scale sensitivity of functions and their assessment poses problems in the analysis of ecological networks and in the context of the conservation and restoration of riverine communities. The selection of target species in the context of ecological network analysis (Van Looy *et al.* 2013a, 2014), as well as the scale of the connectivity measures (Van Looy *et al.* 2013b), and the resolution of the spatial information entered in the analysis (Tormos *et al.* 2014), will strongly influence the outcome of connectivity analyses and the identified ecological networks.

In the IBBHIS project, methodological developments are proposed to incorporate spatio-temporal scales governing biodiversity responses. Emphasis will be for the role of riparian forest in maintaining river ecosystem functions. In the Lab of Quantitative Hydro-ecology we recently developed a series of indicators for the quality of the riparian corridor based on forest cover and fragmentation. An analysis of the spatial and quantitative indicators distribution will determine some contrasting geographical spaces for which biological monitoring data is available, focusing primarily on streams of small size. On these spaces, we will study the influence of the quality of the corridor on some properties of the ecological functioning of watercourses, expressed by features or metrics of interest of macroinvertebrate communities. Species diversity of benthic invertebrate detritivores type shredder, seems to be an interesting candidate metric. This serves as basis for the elaboration of spatio-temporal hierarchical models, seeking to identify the variability of the relations in space and the relative weights of the present variability.

Elucidating mechanisms underlying community assembly improved the understanding of impacts of environmental changes on river biodiversity. In this context, trait-based approaches proved useful to infer community assembly rules at different levels of biological organization and across geographic regions (Van Looy *et al.* 2006, 2014). Determining the characteristics that underlie species sensitivity and/or vulnerability remains crucial for the development of effective conservation and management strategies. Finally, we showed that the evolutionary history of species constrains their responses to landscape processes and environmental changes (Van Looy *et al.* 2009, 2011).

5.2 Continuity and connectivity, contact and exchanges



The PhD work of Kevin Lambeets was centered on the population structure and movement of wolf spiders characteristic for the riparian corridor; Arctosa cinerea (photo), Pardosa agricola et Pardosa agrestis.

Kevin Lambeets 2009. The effects of flooding disturbance on the distribution and behavior of riparian arthropods along a lowland gravel river. Thesis Department Biology, Ghent University.

QUESTIONING

Rivers and their riparian zones play a role as transit zones and exchange areas, both locally as at the landscape and regional scale. To elucidate and understand this corridor functioning, studies of population dynamic structuring and processes in the corridor are needed, and study of population genetics is a primary tool in these, which might provide insight in survival and structuring of populations with regards to landscape dynamics. Further questions deal with the ambiguity of structural and functional connectivity measures to ecological continuity and the cumulative impacts of obstacles over the river network.

STATE OF THE ART

Even though population genetic studies in river corridors were already advocated, no studies documented the genetic structure of riparian populations being influenced by corridor functioning up to then.

Connectivity can be measured either structurally or functionally, and for both approaches many indicators and models exist. Yet, methods to identify ecological networks for species struggled with the choice between structural and/or functional connectivity modelling to be used.

In studies of damming impact, no significant effect is evidenced in general species diversity measures (Maynard and Lane, 2012), and even where certain metrics of aquatic communities prove to respond to obstacles (Brooks et al., 2011; Wooster et al., 2012; Vaughn 2012), no information on accumulation of this pressure over the river network was present apart from energy budgets for sea-migrating fish passing obstacles.

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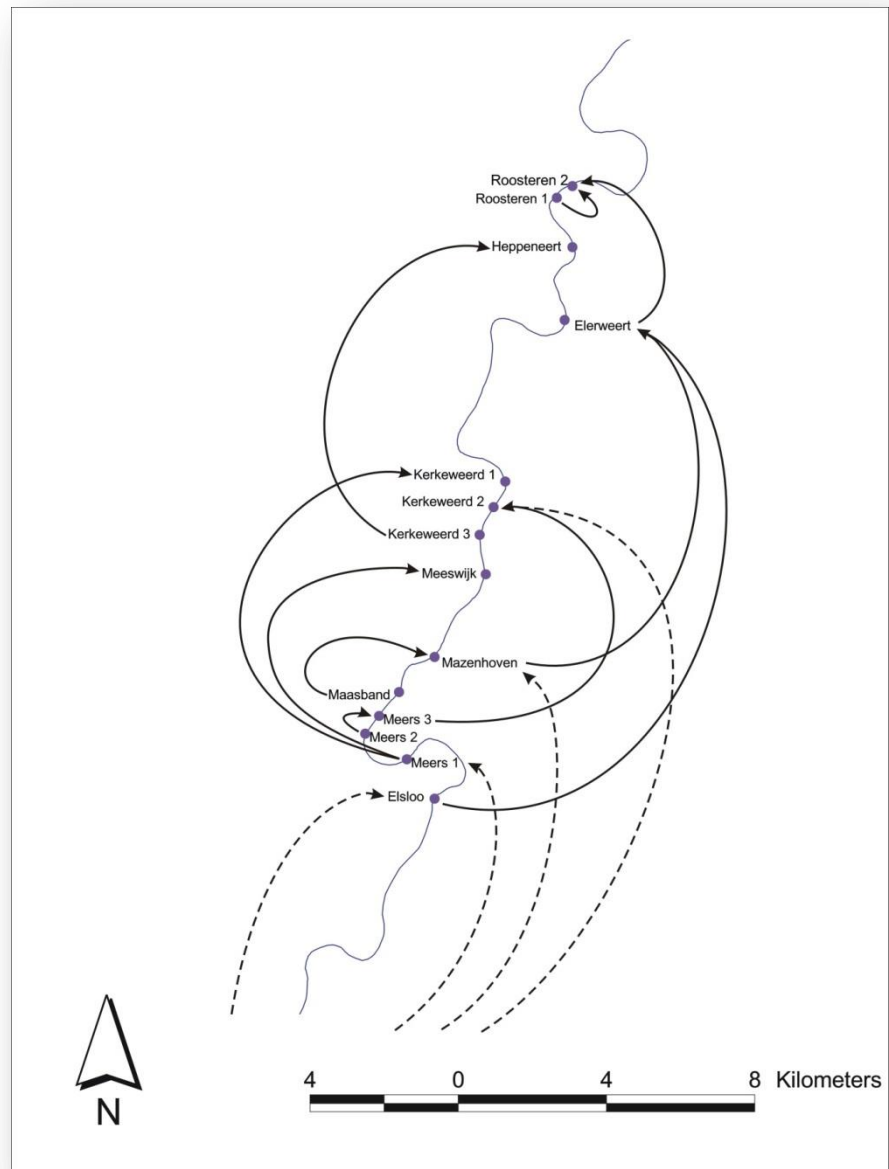
Population genetics

Riparian landscapes offer excellent opportunities for the study of population dynamics and genetics in relation to the processes of fragmentation, alteration and restoration. River regulation results in the disconnection and increased fragmentation of habitats in the river corridor. To this purpose, we studied the genetic structure of riparian populations of plant species.

We were the first to identify the exchanges between populations along the corridors with 'assignment tests', the first to identify the genetic structuring of riparian populations controlled by the intensity of floods and long distance dispersal, and among the first to identify true metapopulations in plants and reveal the responsible mechanisms of dispersal and survival for this structuring of populations in the riparian corridor.

We detected for all species a pronounced hierarchic spatio-temporal structure in genetic variation. This structure could be assigned to the irregular patterns in the flow regime of the River Meuse. Large floods are the major vector of genetic structure, but geographic upstream proximity, probably mediated by small floods, also has an important effect on genetic structure. Assignment tests revealed occasional long-distance seed dispersal with extreme flood events and local colonisation with more regular floods (Fig. 1). With the assignment tests for molecular markers, we were able to identify long distance dispersal between populations >20km apart. Our study species optimally took benefit of the opportunities offered by the river restoration programme, with a strong colonisation after floods, and illustrates the need for maintaining river dynamics to conserve and restore genetic diversity.

Fig. 1 Seed dispersal events between populations of *Sisymbrium austriacum*, inferred from the statistical allocation of individual genotypes to genetic populations based on AFLP markers. Full lines indicate the genetic allocation of an individual to populations within the study area, whereas dashed lines indicate allocation of an individual to outside of the metapopulation sample, suggesting a seed dispersal event from outside the study area.



These genetic diversity studies taught us that for riparian species the rescue effect for populations can depend on long distance (>20km) dispersal events associated with extreme flow events (Jacquemyn *et al.* 2006). Metapopulation dynamics and survival were found dependent of the inter-annual variability of flow regimes (Honnay *et al.* 2009). The general configuration and strength of populations in the riparian zone proved to be ruled by the flood regime (Van Looy *et al.* 2009). Also with regard to the character of exotic species invasions in riparian systems, the study of population genetics and genomics can teach us important elements to understand crucial ecological processes (Jacquemyn *et al.* 2010; Vandepitte *et al.* 2014). Rapid genetic adaptation of our studied exotic species preceded its spread (Vandepitte *et al.* 2014), but also for local species rapid plastic changes of flowering strategies were detected to enhance recovery and spreading in the riparian corridor (Van Looy *et al.* 2011). It is known that the breeding system of a plant species plays an important role

in its genetic response to spatial and temporal habitat dynamics (Honnay & Jacquemyn 2007). Less is known, however, regarding the mediating role of more complex breeding systems such as gynodioecy in the response to spatial and temporal landscape dynamics. Gynodioecious plants have a mixture of hermaphroditic and functionally female individuals. We showed that in adapting its breeding strategy to the local dynamics, the species could benefit from the river dynamics to spread and recover in the riparian corridor (Van Looy et al. 2011)

The downstream hydrochoric spread of seeds of aquatic and riparian plant species, without upstream compensation, can be expected to result in downstream accumulation of population genetic diversity. This idea has been termed the 'unidirectional dispersal hypothesis' and is the genetic equivalent of the more generally known 'drift paradox'. To the risks of this unidirectional dispersal of accumulation of genetic diversity downstream, we evaluated our studies and performed a meta-analysis. We presented a general synthesis of the patterns of population genetic variation across different riparian and aquatic plant species along rivers (Honnay *et al.* 2010). For the studied patterns of within- and between-population genetic diversity among three riparian plant species (*Sisymbrium austriacum*, *Erysimum cheiranthoides* and *Rorippa sylvestris*), there was no evidence for the unidirectional dispersal hypothesis. The meta-analysis on studies reporting on the population genetic structure of riparian and aquatic plant species along rivers, based on 21 data records, did not support the unidirectional dispersal hypothesis either. Also for a riparian spider there was no trace of downstream accumulation of genetic diversity (Lambeets *et al.* 2010). Contact between spider populations was observed over shorter distances, occurring along the shores at low flow conditions, whereas the river channel constitutes a physical barrier for spider species exchange between opposite shores. The proposed restoration of the riparian zones will increase the amount of suitable habitat, the contact between populations and eventually riparian spider populations' persistence.

Recurrent colonization and extinction have profound consequences for the distribution of genetic diversity. Inferring gene-flow patterns from simple measures of genetic differentiation or isolation by distance patterns is inappropriate in these ecosystems. Our results strongly support previous suggestions (Tero *et al.*, 2003) that stream ecology should consistently embrace metapopulation theory to be able to understand patterns of genetic diversity, as well as species diversity. It is important to note that these conclusions have important conservation consequences and that the distribution of genetic diversity along rivers is more than a theoretical issue. Without insights into the general patterns of the distribution of genetic diversity along rivers, the implications of common river regulation measures such as the construction of dams, dikes and embankments are impossible to predict. From these insights, we drew perspectives for further study based on phylogenetics for macroecological studies and on population genetics for restoration potentials.

Model development for structural and functional connectivity

The comparison of the otter's habitat requirements and network colonization potential as a highly mobile generalist, with the beaver's preferences and potential as a habitat specialist were explored over the Rhône basin (Van Looy *et al.* 2013a), revealing the influence of the species studied in network analyses, both to characterization of connectivity and continuity aspects, as to scale sensitivity.

In the same way we identified ecological networks at river basin level and their scale sensitivity in analysis and data entry (Van Looy *et al.* 2013b). The role of river corridors in providing connectivity is questioned in the context of defining ecological networks over large territories (Rouget *et al.*, 2006; Grant *et al.*, 2007). The assessment of connectivity in river networks generally poses specific

methodological difficulties (Peterson and Ver Hoef, 2010), as does more generally the contribution of specific landscape features to the accommodation of biological processes (Simberloff et al., 1992). Attempts to measure this interplay between landscape configuration and species movement, that we call functional connectivity, are still quite uncommon (Wainwright et al., 2011). Connectivity is either *structural*, based on adjacency of landscape features, or *functional*, based on how that adjacency translates to movement of organisms. Structural connectivity is defined as the adjacency or proximity of patches within a landscape and is a measure of the degree to which patches are connected without regard to organism behaviour (Taylor et al., 1993). Alternatively, functional connectivity is conceptually defined as the degree to which a landscape impedes or facilitates movement of organisms among patches (Bélisle, 2005). Functional connectivity is mostly derived from species range or dispersal studies, at best with dynamic process-oriented population or distribution models (Marion et al., 2012; Schurr et al., 2012). Managing for structural connectivity is thought to increase functional connectivity, yet this implication is not so straightforward (Tischendorf and Fahrig, 2000). Ideally, functional and structural connectivity should be integrated when providing guidance for management. We developed a modelling approach that elucidates both aspects of connectivity to identify vital corridors and conservation priorities in a river network. Bayesian inference offered good perspectives to elucidate the functional component of connectivity, as it is renowned for dealing with spatially structured and incomplete data of species occurrence. We estimated the colonization probability for river segments under influence of different potential limiting factors in the riparian corridor based on the observations in the different surveys for the river network of the Loire basin. Furthermore we took advantage of the iterative nature of Bayes' Theorem, in integrating the time steps of observation (5 steps of 5 year) and spatial differentiation of the river network in the analysis. Most analysis methods of connectivity are still based on the uniform percolation theory (Gardner et al., 1989) and in this way do not integrate information on functional corridor quality. Here we used the weighted graphs to integrate not only distances but also the functional corridor quality to the connectivity analysis. Challenges for this integrative approach to functional and structural connectivity for riparian corridors arose at two fronts: both the dendritic structure of the river network that we fully integrated with the graph method, and the functional connectivity inference for the species movement based on spatially structured data (Grant et al., 2007, Peterson et al., 2013), in our case questioned for otter colonization probability. The developed model that integrates both structural and functional connectivity is presented in the paper joined in Part 3.

Damming impacts on continuity and connectivity

The great majority of river systems of the world are subjected to flow regulation and impoundment; over half of the world's large river systems are affected by dams (Nilsson et al., 2005). Recently, questions on the opportunity of dam removal and the ecological benefits of such restoration measures arise, but for specific contexts, the general rationale for restoring natural features often seems to get lost, and not only due to uses conflicts (Lejon et al., 2009). Often there is a local attachment to existing landscape features and scenery, but more importantly river managers encounter resistance of conservationist and fisheries stakeholders that question the potential gains and stress the risks of species loss. Nevertheless there is general agreement to the injurious character of human alterations and to the application of a reference approach (Hansen and Hayes, 2012). But especially the strong emphasis on the river's corridor functioning and the impact of

obstacles to ecological networks, demands for dam removal. As a result, there is need for advanced assessments of the role and effects of dams within river networks to support strategies for mitigating ecohydrological and socioeconomic costs, and recently important efforts are made globally to the inventory of reservoirs and dams (Lehner et al., 2011), or to evaluate their impact on river ecology (Petts, 1984; Acreman and Ferguson, 2010). In France and Western Europe in general, the high degree of flow regulation and the governmental initiatives to address environmental problems under the Water Framework Directive provide the need and impetus for environmental water allocations and the need to monitor and assess the ecological effects.

We showed that dam density measured at supra-reach level shows more significant influence on river health than the local level density, and further that the impact of dams is best estimated with measures for the functional traits of biotic assemblages. An extensive dataset of fish (169 sites) and invertebrate (211 sites) communities in the Loire river basin, described with metrics of density of ecological guilds, taxonomic richness and life history traits, and coupled with reach hydromorphology and catchment characteristics was constructed. With techniques of generalized linear modelling we quantified dam impact and investigated the importance of regional- and local-scale measures of dam density to the structure of biotic communities. The analysis showed that community structure at the basin scale responded significant to dam presence and confirmed that the strongest relationships were observed for specific functional trait-based metrics. For the macroinvertebrates the observed impact counts up to 25% of the variance in the trait-based quality indices, whereas for fish communities the dam density only explains up to 12%. Macroinvertebrate responses were stronger at higher scale level, and especially the upstream context explained on its own 70% of the observed impairment. For fish communities, the local context prevails and explained up to 70% of the dam impact. These results can be explained by the biotic processes ruling community assembly in the specific groups, passive dispersal for the invertebrates and migrations between habitats for fish. The geographic context furthermore explains the differentiation in these responses, reflecting the metacommunity structure of invertebrate assembly over the river basin. We conclude that for upstream parts of the river basin, locally based management actions can be successful in restoring biotic integrity, whereas more downstream, dam removal actions require more integrated measures at regional rather than local scale.

Both for fish as for invertebrates significant relationships with local dam density are only present for specific trait-based metrics and not for the global biotic integrity indices. The integrated network measure of dam density shows stronger correlations than the local dam density also both for fish as invertebrate metrics, indicating the accumulation of dam impact in the river network.

5.3 At the face of global change



Over the last decades, a strong increase in richness and abundance of macroinvertebrates is observed over the river network of France. Especially in the group of the caddisflies (Trichoptera, here a picture of *Oxyethira*, a Hydroptilidae).

QUESTIONING

Observing and predicting global change effects require long term, large scale analyses, of which the rarity nowadays often limit our comprehension. Actual patterns of species diversity and community changes in real ecosystems under environmental change should receive greater attention (Gessner *et al.* 2010; Gilman *et al.* 2010) as up to now only few studies have explored the scale effects on community assembly and biodiversity.

STATE OF THE ART

Streams and rivers are expected to respond strongly to climate change, for their physical controls of hydroregime and water quality are governed by climatic factors, principally air temperature and precipitation (Hughes, 2000). Changes to flow regime and temperature have been evidenced to strongly influence macroinvertebrate community structure (Daufresne *et al.*, 2004, 2007, 2009; Durance & Ormerod, 2007, 2009). As a consequence, altered peak flows, droughts and rising temperatures are expected to reshape stream macroinvertebrates' distributions (Domisch, Araújo, Bonada *et al.*, 2013).

The problem with the detection of clear climatic trends for freshwater communities is that observed elements, like range shifts, are species-specific, with cold-water organisms being generally negatively affected and warm-water organisms positively affected (Poff *et al.*, 2012). Up to now, the lack of a wider knowledge hinders predictions of freshwater biodiversity responses to climate change and other major anthropogenic stressors (Heino, Virkkala and Toivonen, 2009).

Other difficulty lies in distinguishing these Climate Change effects from simultaneous, but unconnected, changes through time. When trying to untangle Climate Change consequences in invertebrate communities not only temperature is to be considered (Poff *et al.*, 2010). Potential changes in water discharge may also contribute to the loss of native biodiversity, jeopardizing ecosystems equilibrium (Palmer *et al.*, 2008; Sheldon & Thoms, 2006). The difficulty in detecting clear climatic trends relies on distinguishing global warming effects from other simultaneous but unconnected anthropogenic disturbances such as warm water. Conversely to this supposed degradation perspective, water quality management over the past decades has successfully contributed to improve biological quality. As a result, future management challenges might now lead to climatic effects becoming increasingly important (Durance & Ormerod, 2009).

Predictions and extrapolations for fish communities over the French river network estimate future loss of functional diversity (Logez & Pont, 2013; Buisson, Grenouillet, Villéger *et al.*, 2013), with consequent strong impacts to present communities. Comparable exercises for macroinvertebrates predict a decrease of around 40% for a majority of species in the amount of climatically suitable areas by 2080 (Domisch *et al.*, 2013). Up to now, impact of Climate Change in invertebrate communities has been addressed either for large datasets but "short periods" of time (Chessman, 2009; Collier, 2008; Scarbrook *et al.*, 2000) or long time series but little number of sites (Mazor *et al.*, 2012; Durance & Ormerod, 2007). Studies combining both spatial and temporal components are scarce.

THE INNOVATION WE BROUGHT

Global warming is assumed to be a threat to temperate stream biodiversity, still many of the processes and mechanisms behind the predicted threats to diversity remain uncertain. We identified current trends and drivers of change for freshwater communities over a large spatial and temporal scale already revealing a strong ecosystem shift.

We analysed diversity and composition shifts in stream invertebrates communities during the last three decades in relation to geographic elements and human stressors over the French river network (circa 1000 km in longitude and latitude).

We observed a 42% increase in the taxonomic richness of stream invertebrate communities, largely caused by climate change (23% purely climate-induced taxonomic richness increase). As a local mechanism, a bottom-up food web productivity response to rising temperature was responsible for this strong increase in site diversity. Stochastic assembly processes (both environmental stochasticity and dispersal related stochasticity) increased the regional scale diversity, giving spatial insurance to biodiversity and lowering the risks of biotic homogenisation.

Thus, stream invertebrate communities show strong resilience to environmental changes thanks to local and regional responses of productivity changes (resource resilience), and thanks to landscape heterogeneity (refugia resilience) and dispersal processes (recruitment resilience). For the French stream invertebrate communities, up to now the resilience mechanisms seem to outweigh the predicted threats. From this knowledge emerge scenarios that enhance the temperate streams' resilience to cope with further global changes.

Our observations over large spatial and temporal scale contrast to predicted functional changes (Domisch *et al.*, 2013; Daufresne *et al.* 2007), the richness increase is on the one hand ruled by a local mechanism; more species can co-exist thanks to more resources in the absence of competitive limitation. Secondly, regional stochastic community assembly processes induce higher diversity among sites with unlimited resources (Chase, 2010). Not so much the local bottom-up food web control but its synchronized manifestation over such a large spatial scale and within such a short time frame is an extraordinary phenomenon. To the question why this trend of biodiversity increase is not earlier noticed, or only partly (Dornelas, 2014), we have to stipulate that analyses of large-scale long-term trends are still rare (see productivity biodiversity project under LTER) (Dodson, 2000). To our knowledge, no reports of three decade continuously sampled sites of stream communities over larger spatial scale exist. Nevertheless, maybe the observed trend is not ubiquitous. We argue that water quality improvement played a trigger role in the synchronicity of the observed diversity increase. Population growth and dispersion over the river network are enabled once water quality reached a basic quality level, also described for English chalk streams (Durance & Ormerod, 2007). Further element that potentially enabled this trend is the high geographical variety for the studied French territories with many preserved headwaters and stream sections. Finally, more than terrestrial and lentic ecosystems, streams and rivers are characterized by strong natural perturbations and their communities are highly adapted to changing conditions.

For other freshwater systems strongly influenced by productivity, such as lakes, no similar observations are made. Signals in the same direction might be expected nevertheless, as it has been shown recently that lake productivity is limited by light and not by nutrients (Karlsson *et al.*, 2009), and that warming will have rapid effects on the productivity of high latitude lakes (Karlsson *et al.*, 2005). Striking temporal coherence of food-web interactions over hundreds of kilometres due to faster population growth of herbivores in warmer water in central European lakes is also reported (Straile, 2002). For Arctic freshwater ecosystems, the projected increase in productivity with climatic changes is accompanied with profound hydroregime changes strongly confounding biotic responses (Prowse *et al.*, 2006). Also for our temperate region running freshwaters, there is a risk of too much productivity and temperature increase. Cold water species obviously do not benefit as strongly as eurythermal species in our observations. Furthermore, predicted changes to flow regime might deteriorate conditions. Projected climate-induced intensification of floods and droughts might provoke species loss in time. Nevertheless, the recent period already showed extreme events in the studied region, which impacted strongly on communities at the local scale (Daufresne & Boët, 2007;

Floury *et al.*, 2013), yet with no evidence on the overall trends in the longer run. These local scale and short-term observations invoked hypothesis testing for a climate-induced trend towards smaller organisms (Daufresne *et al.*, 2009); but in our long time series the tendency towards smaller organisms was only a short-term aspect of the change pattern that occurred. Given estimations that temperate ecosystems are to experience the least biodiversity change (Sala *et al.*, 2000), we conclude, based on the strong changes observed in our study, that uncertainties in the current predictions of global change are many times larger than often presumed (see also Heino *et al.*, 2009).

With some other authors (Woodward *et al.*, 2010; Parmesan *et al.*, 2013) we suggest that new concepts to more functional climate change analysis are needed, oriented to increasing productivity and mobility. At present, global change predictions only depict declines and degradation incurring (Poff *et al.*, 2012). Most studies use distribution-climate models and invoke a lack of adaptation capacity to environmental changes (Heino *et al.*, 2009). In our data, however, we clearly observe an increase in diversity that is not limited to a small group of species appearing everywhere, but a strengthening and stronger expression of regional species pools and a higher productivity that involves the entire food web. An ecosystem containing many diversified species will be able to seize new evolutionary opportunities more easily and will stand up to environmental changes (Loreau, 2001). We plead for an open and less prejudiced approach to future new climates with no-analogue communities that inevitably evolve and bring ecological surprises (Williams, 2007). We observed novel enriched communities that were nevertheless composed by the regional species pools. Biodiversity conservation and restoration strategies need to focus on regional species pools and enhance capacities for dispersal and growth (Heino & Peckarsky, 2014). The current catastrophist view to biodiversity loss induced by climate change needs some counterbalance to reinforce and orient adaptive strategies to biodiversity conservation. The persistent investments in water quality prove to pay off for biodiversity, and here show to be reinforced by climate change effects. Our results may stimulate concerted regional efforts of improvement of water quality and dispersion, to reinforce regional species pools and their resilience to further climate change.

5.4 Resilience and restoration



Bed recharges of gravel to an incised river reach, one of the successful measures applied along the Common Meuse traject on the Belgian-Dutch border.

QUESTIONING

Analysis of community and ecosystem resilience and persistence under changing environmental conditions, in particular human alterations of their environment, can reveal patterns and triggers of biodiversity change in space and time. This knowledge might be translated in novel concepts to deal with the conservation and restoration of biodiversity.

STATE OF THE ART

Various authors have illustrated how resilience aspects act and interact at various scales, yet, it has proven remarkably difficult to isolate resilience agents or to account their relative importance to biodiversity insurance (Urban, Miller *et al.* 2000). Not only it is generally acknowledged nowadays, that setting targets in river restoration needs both a societal and multidisciplinary focus (Pedroli *et al.* 2002) and an extended knowledge of processes of species exchange/dispersal (Honnay *et al.* 2010; Van Looy *et al.* 2013b). In recent years, a large amount of evidence has been gathered indicating that reach-scale river restoration projects often fail to meet their predefined goals. Based on this rapidly expanding body of published case studies (Jaehnig *et al.* 2010; Januschke *et al.* 2014), it is concluded that river restoration research should progress to identifying the drivers that determine the success or failure of restoration projects. Many elements point to landscape level drivers of dispersal and species pools (Kail *et al.* 2012; Tonkin *et al.* 2014; Van Looy *et al.* 2014b). Approaches to identify these drivers and prioritize restoration need to integrate scale-hierarchy of responses and dynamics of metacommunities (Stoll *et al.* 2014; Tonkin *et al.* 2014)

THE INNOVATION WE BROUGHT

Variation partitioning over spatial, environmental and connectivity elements can reveal the part played by the different drivers of change and resilience. For the restored sites along the river Meuse, with a spatially nested sampling design we distinguished between spatial and local environmental factors determining floodplain grassland community recovery (Van Looy 2011). A diversity partitioning approach was used to assess the relative contributions of alpha and beta diversity components to total regional diversity between contrasting restoration techniques. The species pool in the vicinity and isolation aspects of dispersal limitation and river influence were much stronger reflected in the recovering community than the local habitat conditions.

From the observed long term (1980-2010) macroinvertebrate community changes for France (Fig.2), as well as for England (Vaughan & Ormerod 2012), we conclude that patterns of change are not directly explained by temperature or precipitation anomalies, or by water quality improvement.

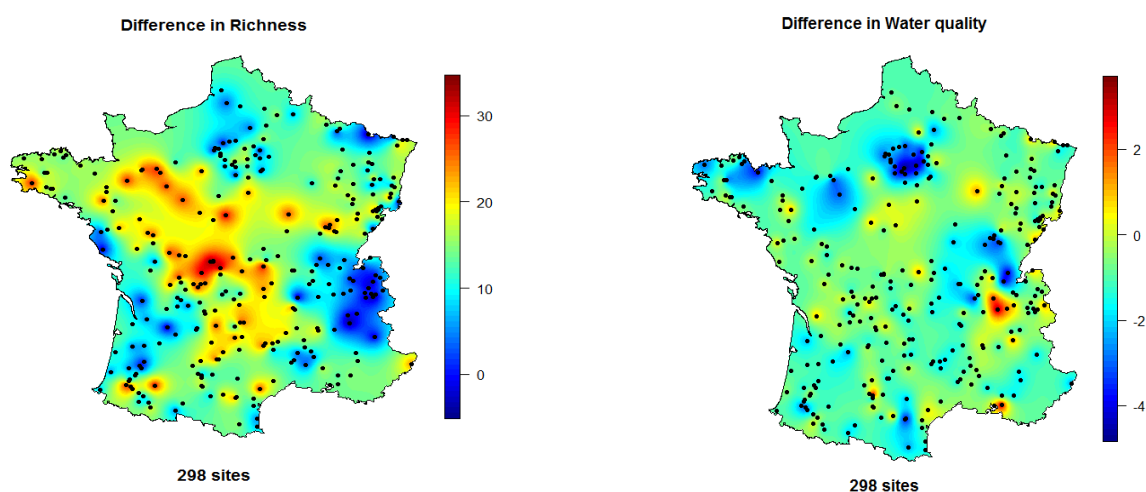


Fig. 2. Change in taxonomic richness and water quality (scale of 10) for the long term series 1980 – 2010.

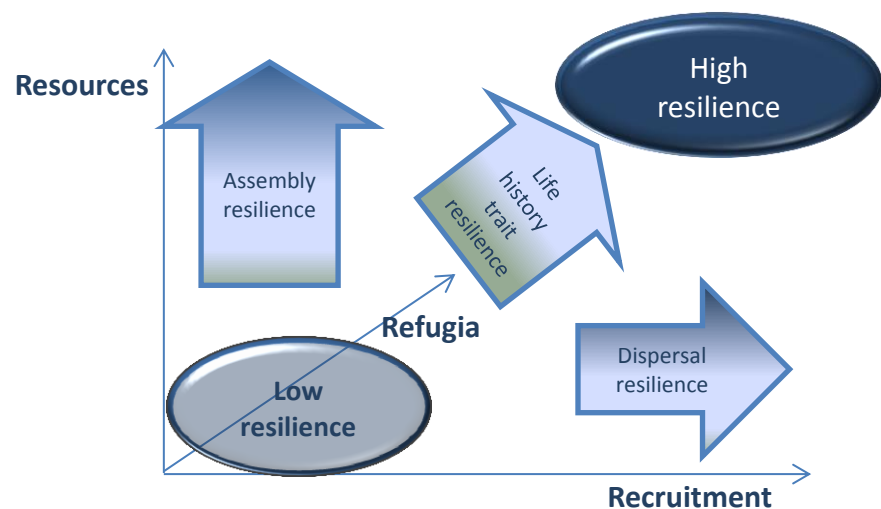
Therefore, we present a novel conceptual framework to identify and deal with resilience of ecosystems. As yet, most of the existing analyses are restricted to either looking at only one driver of change (f.i. temperature), and one measure (drought resistance traits). We identify axes of resilience that are present both in the physical system as in the mechanisms of resilience of the biotic communities.

Ecological resilience is defined as the amount of disturbance a system can tolerate and its capacity to reorganize before it is pushed into a different 'domain of attraction', thereby losing its original functions and processes. Global changes affect the physical template for ecosystem functions and processes. Yet, resilience to these global changes is not purely and simply an asset of the living system. The physical template shows its own resilience, both in absorbing climatic fluctuations, heat and energy fluxes, and attenuating hydrologic and material flow alterations by landscape dynamics. Biotic processes such as demographic mechanisms (establishment, growth, and mortality), intra- and interspecific competition, and dispersal generate a dynamic resilience pattern on this template. We present a conceptual framework of 3 axes of ecosystem resilience: 1) provision of, and competition for, Resources; 2) Recruitment from regional species pools; and 3) geographical and evolutionary Refugia. We hypothesize that these mechanisms independently can explain patterns of biodiversity change and of resilience to disturbances and environmental change.

Refugia resilience is governed by the regional gamma diversity and functional trait diversity developed over centuries to millennia; Resources trigger/enable assembly resilience as the adaptive capacity of local communities to re-organize; Recruitment from regional species pools shapes dispersal resilience through the ability to move, and establish novel communities.

Our central hypothesis is that the landscape context and physical system's resilience determine biotic resilience. This implies that biodiversity insurance is governed by interactions between resource provision and competition, between connectivity and metacommunity dynamics, and between refugia provided by habitat heterogeneity and functional trait diversity.

We further hypothesize that these associations function in the same way along disturbance gradients and environmental changes (c.f. Tonkin et al. 2013). We also postulate that this resilience estimation will enable prediction of restoration potentials and climatic change-induced patterns of change in biodiversity.



5.5 Synthesis and perspectives



*Road sign on mid-channel bar showing the way to continue the river's 'continuity'.
Picture taken in the Dordogne, source of inspiration for my earlier studies of riparian
forest continuity and connectivity (Van Looy, Meire & Wasson 2006).*

Synthesis

Studying river corridor ecology is definitely a collaborative work, addressing multiple disciplines, far demanding for cartography and spatial analysis skills, for hydromorphology, hydrology and geography, for biochemistry and vulnerability of biotic groups, and for complex modelling. These skills are gathered in the river hydroecology lab in Lyon, offering unique opportunities to launch innovative researches. Due to its complexity of structure and processes, the ecological continuity can only be approached with hypothesis-driven study, incorporated in scale-hierarchic, process-based frameworks!

Ecological continuity and corridor functions are driven by processes and structures at different scale levels; processes of exchanges were shown to be scale-sensitive both for population genetic structuring and diversity conservation, as for ecological networks and connectivity for riparian organisms. Hierarchic genetic structures evolved from differential flood regimes, and ecological networks not only differed according to species dispersal capacity, but also according to the scale-level of integration of connectivity for the network and its branches. For obstacles we also showed this differential impact at local or network level, upstream and downstream for fishes and macroinvertebrates. So, strong hypothesis-based researches are needed to identify the drivers and appropriate scales of forcing and structuring in river systems.

Combining trait-based and phylogenetic approaches will further help decipher the mechanisms underlying differences in how species respond to environmental changes, and offer new opportunities in facing conservation challenges. Especially combined with knowledge on metacommunity and macrosystem structures and processes. Macroecological focus on riparian systems offers opportunity to enter the questions of connectivity and continuity in the network and catchment context where they operate essentially.

To explain the network context of observed diversity patterns and resilience in the river corridor, we presented a conceptual framework for resilience based on axes of resource, refugia and recruitment mechanisms. We propose to investigate these three mechanisms to explain patterns of biodiversity change and of resilience to disturbances and environmental change. More confidence is needed in the intrinsic resilience of communities to global changes. Therefore, an identification of the elements in these three axes of resilience is a prerequisite. Restoring functional diversity by local habitat enhancement and habitat heterogeneity conservation can be crucial to preserve the refuges; the connectivity axis requires recruitment (sources) availability and dispersal capacity of organisms; whereas the productivity and assembly axis needs availability and adaptation to changing resources. So, investigations can be for metacommunity dynamics linked to 'connectivity' (see conclusions for difference upstream versus downstream metacommunity structuring Brown & Swan 2010, Van Looy et al. 2014), assemblage dynamics linked to productivity, functional diversity preservation linked to refugia. Opportunities to unravel these relationships are present with the availability of large datasets of biotic and environmental conditions constructed to assess the relationships of ecosystems to human disturbances over time, in their specific spatial context (river basin network) and referring to specific biodiversity baselines assumed for specific conditions (reference conditions). In these studies emphasis must be on regional and landscape contexts as contacts and exchange are crucial in determining the potential for restoration.

And finally, the first prerequisite to attack these challenges is an open mind, allowing the surprises, being prepared to be amazed!

Perspectives

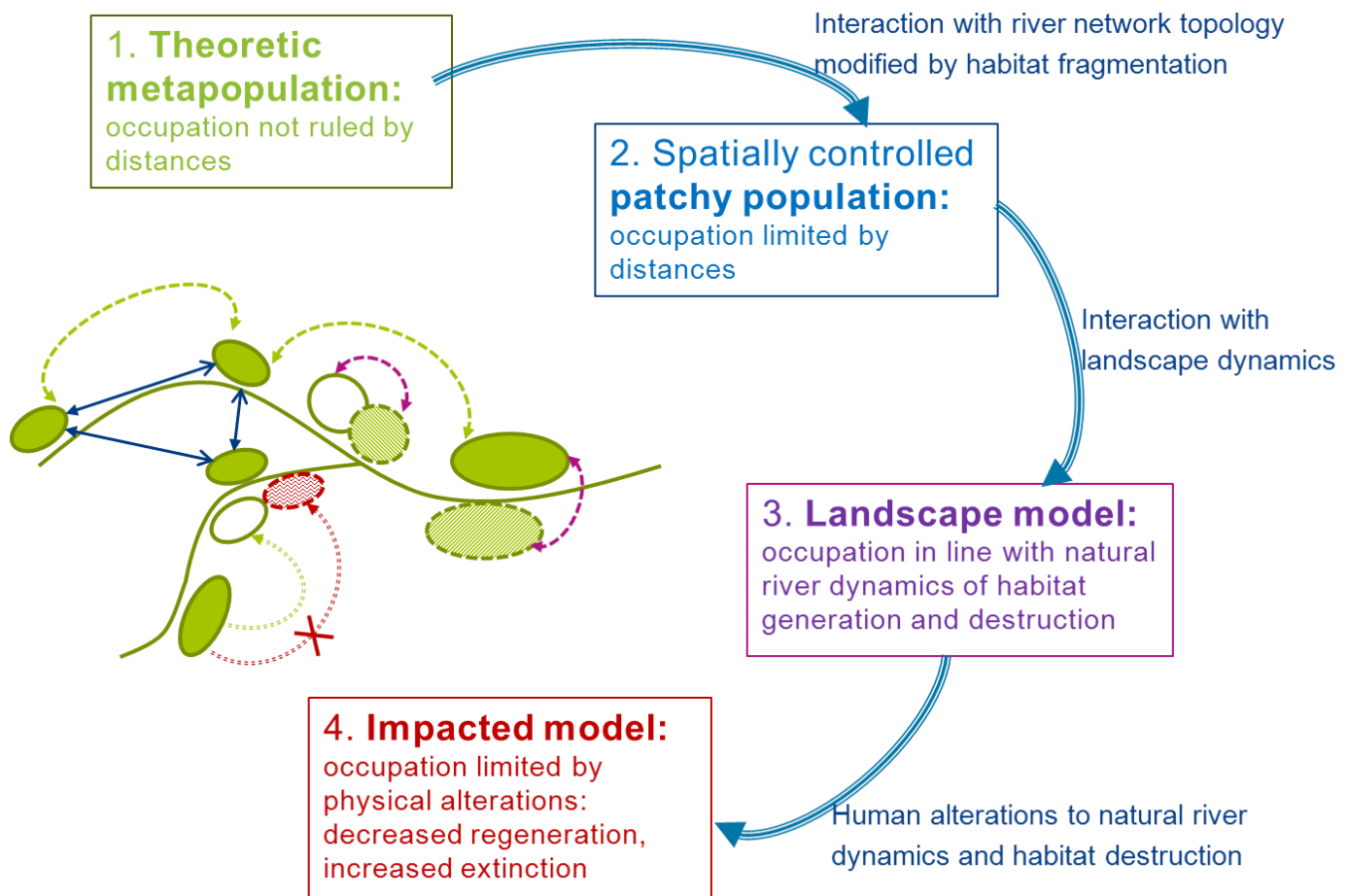
Metapopulation/metacommunity modelling under global changes

Metapopulation persistence in river network

Connectivity of river corridors is highly impacted by physical alterations posing risks to population persistence and restoration. The association of habitat quality and quantity with the landscape dynamics and resilience to human-induced disturbances is still poorly understood in the context of species survival and colonization processes, but essential to prioritize conservation and restoration actions. We present a modelling approach that elucidates these aspects of network connectivity in spatial and temporal context to identify vital corridors and conservation priorities in the Loire river and its major tributaries. A dynamic population modelling framework is used to bring population dynamics in relation to river landscape dynamics and network connectivity. Natural dynamics (resilience) of the river landscape can be confronted with physical alterations in such models and measured in population persistence. Disconnection and alteration of flooding and flow regimes is believed to be critical to population dynamics in river ecosystems. Still, little is known of critical levels of alteration both spatially and temporally, or the role of the river landscape resilience in this.

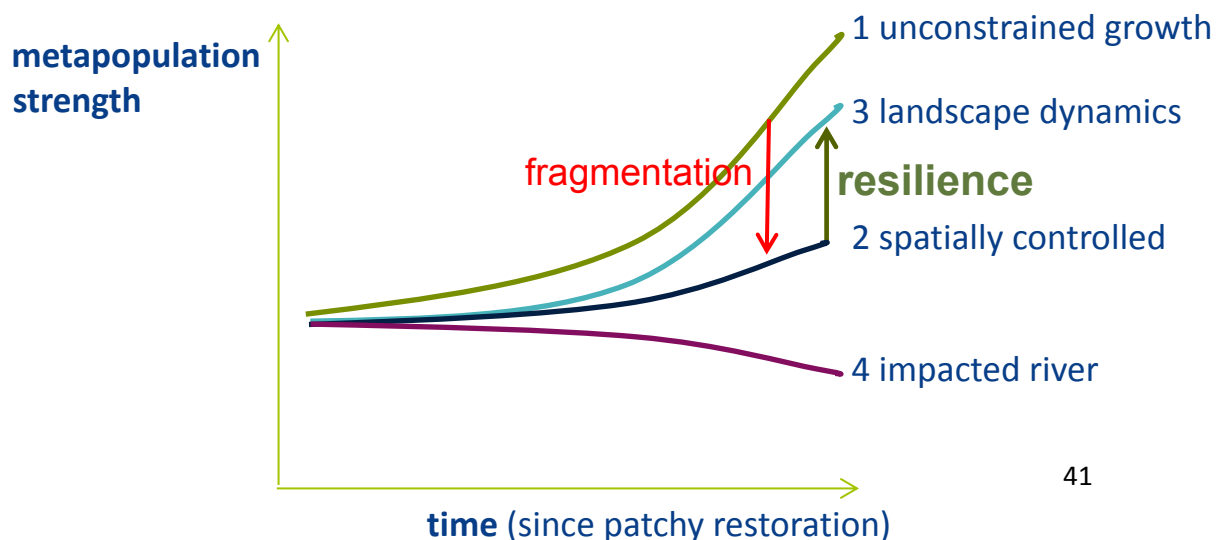
We proposed metapopulation modelling approaches to population dynamics for a dispersal-limited tree species, black poplar; and a recruitment-limited tree species, white elm. The links with landscape dynamics are explicit in metapopulation models as they integrate the spatio-temporal dynamics of habitats and populations in river networks. Identifying metapopulation persistence for the two tree species over the larger rivers in the basin highlights crucial connections and network structure influence to extinction risks in relation to habitat quality and connectivity.

We construct contrasting metapopulation scenarios starting from the two model species, and three model types: connectivity-ruled or seed-rain model, landscape dynamics model (integrating habitat creation and destruction additionally) or stable habitat model, alterations model versus undisturbed.



The models grow in complexity to answer the questions 1) what role river network connectivity plays, 2) what role river dynamics play and 3) what role alterations play.

The first step is to integrate connectivity in the metapopulation model. Therefore, with inclusion of a connectivity factor, the model must additionally be adjusted to whether or not extinction or colonization depends on occupancy patterns. The simplest model assumes that colonization and extinction are constant. More specifically, this means that the number of occupied patches does not affect the number of colonization events in the metapopulation, which is the signature of external colonization. We hereafter refer to this as the propagule rain model.



Meta-community analysis of resilience

Questions and topics for our current research proposals deal with the resilience and recovery potential of communities in a regional geographical hierarchic context to restoration efforts. Knowledge on metacommunity structuring and dispersal abilities are discriminated as key elements to restoration context, and will be investigated through functional groups over different scales and in response to specific abiotic and biotic drivers of success for restoration.

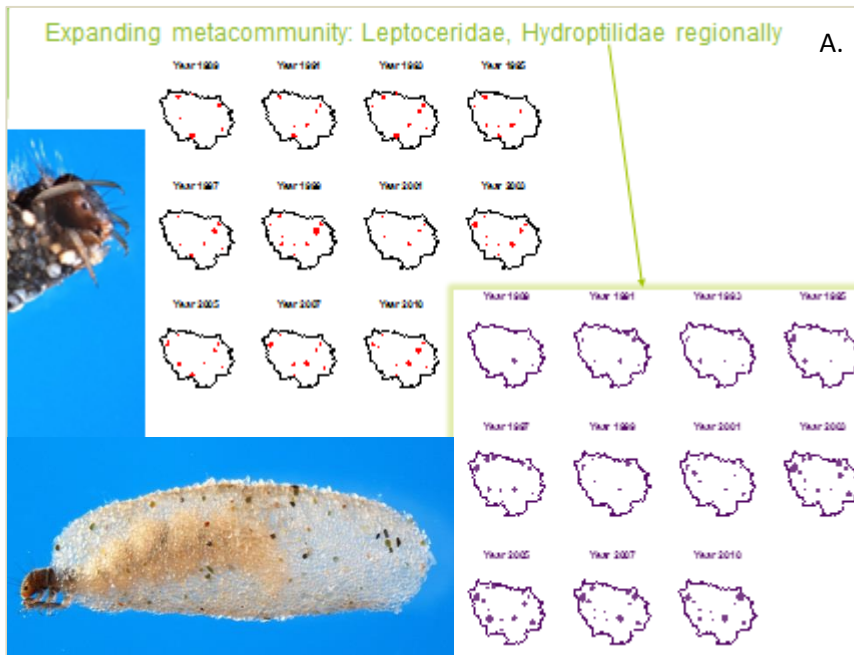
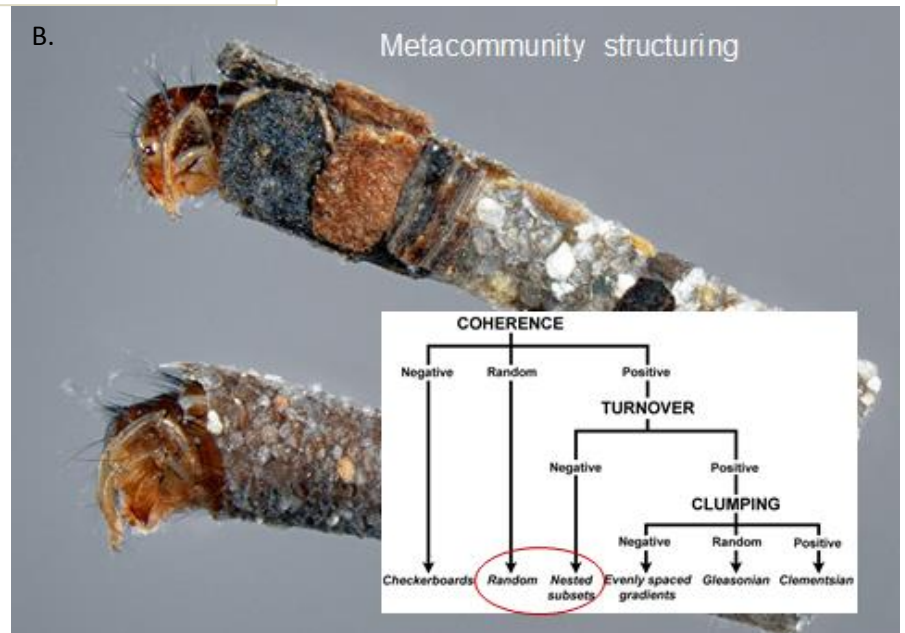


Fig. 3 A. The strongly expanding Caddisfly families, gave way to a metacommunity analysis at regional scale. B. Metacommunity structuring for the Caddisfly group shows both random and nested subset patterns.



Up to now we determined metacommunity structuring patterns for specific macroinvertebrate groups (Trichoptera mainly) in the long time series analysis over specific regions, and detected main structuring patterns of random coherence and nested subsets (fig. 3). Currently, new orientations are explored with macro-ecology and meta-community approaches. Still, up to now, these frameworks are only applied to very local or coarse grained studies. Here, there is still plenty of possibilities for innovative science (see Heino 2013).

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Partie 3. Publications significatives

1. Unravelling river system impairments in the stream network of France with an integrated risk approach, submitted to Environmental Management
2. Global warming induces strong shifts in temperate stream invertebrate communities through local and regional scale mechanisms, submitted to Oikos
3. Integrated modelling of functional and structural connectivity of river corridors for European otter recovery. *Ecological Modelling*, 273, 228-235.

Unravelling river system impairments in the stream network of France with an integrated risk approach

Kris Van Looy*, Jérémy Piffady, Thierry Tormos, Bertrand Villeneuve, Laurent Valette, André Chandesris & Yves Souchon.

Irstea Lyon – UR MALY – River hydro-ecology research unit Onema-Irstea

Keywords: holistic framework – ecosystem functions – uncertainty – Bayesian Belief Networks – hydromorphology

Abstract

Rivers are complex systems for which it is hard to make reliable assessments of causes and responses to impairments. We present a holistic risk-based framework for river ecosystem assessment integrating all potential intervening processes and functions. Risk approaches allow us to deal with uncertainty both in the construction of indicators for magnitude of stressors, and in the inference of environmental processes and their impairment. Yet, here we go further than simply replacing uncertainty by a risk factor. We introduce a more accurate and rigorous notion of risk with a transcription of uncertainty in causal relationships in probability distributions for the magnitude of impairment and the weight of different descriptors, with an associated confidence in the diagnostic. We discuss how Bayesian Belief Networks and Bayesian hierarchical inference allows us to deal with this risk concept to predict impairments and potential recovery of river ecosystems.

For the French national territory, we developed a comprehensive approach for river ecosystem assessment, which offers an appealing tool to facilitate diagnosis of the likely causes of impairment and predict future conditions. The ability of the risk approach to integrate multi-scale quantitative and qualitative descriptors in the identification of multiple stressor sources and pathways in the stream network, and their impairment of specific processes and structures is illustrated for the national level risk analysis for hydromorphology and pesticide pollution. Not only does the risk-based framework provide a more complete picture of environmental impairments, it also offers a comprehensive, user-friendly tool to instruct the decision process.

1 Introduction

Ecological assessment methods are increasingly being used to determine the presence and degree of environmental impairment. In most cases, however, assessment results cannot be used to confidently identify suitable management options unless the causes of impairment have been identified explicitly (Suter 1993). Survey-based assessment methods typically include more integrated measures – so-called integrity indices that are designed to reduce complex arrays of ecosystem responses to various disturbances into a single number, but they do not unravel the causalities (Dyer et al. 2000). This challenges scientists to develop new tools to structure and analyse information and uncertainties from different levels of river ecosystem functioning (Page et al. 2012; Ocampo-Duque et al. 2013).

During the last decade, scientific progress has been characterized by a tendency to use ever more complex models built on relationships observed locally, neglecting many important aspects of ecosystem functioning that occur at larger temporal and spatial scales (Wiens 2002). The lack of scientific information gathered at appropriate scales has prevented management actions from being effective (Palmer et al. 2007). Thanks to technical and methodological improvements in data gathering, interpretation and extrapolation, new perspectives of risk-based approaches for holistic scale-hierarchic ecosystem analyses have recently been explored (Jones 2006; Esselman and Allan 2011; Fock 2011). However, even these advanced methods have limited diagnostic power to quantify environmental risks with multiple causalities, which is the prevailing situation in multi-stressor stream contexts.

The effects of human-induced alterations in hydrological regimes, water quality and physical structure on the functional attributes of riverine systems are multiple and complex (Ormerod et al. 2010; Leigh et al. 2012). Causal relationships between ecological integrity and the multitude of river system impairments and stressors in catchments are often difficult or even impossible to identify (Downes et al. 2010; Norris et al. 2012). Hence, there is a need for methods to assess the combined and relative risks of multiple stressors to ecosystem functioning at multiple scales (Camargo and Alonso 2006; Dudgeon 2010; Ormerod et al. 2010; Rasmussen et al. 2013). Furthermore there is need for improvement in ecological information, in particular in determining landscape features that can have a profound influence on the estimated exposure to stressors, and that can therefore significantly improve ecological risk analysis (Heathwaite 2010; Kapustka 2005).

Here we illustrate the novelty and strength of the integrated, scale-hierarchic framework and Bayesian Network approach developed for the French river network that is now nationally in use for the assessment of both hydromorphological impairment and pesticide pollution. Assessments from this framework infer the impairment risks for specific ecosystem functions and processes, using a diagnostic approach to determine the magnitude of stressors and impairments. We first introduce the principles of scale-hierarchy and the notion of risk in the probabilistic framework, as introduction to the integrated risk assessment framework that we illustrate with the assessment of hydromorphological impairment of riparian zones and pesticide contamination risks.

2 General framework and methodology

The scale-hierarchic audit framework

A scale-hierarchic approach is essential for ecological risk assessment that views integrity in terms of dynamic states influenced by factors at multiple levels (Suter 1993; Kapustka 2005). The scale-hierarchic framework is also crucial for inference methods that model hierarchically structured spatial data. Hierarchic structuring is a basic step in eliminating a large fraction of the uncertainty in causal relationships, as it can discriminate effects at different scales and determine their relative contribution to ecological impairment (Page et al. 2012). Instead of focusing on local causes, we attribute weight to the driving forces at higher (e.g. regional) scales, given that risks associated with factors acting at these scales can often be quantified more straightforwardly (Van Sickle and Johnson 2008; Norris et al. 2011).

The scale-hierarchic river audit system for France (Chandesris et al. 2009) is based on a spatial classification and attribution of multi-scale descriptors of human-induced disturbances. At the highest level, we distinguish hydro-ecoregions (10^3 - 10^4 km²) as large climatic geological entities. The French Hydro-EcoRegion (HER) classification comprises 22 geographical entities in which stream ecosystems should exhibit common characteristics (Wasson *et al.*, 2002). Geology, relief and climate are the determinants for hydro-ecoregion delimitation. The HERs provide a framework for grouping data in terms of natural river features and human activities. The HERs are divided in Hydrological Units (1093 entities of 10^2 - 10^3 km²) of connected sub-catchments, in order to enable gathering relevant data on land cover and land use for upstream catchments. Finally, a systematic segmenting of the 230 000 km French river network identified 69500 reaches, ranging from 1 km on average for small streams to up to 10 km on average for large rivers. The segmenting into hydro-morphologically homogeneous reaches is based on a semi-automatic Gis-process that distinguishes confluences, geomorphological boundaries, and changes in channel form, sinuosity and valley floor width. For each of these river reaches natural and stressor descriptors are aggregated from two spatial scales; catchment land cover information is gathered from the Hydrological Units, and locally, information on land cover and hydromorphology is extracted for the individual river segment for summer and winter bed and over different dimensions (i.e. buffer sizes) for the riparian corridor (valley floor, floodplain, 100 m, 30 m and 10 m).

This smallest spatial unit of the river reach has unique local and network catchment boundaries, and unique descriptors of river network position and connectivity. River reach characteristics are defined as a function of influences of natural elements (climate, elevation, geology, soil, land cover, river network position and connectivity), human activities in local and network contexts and other interactions across spatial hierarchical units (Frissell et al. 1986; Thorp et al. 2006). The descriptors of these characteristics are gathered in a uniform way from national databases, geospatial datasets and GIS derived features. The nested structure reflects the notion that factors operating at lower hierarchical spatial levels may be influenced by factors at a higher spatial level. Information gathered at different scale levels will be integrated in multi-scale descriptors in order to describe the occurrence and impact of human alterations to river functions.

Not only has this approach the strength of a full length assessment of the river network – not biased by sampling strategy – it furthermore allows working with an oriented, connected network structure (Grant et al. 2007). Upstream stressors do not only operate on a different scale level than downstream stressors, they can also be arranged according to stream flow, for their effects strongly depend on distance and quality aspects of the corridor (Van Sickle and Johnson 2008). Ecosystem impairments and pressures are propagated through the network mediated by the riparian corridor (Cormier et al. 2000). Moreover, as river functions and structure are tightly linked and strongly related to dendritic network structure, not only is a scale-hierarchic approach to the river basin context required, but a truly spatially interconnected network to identify functional relations is called for (Grant et al. 2007; Peterson et al. 2011). For this purpose, a topological structure of the river network, based on graph theory and stream flow model approaches, is constructed in which all segments along the branches of the dendritic network structure are embedded both in the downstream and upstream directions, so as to enable weighting connection by distance, and weighting segments as nodes in the network (Van Looy et al. 2013).

Causal relationship structuring in Bayesian Belief Networks

Bayesian Belief Networks (BBNs) are emerging as tools to aid in the conservation, restoration, and management of ecosystems (see McCann et al. 2006; Nyberg et al. 2006; Allan et al. 2012; Shenton et al. 2011). They consist of two components: a qualitative graphical structure that describes the causal relationships between the different considered variables, and a quantitative description of the strength of these relationships that relies on conditional probability tables (Naïm et al. 2007). Since the nodes are modelled by means of probability distributions, uncertainty can be estimated more accurately than in models where only mean values are taken into account. In this way, BBNs allow scientists to combine measured responses to environmental change with a conceptual understanding of the ecosystem in question within a probabilistic framework that depicts the chain of hypothesized causal relationships and quantifies the relative influence of individual linkages with explicit uncertainty (Borsuk et al. 2004). This enables ecosystem responses to potential, human-induced, change in environmental drivers to be predicted (Leigh et al. 2011; Stewart-Koster et al. 2011). In this regard they are especially suitable to risk approaches in order to detect injuries and predict responses in river systems.

The strength of BBNs lies firstly in their ability to handle data sources of different origin. Multi-scale and multi-source descriptors, including both direct sources and influential factors for impairment risks, can be included in the model. Secondly, the probabilistic framework allows both empirically-based parameters and non-parametric expert knowledge-based probabilities to be entered as priors in the inference process. Prior probability distributions can be obtained through expert elicitation of probabilities, which can subsequently be updated with the information contained in an empirical dataset. The result of such an inference is a new, more accurate assessment of the relationships between the considered variables, described by a Bayesian *posterior* probability distribution.

BBNs are particularly well adapted to deal with complex systems, for the state of a node only depends on the states of its immediate parent nodes, thus allowing one to work on smaller sub-models, which can then be linked to each other and integrated into the complete model. This property also allows for the modification of a model part without having to modify the entire model. This flexibility in structuring a model through smaller sub-models that integrate variability in the explanatory variables or in the modelled processes (Biggs et al. 2009) makes BBNs attractive tools both for informing on knowledge gaps and uncertainties, and for the construction of scenarios and presentation of possible futures.

Finally, the graphical structure of BBNs allows for the visualisation of functional links and relationships between variables and scales. The underlying graphical structure makes it easier for experts from different fields and stakeholders or decision-makers to discuss the various hypotheses depicted in the BBN and define a common language.

3. Resulting river impairment assessment over the river network

The integrated risk-based framework

The risk assessment framework (Fig. 1) simultaneously considers ecosystem functions and impairments in physico-chemistry, hydromorphology and ecology. Both within and in-between these components, functional relationships can be modelled with hierarchic Bayesian frameworks, by either quantitatively or qualitatively modelling causal relationships. The modelling framework therefore relies on the identification of natural baselines and the analysis of stressor influence on the processes and structures of river systems. Three successive steps are distinguished in our risk assessment approach (Fig. 1): 1) the *aggregation* of relevant information from different scale levels into multi-scale descriptors using typological and hierarchical spatial filtering; 2) the *integration* of descriptors into impairment indicators for processes and structures, which are implemented through BBNs (under Netica) to assess the relative contributions of the descriptors to the impairment magnitude; and 3) the *integrated modelling* of relationships between specific ecological processes and structures and their combined influences on ecosystem functioning. Uncertainties in impairment levels described at step 2 are included so as to provide a complete risk analysis. It is important to note that two kinds of statistics are provided for each node in the BBN: the most probable impairment level and the diagnostic confidence in the causal relationships for the impairment, given in the probability distribution.

Spatial filtering based on typologies can serve to better characterize and qualify environmental conditions and descriptors and thus adjust probability distributions of the impairment levels. For this purpose a chemical, hydromorphological and ecoregional typology was developed that frames natural gradients and climatic, geographical variance. For example, Van Looy et al. (2013) looked amongst chemical river types to determine relationships between nutrients and riparian conditions based on type-specific responses. When ecological data are available, the previously elicited prior conditional probability tables in the BBNs can be empirically updated using Bayesian inference. In this manner, the inferred process-based relationships can return information to descriptors and the characterisation of the river system. These feedback loops are an intrinsic part of the hierarchic inference process. As an example, Piffady et al. (2010; 2013) assessed the impacts of inter-annual variations in temperature and hydrologic regimes on the fish community using a Bayesian hierarchical generalized linear model.

Finally, outcomes of the analyses can be: a nationwide homogeneous identification of impairment risks covering the entire network, a spatial interpretation of risks of specific impairment, and a weighting or comparison of different stressors for specific functions or regions. The construction of BBNs can therefore result or evolve in accordance to specific questions for management or strategic purposes. We illustrate the framework in the following paragraphs through the hydromorphological sub-model and the pesticide pollution risks.

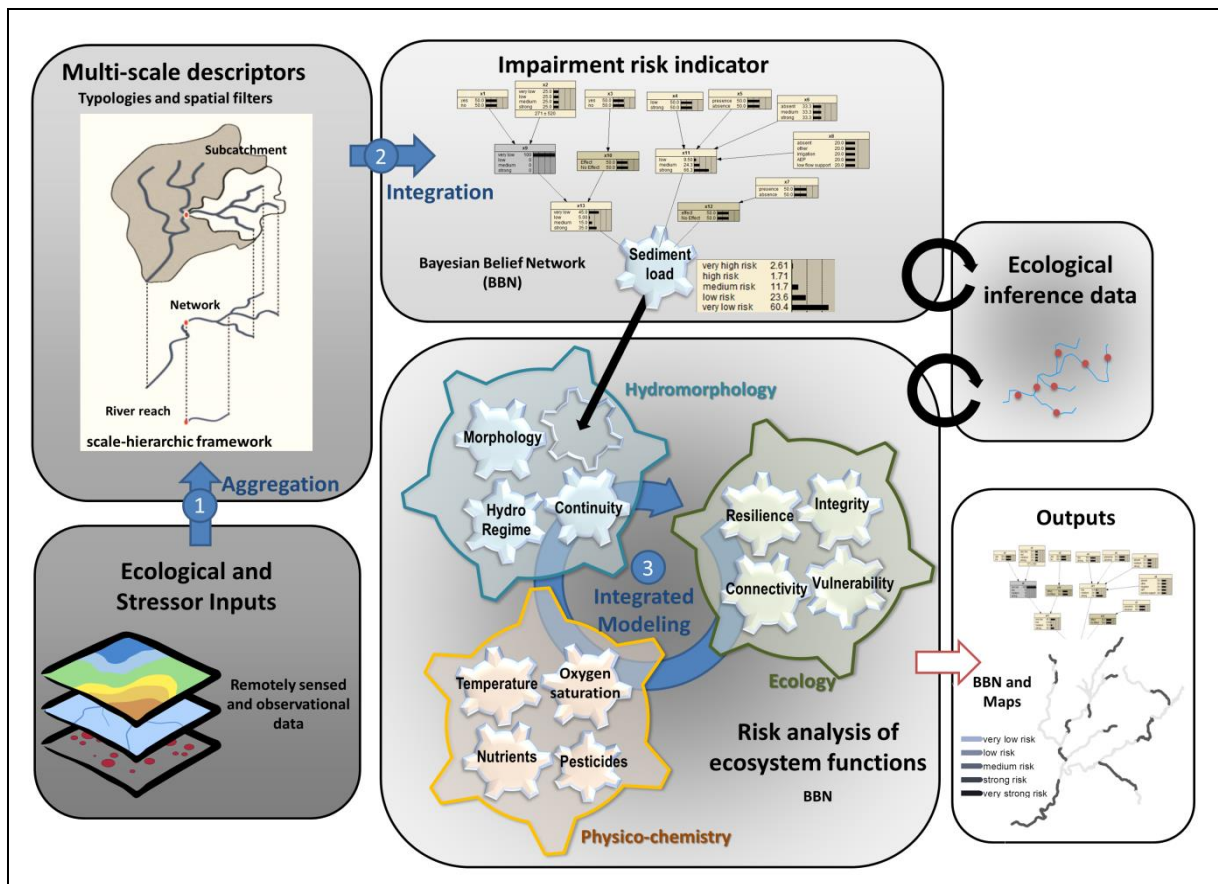


Fig. 1. Scheme of the risk-based framework of river system impairment assessment. Main steps in the framework concern the aggregation of relevant data into multi-scale descriptors, the integration in impairment indicators for ecosystem processes and structures (for which risks are assessed in the framework) and the integrated modelling of ecosystem function impairment. The central part of the scheme shows how the three ecosystem compartments interact to determine ecosystem functioning.

Risk assessment to hydromorphological impairments

Rivers have long been modified by human activities, which have impacted on three main physical components: (i) flow regime (flow quantity, dynamics and groundwater connectivity), (ii) river continuity (connectivity) and (iii) morphological conditions (width-depth variance, bed structure and substrate, river bank structure). As human impacts can act at different scales and through different pathways upon a river's hydromorphology, the advent of the European Water Framework Directive challenged the scientific community and Member States to nationally address these issues, and to synthesize elements of hydrology, geomorphology and riparian zone characteristics whilst linking them to human pressures (Gottardo et al. 2011).

BBN's are constructed for each hydromorphological indicator, with causal relationships that were primarily quantified with expert elicited prior conditional probability tables by an expert panel. These constructed causal chains are based on both natural and stressor multi-scale descriptors, taking into account natural filters (i.e. altitude, climatic-hydrologic regime) and the spatial network context (i.e. presence of dams or weirs in the upstream or downstream parts of an analysed reach). For example for the impairment indicator of river bed structure, the BBN is based on alteration probabilities of channel straightening (causing increase in flow velocity and shear stress) and local damming (causing

upstream sedimentation and downstream erosion), combined with upstream risk of sediment load blocking and the network position of large dams upstream. This indicator construction illustrates both the use of an integrative approach to stressors of different origin and scales (local and upstream network) and their interpretation in the river network. Two different and complementary statistics are provided: the magnitude of the river bed alteration depicted by the discretized state within the Bayesian network node taken by a variable and a probability distribution for the variable to take this state.

Confidence in the causal networks

Confidence in the judgment is depicted through the probability distribution among states: the more one state tends to 100% probability; the more confident we can be in assigning this state to the variable. In this work, we insist on the importance of providing two statistics; the most probable impairment and the level of confidence in this judgment. The confidence expressed in the probability distributions is given by the expert panel, based on the strength of causal relationships and the weighting of different causalities. The complexity and difficulty of this choice is then apparent in the number of parental linkages in the BBN. For this reason, the discretization of intermediate latent variables that have better identified causal links can add to the overall confidence in the BBN. So, confidence in causalities can be ensured high up in the network with the availability and accuracy of relevant information (data), or lower down in the BBN with increased knowledge for weighting the (multiple) causalities – ideally with inferred posterior distributions.

This aspect is illustrated in figure 2 with the assessment of impairment risk to river bank structure. The impairment risk indicator has two contributing latent variables; the nature of the river bank and riparian forest cover. Presence of urbanization and roads in the riparian zone are identified as causes of river bank stabilization, whereas river bank functionality is represented by riparian forest cover. Two descriptors for the riparian forest cover were retained: riparian forest cover within a 10m buffer is considered an indicator of potential shading and organic matter provision to the aquatic environment; whereas the 30m buffer riparian forest cover informs on buffering capacity (nutrient retention, diminishing impact of adjacent land use). The descriptors of riparian forest cover give good confidence with narrow probability distributions of the riparian forest latent variable in the two cases (A and B of fig. 2), whereas for the nature of the river bank, the information at hand gives less confidence, leading to more uniform probability distributions. The descriptors of roads and urbanization in the corridor give less confidence to the impairment risk to the nature of the river bank, resulting in more uniform probability distributions. Still, for the overall river bank structure we can reach quite high confidence in the case of an established riparian forest cover.

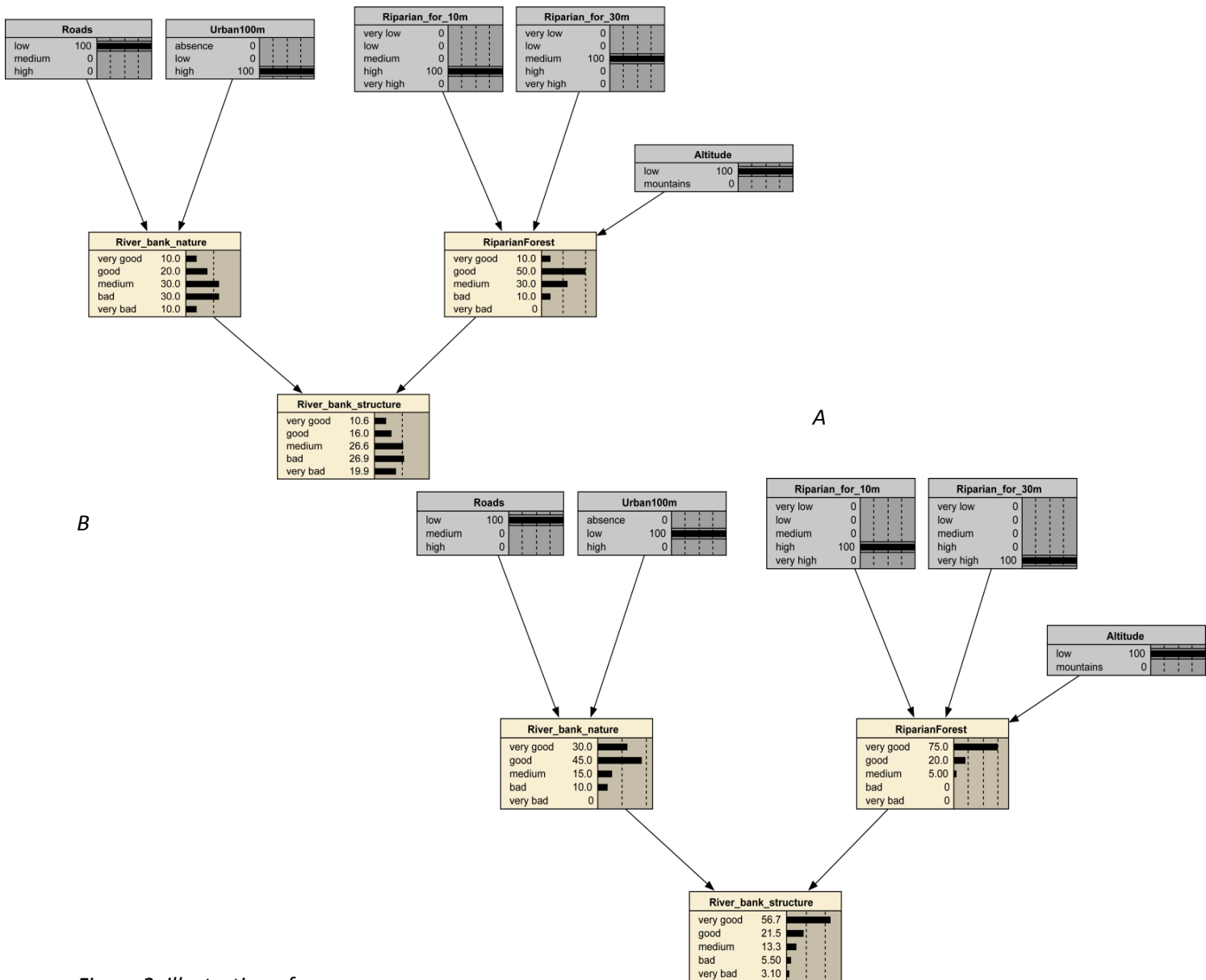


Figure 2. illustration of confidence in the BBN.

The network for the indicator of river bank structure shows causal links to two latent variables for the nature of the river bank and for the riparian forest cover. The confidence in risk judgment is present in the probability distributions for the latent variables and for the final integration in the indicator. A rather uniform probability distribution and thus little confidence in the judgment is present in case A. High confidence in the judgment is present in case B, with a highly skewed probability distribution.

Based on the observed relationship between riparian forest cover descriptors and the physico-chemical and biological quality of the river reach, boundaries for a sufficient (i.e. functional) riparian forest cover were determined (Van Looy et al. 2013). These boundary values were entered as descriptor classes into the BBN, resulting in higher confidence for the riparian forest cover latent variable in the integration and thus in a stronger foundation to the risk mapping of impairment to the riparian zone structure (Fig. 3). Mapping these associated confidences in judgments furthermore allows identification of knowledge gaps linked to geographical context (see inset in figure 3).

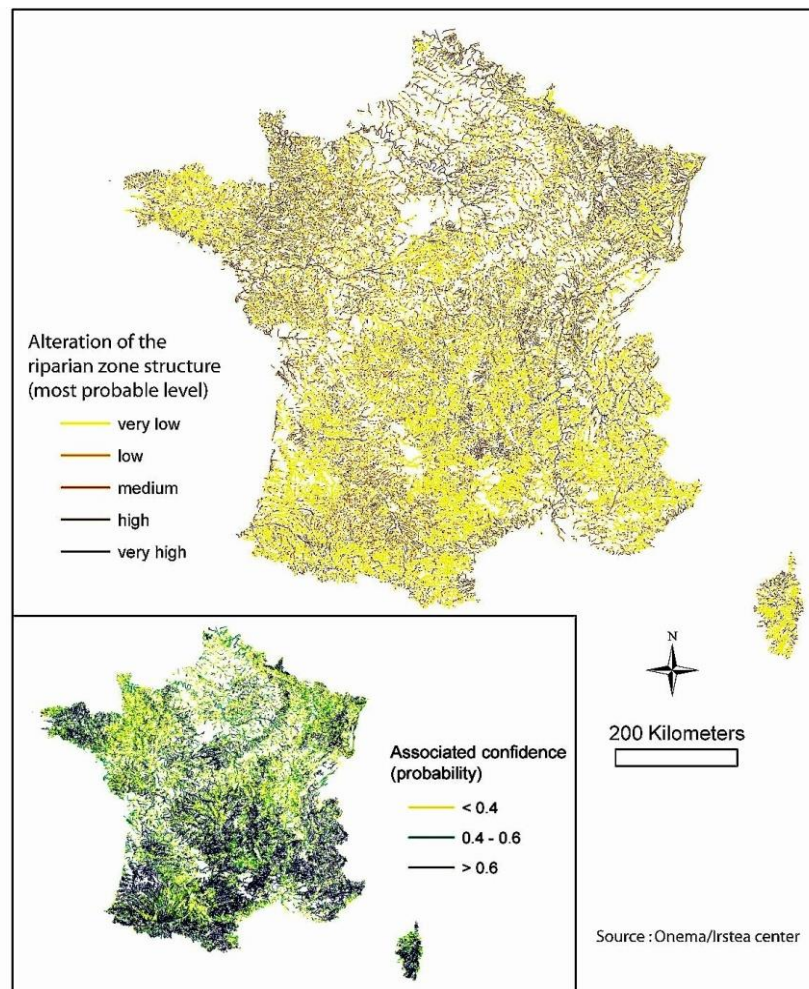


Figure 3. Impairment risks to the riparian zone structure for the French river network. The risk assessment is presented in terms of the most probable level of impairment of the riparian zone structure in France. The inset figure map shows the associated confidence to this level of impairment, for the 230 000 km French river network.

Risk assessment for diffuse pollutions

The potential impacts of agricultural pesticides on watersheds' ecological status are a further important concern in the European water strategies. There is a major interest in developing models that can reliably assess the risk for rivers of being contaminated in view of the complexity of multiple stressors in the watershed (Harris and Heathwaite 2012, Heathwaite 2010). At first, such approach demands a diagnosis of physical properties of soils at the basin scale to determine the main way of transfer from the field to the river. Existing methods did not account for the different chemical component properties in the pollution transfer, such as persistence or water affinity that can either positively or negatively interact with the contamination risk. The Arpeges (Risk Analysis of Pesticides for Surface Water management) model ambitions taking the soil and the molecule properties into account to provide a unified model of contamination risk over the French national territory. It provides a robust tool for the French Water Authorities in assessing the status and the risk of failing to meet the environmental objectives.

The model is developed within the risk assessment framework. It combines catchment-scale descriptors into indicators of seasonal acute and chronic pollution magnitudes. Descriptors, related to main ways of pollution transfer, chemical component properties and pesticide use, are derived from national GIS databases.

In the BBN, the pollution process has been decomposed according to the three main ways of transfer to the river (surface run-off, leaching of water-soluble pesticides through permeable soils, and tile drainage) that were described for their intrinsic vulnerabilities. The intrinsic vulnerabilities refer to the physical soil properties, aquifers, hydrographical network and drainage density, and potential interactions with biological characteristics of the riparian corridor that can slow down water transfer and actively extract solutes. The considered properties of pesticides are the persistence (half-life duration), the soil organic carbon-water partitioning coefficient (water affinity) and the solubility. By crossing the intrinsic vulnerabilities with chemical properties of molecules, the specific vulnerabilities are determined. Two specific vulnerabilities were considered: vulnerability to chronic and acute pollution.

In addition to the vulnerability, information on pesticide use is entered in the model. Both the processes of transfer as the application practices have been considered as being influenced by climatological variables. These are principally the frequency and quantity of rainfall, which were retained as factors to a spatial and temporal hierarchic approach: based on a geoclimatic zone delimitation (Champeaux and Tamburini 1996) and time periods for the seasonality (spring/summer and autumn/winter). Finally, the information on the quantity of pesticides used is crossed with the specific vulnerabilities to give the resulting seasonal acute and chronic pollution risk level. Class boundaries and conditional probability tables have been set up accordingly with expert judgments for presentation at a national scale level. See Figure 4 for an example of model result over the French territory (for the 1093 Hydrological Units).

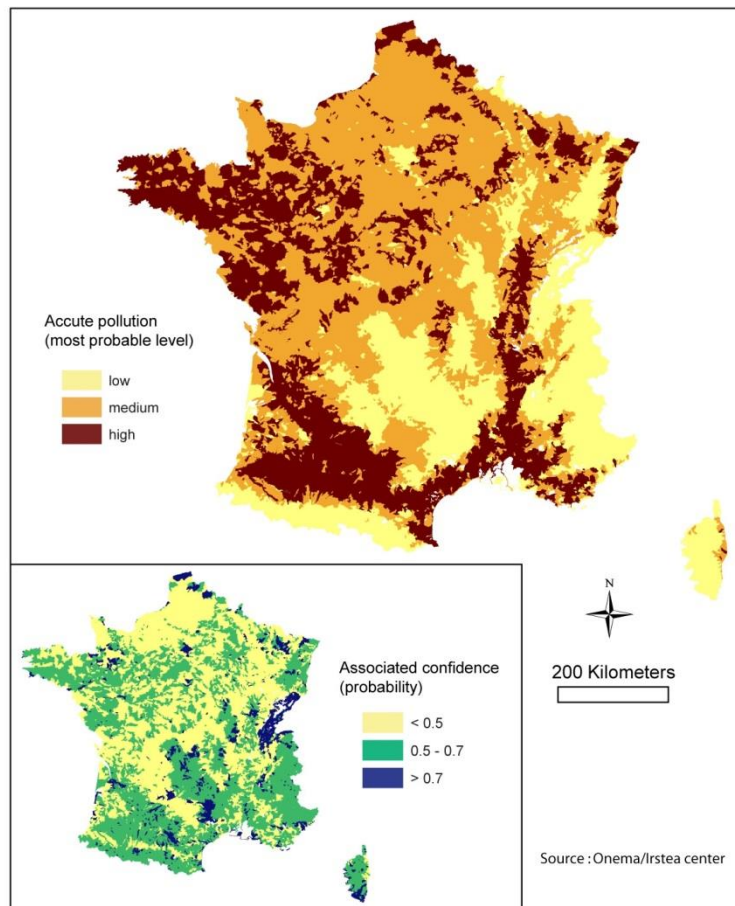


Figure 4. Risk assessment for acute pollution of pesticides with presentation of the most probable level of pollution and the associated confidence for the French national territory.

4. Discussion

The examples described above demonstrate the potentials of the integrated risk-based framework to better frame and determine the relative contributions of stressors to the impairments of river systems. The presented hydromorphology assessment covers the entire stream network of France and was used by the river management authorities in elaborating the 2013 status report under the Water Framework Directive. Local validation by the water authorities' experts confirmed the assessment in 80% of the cases. To our knowledge, few similar comprehensive assessment systems exist at such large scales using spatial hierarchic frameworks (see Davies et al. 2010; Davies et al. 2012; Wang et al. 2011; Esselman et al. 2013). Those examples are habitat-oriented audit frameworks assembling relevant natural factors and human disturbances in order to assess ecosystem types. Still, it is difficult to bring all the relevant elements into the picture, both due to gaps in information, and to the complexity of interactions. We believe the proposed risk approach provides a promising additional field for most comprehensive assessment systems, as it allows the inclusion of all environmental insights and at the same time highlights shortcomings in both information and understanding of relationships.

This is also illustrated by the Arpeges model that brings a comprehensive pesticide pollution risk assessment, combining strengths of different existing model types. The aggregation and integration of the information entered in this model is quite unique; most diffuse pollution models are or small-scale pathway models or catchment scale models at best combining hydrological and river quality models (Arheimer and Olsson 2003). The Arpeges model is oriented at sub-catchment scale risks while integrating individual molecule pathways and both local soil biogeochemical processing aspects as large scale climatic and geologic-geographic factors. Thus we follow the recommendations for diffuse pollution modelling to combine the approaches and results of chemometric data analysis methods that are based on observation and analysis of experimental data, and deterministic models that are defined as numerical methods based on theoretical principles (Terrado et al. 2009).

The risk approach allows weighting of the different sources of evidence in the integrated assessment model, where drivers may operate at different scales. The innovative elements in the proposed framework consist firstly in the presentation of both the confidence for the appraisal and for the understanding of processes and causal relationships. Secondly, the integrative character of the BBN structure translates the complexity of the relationships studied. They can be associated with evidence weighting to determine the incidence, distribution, and causes of impairment (Cormier and Suter 2008; Norris et al. 2012; Webb et al. 2012), and probabilistic frameworks that allow modelling and predicting possible futures for the relationships between environmental stressors and stream condition (Stewart-Koster et al. 2010; Allan et al. 2012; Sheldon et al. 2012). In this formalized risk model structure, expert judgment can lead to a better understanding of causal relationships between environmental stressors and ecological responses (Beven and Alcock 2011; Allan et al. 2012). Inferring posterior values to prior estimates in integrated modelling of ecosystem processes is a necessary step to ensure a rigorous weighting of conditional probabilities. However, observational data are not always available, and not for all descriptors. This can be due to many factors, such as costs of field campaigns in a national network survey or the difficulty of developing a coherent experimental protocol. The main strength of this risk approach is that it can reach conclusions (albeit with less certainty) without having full data. Furthermore, in the context of very complex systems, it can be significantly helpful in identifying knowledge gaps for a full understanding of the studied process.

The second strength of the proposed framework is the elucidation through BBNs of the pathways of impairments to ecosystem processes. All existing knowledge and expertise can be integrated in a network that depicts the chain of causal relationships, while at the same time quantifying the relative influence of individual linkages with explicit uncertainty (Borsuk et al. 2004), and taking into account complexity through a multitude of links between stressors and causalities (Biggs et al. 2009). Although relationships that can be identified in this way are not necessarily causal, the ability to predict aspects most at risk using broad scale predictors should serve as a useful management tool (Cormier and Suter 2008; McGinnis and Kerans 2013). With such a model, permanently taking the uncertainties associated with the processes into account, the effects of different management options for stream systems can be assessed fairly, as future possible conditions and their probabilities of occurrence can be predicted based on forecasts of land-use change or implementation of best management practices.

In conclusion, the framework with Bayesian estimation of risks presented here provides a comprehensive and rigorous assessment approach to river impairments. Particular attention has been paid to the development of visually attractive, user-friendly, flexible and evolving approaches to improve their transfer. Both indicator selection and restoration decision are founded on a balance of environmental and social principles (Pedroli et al. 2002; Bouleau et al. 2009), and effective management solutions are only achieved when based on thorough and sound science that evolves with the changing environment.

Acknowledgments

The authors gratefully acknowledge the financial and structural support for the SYRAH hydromorphology audit and ARPEGES model project of the ministry of ecology, the water authorities and the French National Agency for Water and Aquatic Environments (ONEMA). The international collaboration and the scientific harmonisation of the public water policies to the European WFD since 2000 started the flow of ideas at the basis of the presented framework. We would like to thank Ricardo Simon, Angus Webb, Catherine Leigh and Martin Thoms for their valuable comments and suggestions to earlier versions of the manuscript.

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Global warming induces strong shifts in temperate stream invertebrate communities through local and regional scale mechanisms

Kris Van Looy¹, Martial Ferréol¹, Marta Prieto-Montes¹, Mathieu Floury¹, Yves Souchon¹.

¹: Irstea, National Research Institute of Science and Technology for Environment and Agriculture, UR MALY, River hydro-ecology unit, 5 rue de la Doua, Lyon-Villeurbanne, France

Abstract

Global warming is assumed to be a threat to temperate stream biodiversity, but many of the processes and mechanisms behind the predicted threats to diversity are uncertain. We aim at identifying current trends and drivers of change for freshwater communities over a large spatial and temporal scale. From a large-scale long-term dataset on stream invertebrates from the river network of France, ranging over 1000 km in longitude and latitude, we analysed diversity and composition shifts over time in relation to geographic elements and human stressors. Mechanisms for local site community change were investigated with a fourth corner analysis of biological traits. For spatial and temporal diversity patterns and changes the dissimilarity was investigated and partialled out over turnover and nestedness components.

We observed a 42% increase in the taxonomic richness of stream invertebrate communities over the last 25 years, largely caused by climate change (23% purely climate-induced taxonomic richness increase). A bottom-up food web productivity response to rising temperature was responsible for the strong increase in local site diversity. Stochastic assembly processes increased the regional scale diversity, giving spatial insurance to biodiversity and countering the risk of biotic homogenisation. Stream communities appear to be highly resilient to environmental changes due to local and regional factors that promote productivity, stochastic assembly and dispersal processes.

Key words: biotic homogenisation, trophic amplification, stochastic assembly, large scale, long term, productivity, response diversity

INTRODUCTION

Climate change is depicted as a threat to biodiversity in all its forms; both by increasing extinction risks of species locally, and homogenisation of communities regionally (Cardinale et al. 2012). Freshwater ecosystems around the world are subject to frequent and pervasive invasions and spreading of ubiquitous generalist species (Olden and Poff 2004); the two main causes of biotic homogenisation identified as global threats to river biodiversity (Vörösmarty et al. 2010). Aquatic invertebrate communities are well known for their sensitivity to warming and high susceptibility to both biological invasions and dominance by generalist species (Poff et al. 2012). Furthermore, climate change is always associated with multiple other stressors (Heino et al. 2009) which likely generates interactive effects (Ormerod et al. 2010).

Observing and predicting global change effects requires long-term, large-scale analyses. Patterns of species diversity and community changes in real ecosystems under environmental change require our attention (Gilman et al. 2010). To this end, we have constructed a long-term series of annually sampled stream and river sites that employs standardized methods, spanning the three last decades and over 1000 km in both longitude and latitude; sufficiently large spatial and temporal scales to attribute biodiversity changes with high confidence to climate change (Parmesan et al. 2013). The drivers of biodiversity change are determined independent of scale (Chase and Knight 2013), by comparing individual sampling sites over time and by analysing community changes in a selected group of taxa. This analysis is complemented with diversity partitioning for several spatial and

temporal scales in components of turnover and nestedness (Baselga 2010). Our overall aim was to test two hypothesized trends: diversity declining with rising temperature, and homogenisation occurring over large spatio-temporal scales.

For both hypotheses, the challenge is to discern the specific drivers of local and regional biodiversity and compositional changes in the complexity of environmental changes. For the homogenisation hypothesis, the changes at higher spatial scales have to be investigated, whereas for the thermal and trophic regime perturbation, the response of local diversity and loss of taxa is at stake.

For the local diversity, other mechanisms besides temperature sensitivity, habitat deterioration, invasion or dominance may also contribute to responses to warming stream systems. Higher productivity and trophic amplification (Beaugrand et al. 2014), higher dispersal abilities and species shifts in general might counter the hypothesized decline.

For the regional scale level, community assembly mechanisms that can maintain diversity involve either deterministic or stochastic processes (Vellend et al. 2014). Species diversity and composition vary deterministically along environmental and/or spatiotemporal gradients. With global changes (homogeneous overall trends), convergence in these gradients and thus biotic homogenisation is to be expected with time. Still, stochastic processes can increase site to site variation in species composition (β diversity) under such conditions (Rosindell et al. 2012). Stochastic processes may therefore override deterministic processes of community assembly, driving response diversity (Elmqvist et al. 2003) and providing some spatial insurance against broad-scale homogenisation (Ruokolainen et al. 2009, Chase 2010). We tested the hypotheses of local and regional scale responses in taxonomic and trait-based diversity and dissimilarity changes.

MATERIALS AND METHODS

Dataset construction

We constructed a dataset spanning over 25 years from 91 sites throughout France sampled annually for aquatic invertebrates. Sites ranged from streams to large rivers (mean annual discharges between 9 - 192 m³/s) and spanned over 1000 km in longitude and latitude, between 8 - 977 m above sea level. The sampling protocol for all sites consists of sampling a reach ten times the stream width, for which a number of unitary samples are collected with a Surber of 500 μ m mesh size and 0.05m² large. Each sample corresponds to a mesohabitat categorised by both substrate type and water velocity. Mesohabitats are sampled in a hierarchical order, according to their potential to host different taxa. In 2007, the number of unitary samples raised from 8 to 12. The first 8 subsamples correspond to those of earlier protocols. For this study, only the first 8 unitary subsamples were considered, allowing to construct a harmonized data set from the different protocols.

All invertebrates in the samples are identified, but the level of taxonomic resolution varies depending on time period and region and therefore we retained the finest, most consistent level available: the family level. This level is the most robust when analysing macroinvertebrate data at large spatial scales because regional differences in species pools limit the detection of general patterns at finer levels of taxonomic resolution (Heino 2014). Regardless of the resolution chosen, analysis of both abundance-weighted community composition and presence-absence data is needed to infer environmental relationships and trends (Heino 2014). Therefore we conducted our analysis on both these types of data.

All sites at the national scale are monitored to assess general trends in biodiversity, with a spatial spreading that is based on river type and catchment. They do not correspond to undisturbed reference conditions and cover all the gradients of human presence over catchments. We therefore added to the above set of sites a set of annually sampled reference-condition sites to allow us to cross-check our findings from the above analysis against those associated with no immediate human impacts; i.e. to separate direct human-induced effects from global trends. This set of reference-condition sites consists of samples from 51 sites covering the period 1992 - 2011. They are selected

according to national reference-condition standards for chemical water quality and catchment land use, and we verified for the reference sites the absence of trends for chemical water quality parameters in time. For the chemical water quality, the systematically measured pollution and trophic state variables of dissolved oxygen content, pH, chlorophyll a and pheopigment concentration, ammonium, nitrites, nitrates and orthophosphates were retained and mean values were calculated on the monthly water samples for a time span of eleven months before and one month after the biological sampling. For robustness of the data set, in the light of the single annual biota sampling, the accidental gaps in the series and to dampen meteorological irregularities, we constructed eight three-year periods of analysis.

Catchment disturbance - determined with the proxy naturalness of the catchment land use (based on CORINE Land cover data category near-natural land use) and water pollution (based on monthly chemical water quality sampling) were used as the environmental factors representing the main stressors to river biodiversity (Vörösmarty et al. 2010). Altitude and river size (Strahler order) were entered into the analysis as geographical parameters, to complete the environmental gradient of river conditions potentially explaining macroinvertebrate community structuring. Temperature increase for the studied region is gradual and reaches 1°C over the three decades for air temperature measurements; whereas for water temperature an average increase of 2°C over the same period is reported (Daufresne and Boët 2007, Floury et al. 2012).

Analysis of local scale changes

To detect local scale changes of taxonomic diversity and functional changes, at first a site occurrence frequency regression analysis for the taxa over the long-term series dataset was executed to identify general richness and taxa specific trends. The use of taxonomic composition alone may be insufficient to unambiguously distinguish local effects from natural biogeographic variation of populations (Webb et al. 2010). The biological trait profile of a community offers an alternative approach for assessing responses in stream communities (Poff et al. 2010). We therefore used biological traits to determine functional relationships between biota and environmental characteristics, and community response to climate change (e.g. Poff et al. 2010). Community traits were calculated by implementation of a fuzzy coding approach to quantify the affinity of each taxon for each modality within a trait. This established method (Usseglio-Polatera et al. 2000, Bêche et al. 2006) demands an affinity assignment to each trait modality for each taxon. For each of the taxa, we documented 15 biological traits divided into 50 trait modalities (Table 1). The traits relate to the life history of organisms (e.g. size, number of reproductive cycles) or features that confer resilience or resistance beyond that provided by life history traits (e.g. attachment), as well as more general biological and physiological features (e.g. feeding groups, respiration).

To analyse community traits and properties of sites through time, a fourth-corner analysis approach was used (Dray et al. 2013) that distinguishes significant differences in trait composition over time. Fourth-corner outputs are statistical parameters to be incorporated into causal ecological models describing the mechanisms determining the observed associations or correlations, rather than modelling technique outputs. Here, we use time as single variable to analyse trait compositional changes over the sample sites. Autocorrelation of the successive time periods is not discussed as we consider each period as independent from the others (i.e. investigated in terms of disjunctive variables). Results are Pearson correlation coefficients for each pair between trait modalities and periods. Their significances are respectively tested by a permutation of both rows (samples) and columns (taxa). For the eight time periods, trait modalities that were significantly positively and/or negatively ($p < 0.05$) associated to a period were detected.

Dissimilarity and community turnover

To test at the regional level for biotic homogenisation and community turnover patterns we examined both spatial and temporal β diversity changes for the whole survey period, as well as for distinguished specific trend periods. Spatial β diversity was measured for abundance data as Bray-

Curtis dissimilarities between sites for different periods, whereas temporal β diversity was measured as Sørensen diversity for individual sites over time periods. Dissimilarities among communities result from two different processes: species replacement (turnover) and nestedness (directional species gain and loss). We partialled out the temporal β diversity in its components of species replacement, as measured by the Simpson dissimilarity index, and nestedness-resultant dissimilarity, which is estimated by subtracting the turnover effect from the total β diversity (Baselga 2010). We are aware of different opinions how β diversity partitioning should be done (Podani and Schmera 2011, Carvalho et al. 2013) and believe that for the interpretation in our temporal analysis the turnover and nestedness indices of Baselga (2010) provide the most appropriate information (Legendre 2014). To test for functional homogenisation, Rao's functional diversity index (Champely and Chessel 2002) for the community traits was calculated and compared over the time periods.

To counter homogenisation and provide insurance to taxonomic diversity, community assembly has to show a response diversity that has only minor spatial structuring; i.e. it must not be fully governed by geographical and environmental gradients. This is because homogenisation will occur in the long run if community changes are spatially structured, i.e. driven by deterministic processes. As the calculation of β -diversity can vary when the size of the regional species pool varies (Chase and Myers 2011), we selected a 'constant' species pool within a specific taxonomic group — a community module in the sense of Gilman (2010) — to disentangle the relative contributions of deterministic and stochastic processes (Vellend et al. 2014). The group selection compensates for the lack of detailed information on local species pools and environmental conditions, to better understand how large-scale processes influence biodiversity and community assembly (Ricklefs 2004). The selected group consisted of 12 families of the Trichoptera order, for which sites are selected with at least 6 out of 12 families present and with continuous presence before and after the year 2000, thereby ensuring temporal continuity. Seventy-nine sites from the long term series had data that met the group-selection criteria. The composition of the group should converge or at least show some spatial structuring if environmental forcing is present. To test for this, we performed a Mantel test of similarity between communities over the spatial gradient present in the dataset. Partial mantel tests for the environmental factors and the geographical distance then allowed us to decouple pure spatial from environmental structuring.

Results

We found a strong continuous diversity increase in the long-term time series whereby average taxonomic richness rose by 42% over 25 years (Fig. 1). Taxa with the strongest increasing trends ('winners') over the long-term time series (Fig. 1) belong to the Diptera, Odonata and especially the Trichoptera, with more than half of the strongly increasing taxa in this order. The two taxa with decreasing trends ('losers') are associated with lentic environments.

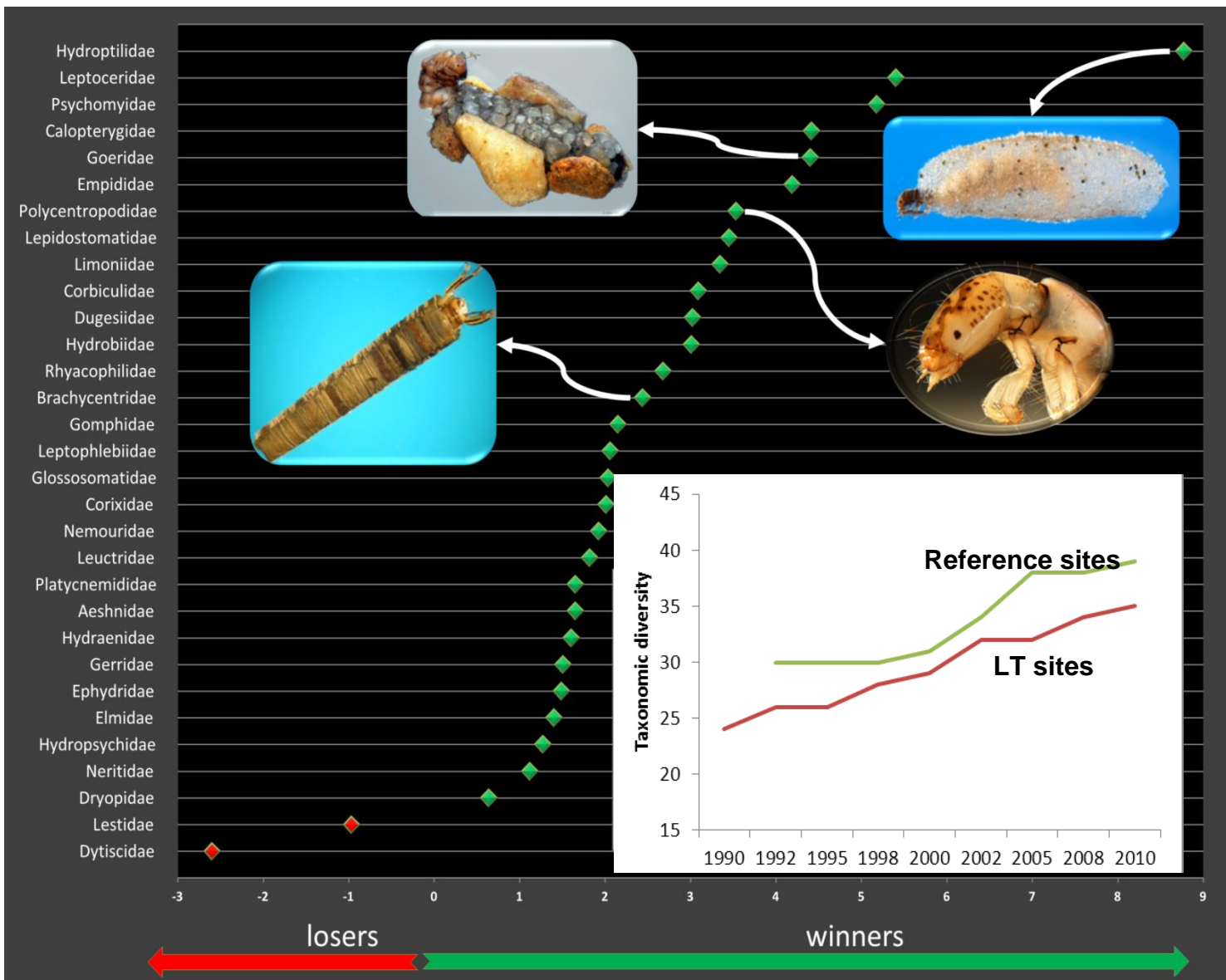


Figure 1. Significant winners and losers over the long-term time series; taxa with significant trends (regression slope values for presence frequency over the sites in time). The inset graph shows the evolution of taxonomic diversity for the long-term time series (91 sites) and the undisturbed reference sites (51 sites) average richness values. Photo credits Fabrice Parais.

We checked the above trend — caused by water quality improvement and climatic change together — with those in the set of near-pristine sites considered to be in reference condition. For the reference sites, the period before 2000 shows constant diversity, in contrast to the recent period (after 2000) which shows a 23% increase in taxonomic richness (Fig. 1). The trend for the new millennium is comparable to that of the long-term time series. This diversity increase represents a trend which we believe is solely induced by climate change, as water purification or restoration measures are not relevant for these undisturbed reference sites.

Trends in some physical-chemical water parameters were also present for the recent period (Fig. 2). General water quality improvement over the entire period shows diminishing concentrations of orthophosphates (average decrease over all sites - 0.09mg/l) and nitrites (- 0.05mg/l). Since 2000 oxygen content has increased (+ 0.5mg/l on average 2000-2010) and ammonium declined (- 0.05mg/l). These latter two trends we associate with higher primary production (and nutrient cycling) due to temperature increase. Climate change increases primary production as higher temperatures result in higher bacterial and photosynthetic activity. For streams, bacterial and algal production occurs in biofilms. Increased biofilm growth is suggested by the increasing pheopigment concentrations (which measure degraded plankton, including benthic plankton) observed over the time period.

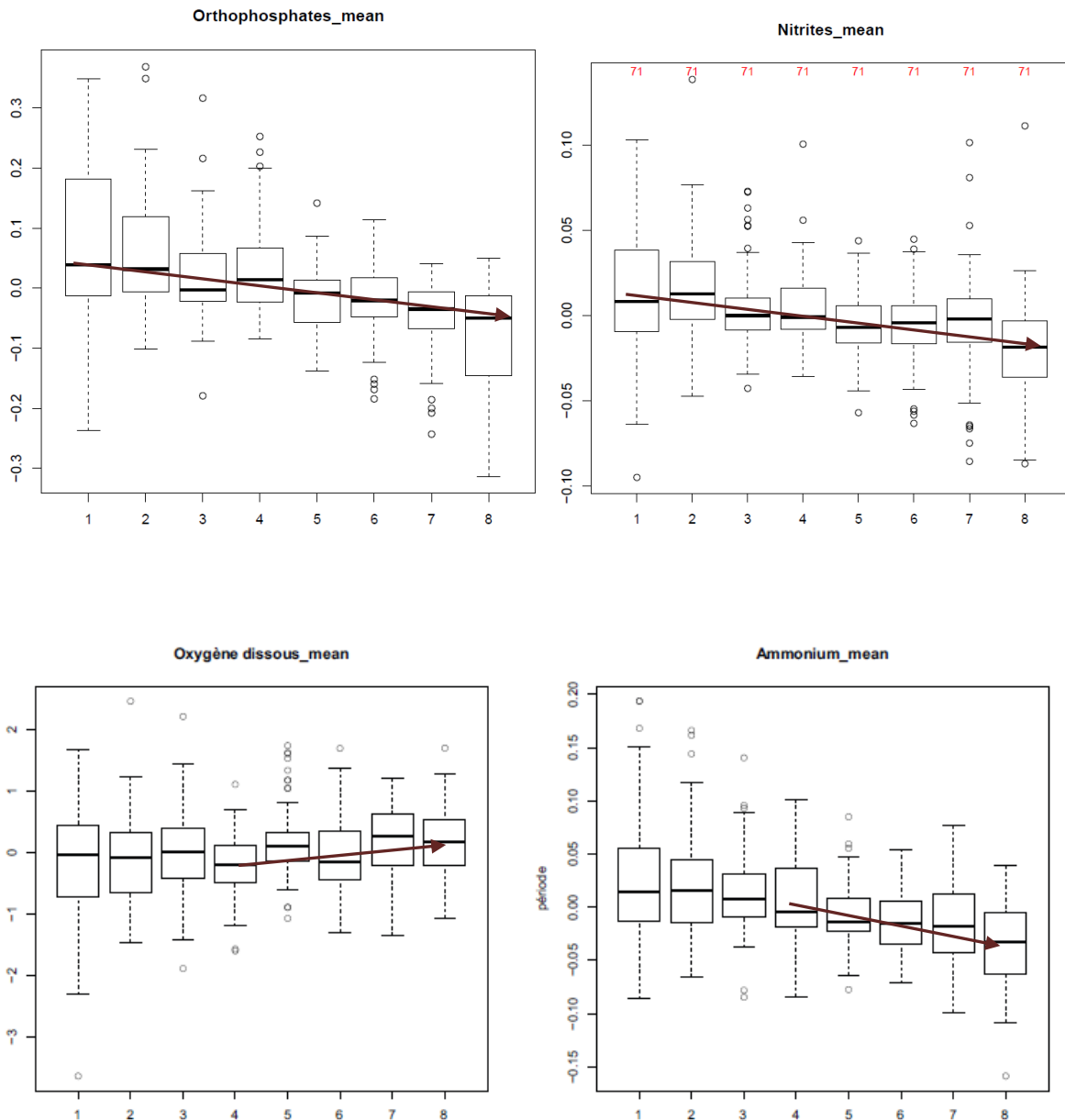


Figure 2. Water chemistry parameters with significant trend over the time series, in a centred-weighted presentation over the sites for each period. Orthophosphates and nitrites showing trend over the entire period, whereas for oxygen and ammonium trends are only present since 2000.

Bottom-up food web mechanism of productivity-biodiversity increase

Our community traits analysis also revealed strong trends since 2000 for the trait categories of functional feeding groups and food resources (Fig. 3). Functional changes describe a gradual bottom-up trophic amplification (Fig. 4a) starting from a stable period before 2000 that was associated with filter feeders. The first years of the new millennium (2000-2002) are then associated with significantly more microphyte scrapers, followed by piercer herbivores which are significantly associated with the 2003-2005 period, followed by a period of predator increase. This mechanism of bottom-up food web response to productivity increase or trophic amplification is significantly reflected in the strongest increasing taxonomic group of the caddisflies (Fig. 4b), as this order includes a variety of life strategies covering the full extent of the food web occupied by the invertebrate fauna. The trophic amplification in the caddisfly families is stepwise: response to productivity increase of bacterial and planktonic growth is reflected in strong increase of small biofilm-feeding taxa (Hydroptilidae, Psychomyidae); a more gradual increase of larger herbivores (mixed group feeding on detritus, algae and macrophytes); a third and final strongly increasing group consisting of medium sized predatory Polycentropodidae, Leptoceridae, Ecnomidae and Rhyacophilidae that show a retarded response, yet with a strong and rapid increase a few years after the first group that consists of prey species.

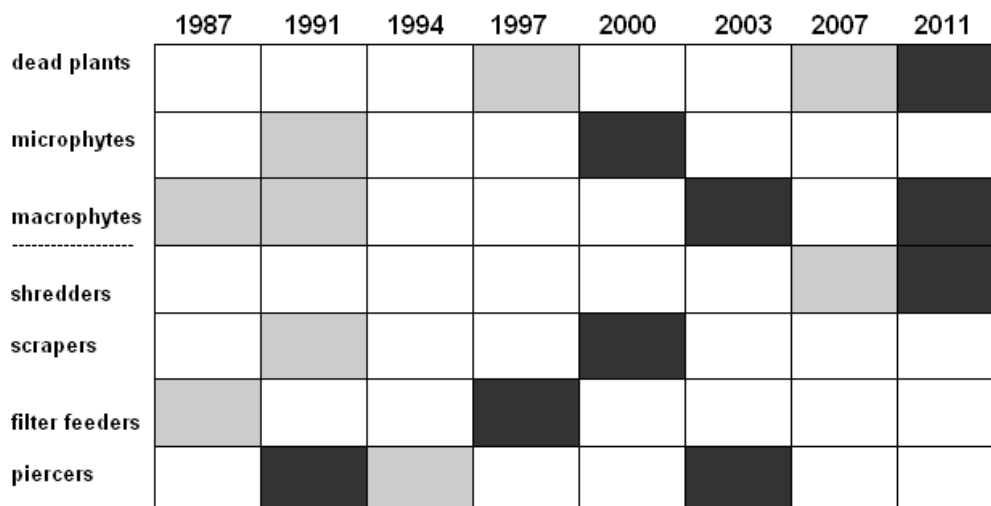


Figure 3. The significant community trait associations to specific periods (mid-period year as column header) in the time series, for the food resources and the functional feeding groups. This fourth corner analysis output gives in grey negatively associated periods, in black periods with significant association of the specific trait modality.

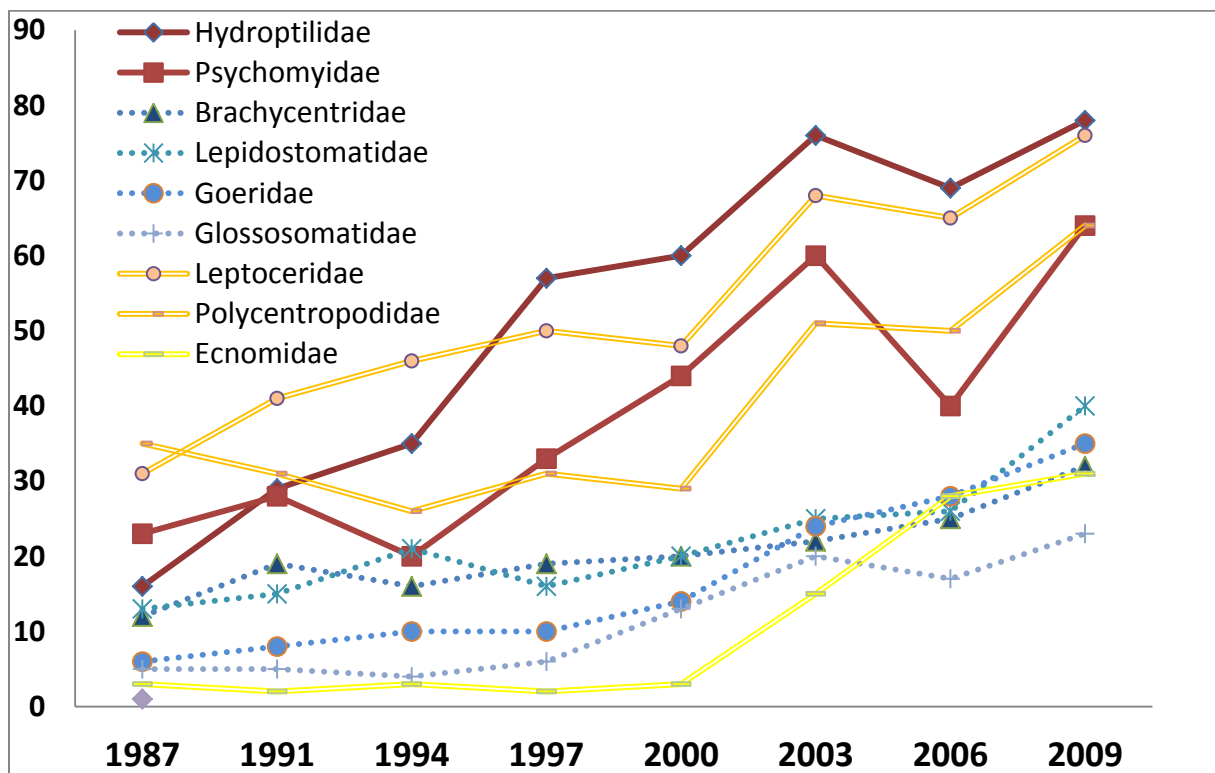
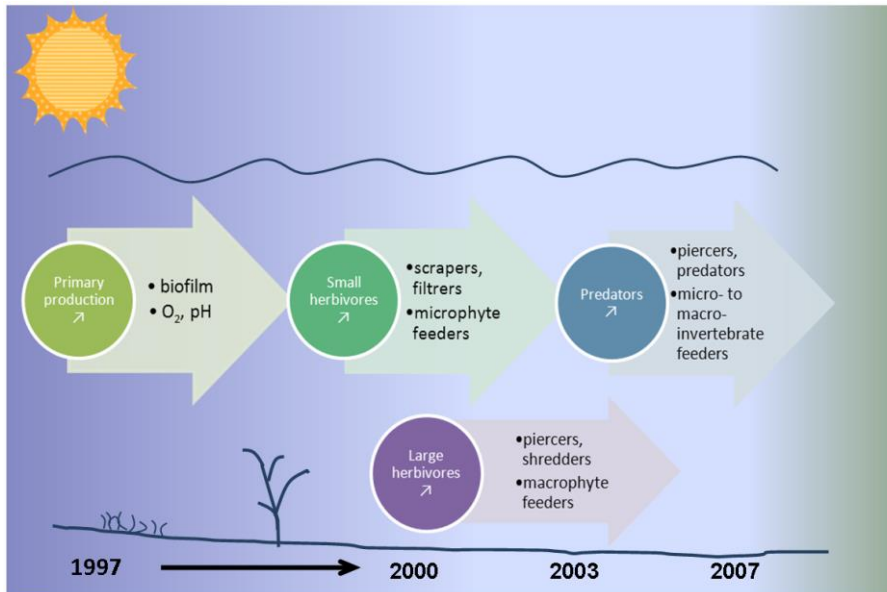


Fig. 4. (a) Observed bottom-up control of food web amplification with identified community trait changes for feeding guilds and habits in time, explaining temperature-productivity-biodiversity relationship of streams in temperate zones. (b) Frequency of caddisfly families over the long term series (presence of taxa over 91 sites; on first axis the centre year of period). Three groups can be distinguished: 1) in red solid lines the first step responding group of the smallest caddisfly families feeding directly on biofilms; 2) a large herbivore group with gradual increase in blue dotted lines; 3) in orange dashed lines the last responding strongly expanding group consisting of medium sized predatory taxa.

Spatial and temporal pattern of β diversity

Spatial and temporal β diversity show high and similar values over the long term series (temporal β diversity: 0.63 SD 0.05, spatial β diversity: 0.60 SD 0.05). The pattern shows little change through time, even when we partition β diversity (Baselga 2010) into community turnover and nestedness. The community β diversity changes across all sites are very small ($<2000 \beta$: 0.46, $>2000 \beta$: 0.44), associated primarily with a small turnover change (0.36 and 0.33 respectively). No significant differences are observed for nestedness, even if values are slightly higher for the period after 2000, in line with higher increase in species richness observed. No homogenizing trend towards increasing similarity among sites is present, especially not for the period after 2000 – associated with climate-induced changes – showing an increase in β diversity from 0.51 to 0.56. Nor are there changes in functional diversity of the community traits over time which might indicate functional homogenisation (Hillebrand and Matthiessen 2009, Baiser et al. 2012).

For our caddisfly community module strong response diversity is observed with high dissimilarities (mean dissimilarity 0.47), resulting in strong spatial differentiation in abundances and dominance (Fig. 5). Mantel tests for dissimilarity within this group and spatial distance between sites revealed the absence of overall spatial structuring. With partial Mantel tests for dissimilarity considering the environmental factors, the absence of pure spatial structuring for Euclidian distances is shown. When geographic distance is partialled out, the environment only marginally correlates to dissimilarity, for river size ($r(\text{AB.C})= 0.12$, $p<0.0001$), altitude ($r(\text{AB.C})= 0.07$, $p<0.01$), naturalness ($r(\text{AB.C})= 0.11$, $p<0.0001$) and not to water pollution. This confirms the principal role of stochasticity in assemblage structuring for the group/community module, with only a minor role being played by geographic and environmental gradients.

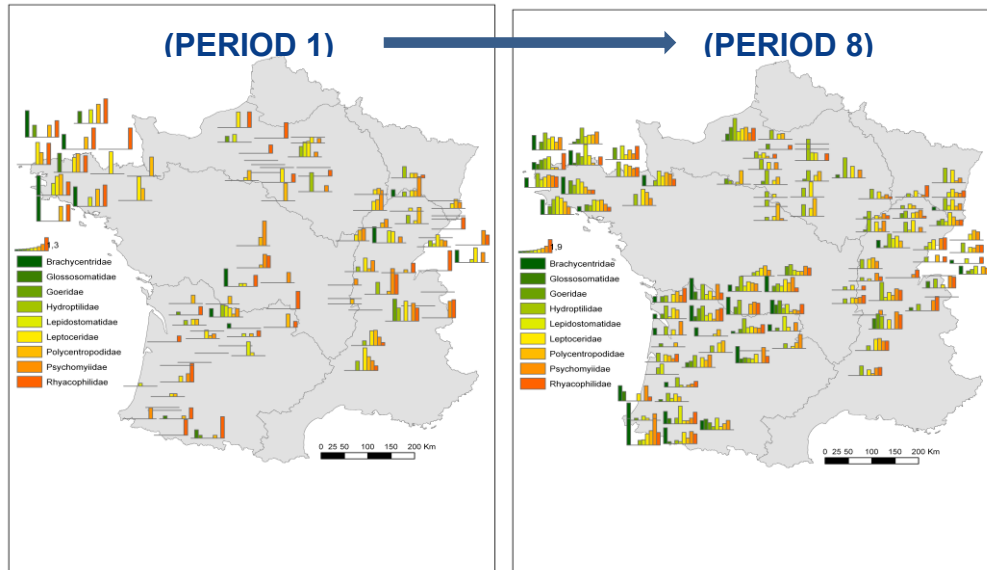


Figure 5. The site abundances for the first (1987-1990) and the most recent period (2008-2011) of the selected taxon group (Caddisfly families with significant abundance tendencies are presented). Strong increases both in abundances and evenness are present (notice in the figure that the logarithmic scale for the two periods is different; for the first period logarithmic abundance scaled 1.3 corresponds to 1.9 in right hand figure). The recent period shows highly diverse communities with high abundances of caddisflies showing both locally as regionally strong evenness.

Discussion

In contrast to presumed slow and gradual climate change impacts (Parmesan and Yohe 2003), we show strong community shifts occurring due to warming. No loss of taxa is observed; on the contrary, we observe a strong and continuous increase in diversity. Our observations are in line with the suggested absence of competitive exclusion for stream invertebrates (Death 2002), enabling higher diversity with increasing productivity (Tonkin et al. 2013). As described, α diversity for aquatic invertebrate communities increases with productivity through the local trophic amplification mechanism. It does not decline after an optimum as assumed in the productivity-disturbance hypothesis (Townsend et al. 1987). A more log linear relationship between diversity and productivity has already been postulated for aquatic invertebrate communities, even at finer spatial grain analyses (Death 2002, Tonkin et al. 2013). For the productivity-driven α diversity increase, we assume that local scale biotic processes of differential competition and resource use are at play, like the facilitation process that is documented for the caddisfly families (Cardinale et al. 2002).

Both for the trophic amplification and for the stochastic assembly process, the caddisfly community module analysis brought the most striking evidence. The analysis within this restricted group allowed to overrule scale dependency of β diversity and distance decay relationships. The overall low taxonomic resolution to the analysis might appear as a limitation to detect climate-induced changes. We verified the observed tendencies with genus-level data present for the first and last period and for the community module analysis; the general tendencies of diversity increase and β diversity maintenance over the entire period and spatial differentiation within the community module was confirmed.

At the regional scale, the observed change in diversity does not find its origin in organisms following the temperature shift northwards. With spatial differentiation remaining unchanged a boosting of regional species pools is revealed. There is only a small number of (invasive) species that are detected spreading throughout the studied territories, and range expansion northwards of typical southern species is only observed for a few species in our data. Although all ingredients for homogenisation are present; obtrusive invasive species and a gradual large-scale recovery process with water quality improvement, still no trace of homogenisation is present. Of course biotic homogenisation is mostly associated with species loss (Baiser et al. 2012), but it is also presented in contexts of increasing species numbers when species invade while no resident species go extinct (Olden and Poff 2004). Homogenisation is furthermore identified as a risk in recovery processes (Erwin 1998). Here, on the contrary, strong spatial insurance is observed.

The generation of β diversity under conditions of productivity increase is ruled by stochastic processes of species arrival and mortality in community assembly (Chase 2010). Several stochastic processes can be at the origin of the spatial differentiation in community assembly. First, colonization and extinction dynamics can create high β diversity among localities. Second, stochasticity in arrival of species can lead to priority effects which create multiple stable equilibriums of community structure in different localities, leading to high β diversity (Chase 2010). Furthermore, environmental stochasticity is described to be source of increasing β diversity (Ruokolainen et al. 2009). We presume that both the biotic and environmental stochastic processes are at the origin of the observed response diversity in the caddisfly community assembly. Furthermore the described biotic process of facilitation can additionally cause stochasticity in the spatial differentiation of communities (Cardinale et al. 2002). The observed evenness in the caddisfly communities (see Fig. 5), is in line with this assumption. High regional evenness is furthermore supposed to offer insurance to biodiversity (Hillebrand and Matthiessen 2009).

Thus, richness increase is ruled by a local mechanism; more species can co-exist thanks to more resources in the absence of competitive limitation. Secondly, regional stochastic community assembly processes induce higher diversity among sites with unlimited resources (Chase 2010). Not

so much the local trophic amplification but its synchronized manifestation over such a large spatial scale and within such a short time frame is an extraordinary phenomenon. To the question why this trend of biodiversity increase has not been noticed previously, or only in part (Dornelas et al. 2014), we have to stipulate that analyses of large-scale long-term trends are rare (see productivity biodiversity project under LTER) (Dodson et al. 2000). To our knowledge, no reports of three-decade, continuously sampled sites of stream communities over as large a spatial scale as the dataset we have analysed exist. Nevertheless, maybe the observed trend is not ubiquitous. We argue that water quality improvement played a trigger role in the synchronicity of the observed diversity increase. Growth and dispersion over the river network are enabled once water quality reaches a basic quality level, as was already documented for English chalk streams (Durance and Ormerod 2007). One further element that potentially enabled this trend is the high geographical variety of the studied French territories with many preserved headwaters and stream sections. Finally, more than terrestrial and lentic ecosystems, streams and rivers are characterized by strong natural perturbations and their communities are highly adapted to changing conditions.

Where this observed trend is synchronous with observations in this region's marine environment with a similar abrupt ecosystem shift for the period 1997-2003 also explained by trophic amplification (Beaugrand et al. 2014, Goberville et al. 2014), for other freshwater systems strongly influenced by productivity, such as lakes, no similar observations have been made. Signals in the same direction might be expected nevertheless, as it has been shown recently that lake productivity is limited by light and not by nutrients (Karlsson et al. 2009), and that warming will have rapid effects on the productivity of high latitude lakes (Karlsson et al. 2005). Striking temporal coherence of food-web interactions over hundreds of kilometres due to faster population growth of herbivores in warming water in central European lakes is also reported (Straile 2002). For Arctic freshwater ecosystems, the projected increase in productivity with climatic changes is accompanied with profound hydroregime changes strongly confounding biotic responses (Prowse et al. 2006). Also for our temperate-region running freshwaters, there is a risk that too much productivity and temperature increase may induce negative responses. Cold water species obviously do not benefit as strongly as eurythermal species in our observations. Furthermore, expected changes to flow regime might deteriorate conditions. Projected climate-induced intensification of floods and droughts might provoke species loss in time. Nevertheless, the recent period includes extreme hydro-climatic events in the studied region that have impacted strongly on communities at the local scale (Daufresne and Boët 2007, Floury et al. 2013), yet with no evidence of impact on the larger-scale, long-term trends. Given estimations that temperate ecosystems are to experience the least biodiversity change (Sala et al. 2000), we conclude, based on the strong changes observed in our study, that uncertainties in the current predictions of global change are many times larger than often presumed (see also Heino et al. 2009).

With some other authors (Woodward et al. 2010, Parmesan et al. 2013) we suggest that new concepts to more functional climate change analysis are needed, oriented to increasing productivity and mobility. At present, global change predictions only depict declines and degradation incurring (Poff et al. 2012). Most studies use distribution-climate models and invoke a lack of adaptation capacity to environmental changes (Heino et al. 2009). In our data, however, we clearly observe an increase in diversity that is not limited to a small group of species appearing everywhere, but a strengthening and stronger expression of regional species pools and a higher productivity that involves the entire food web. An ecosystem containing many diversified species will be able to seize new evolutionary opportunities more easily and will stand up to environmental changes (Loreau et al. 2001). We plead for an open and less prejudiced approach to future new climates with no-analogue communities that inevitably evolve and bring ecological surprises (Williams 2007). We observed novel enriched communities that were nevertheless composed by the present species pools. Biodiversity conservation and restoration strategies need to focus on capacity and enhancing of dispersal and growth of regional species pools (Heino and Peckarsky 2014). The current

catastrophist view to biodiversity loss induced by climate change needs some counterbalance to reinforce and orient adaptive strategies to biodiversity conservation. The persistent investments in water quality have proven to have positive effects on biodiversity, and here show to be reinforced by climate change effects. Our results may stimulate concerted regional efforts to improve water quality and species dispersal, to reinforce regional species pools and their resilience to further climate change.

Acknowledgements We gratefully acknowledge the Regional Directories' Environmental Agencies (DREAL) for their collaboration to harmonise invertebrate sampling data series for this study and the highly motivated macro-invertebrate biologists that secured the quality and continuity of the sampling network. Thierry Tormos and Ricardo Simon improved the figures and language of the manuscript. Jani Heino and Catherine Leigh offered valuable comments and suggestions to an earlier version that greatly improved the manuscript.

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Table 1 Trait categories and modalities used in the analysis.

Trait category	Biological trait	Trait modalities		
Life history	Maximum potential size (mm)	<5		
		5-10		
		10-20		
		>20		
	Maximum number of reproductive cycles per year	Univoltine		
		Plurivoltine		
	Number of reproductive cycles per individual	1		
	Life duration of adults (days)	>1		
		≤1		
		1-10		
10-30				
Reproductive technique	>30			
	Single individual			
Oviposition site	Hermaphroditism			
	Male and female			
	Water surface			
Egg/egg mass	Beneath the water surface			
	Terrestrial			
	Free eggs			
	Cemented eggs			
Resistance and resilience	Dissemination potential (all stages)	Female bears eggs in/on body		
		Low (10 m)		
		Medium (1 km)		
	Attachment to substratum of aquatic stages	High (>1 km)		
		Swimmers (water column)		
		Crawlers (epibenthic)		
		Burrowers (infauna)		
		Attached		
		General biological characteristics	Feeding groups	Shredders
				Scrapers
Filter-feeders				
Food resources	Predators			
	Algal piercers			
	Detritus			
	Algae			
	Microphytes			
	Macrophytes			
Dietary preferences	Micro-invertebrates			
	Macro-invertebrates			
	Strong (specialist)			
Respiration of aquatic stages (excluding eggs)	Moderate			
	Weak (generalist)			
	Tegument			
	Gills			
Aquatic stages	Plastron			
	Aerial			
	Adult and larva			
	Adult or larva			
		Larva and pupa		

