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Influence de la dispersion endozoochore sur la composition des communautés végétales :

une approche fonctionnelle basée sur trois ongulés sauvages

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Influence de la dispersion endozoochore sur la composition des communautés végétales : une approche fonctionnelle basée sur trois ongulés sauvages

La dispersion est un processus clé dans les dynamiques de populations. Chez les organismes à dispersion passive, dont les plantes, la dispersion de la banque de graines fait appel à un vecteur biotique ou abiotique. En particulier, la zoochorie influence les patrons spatiaux de distribution et de diversité des plantes à travers une interaction entre les traits écologiques du vecteur animal et de la plante transportée. Ma thèse vise à étudier l'effet de cette interaction sur la composition taxonomique et fonctionnelle des communautés floristiques. Je me concentre sur trois questions principales : (1) Comment les traits écologiques des plantes et des vecteurs influencent-ils le processus de dispersion endozoochore? ; (2) La zoochorie constitue-t-elle un filtre d'assemblage sur les traits fonctionnels des plantes dispersées? ; (3) La zoochorie imprime-t-elle un signal sur les patrons spatiaux de diversité? J'adopte à cet effet une approche expérimentale, en me concentrant sur la flore d'Europe de l'Ouest et sur les trois ongulés sauvages les plus communs dans cette région : le cerf (*Cervus elaphus*), le chevreuil (*Capreolus capreolus*) et le sanglier (*Sus scrofa*). Je montre que l'interaction entre les traits des plantes et des vecteurs influe sur les durées de rétention des graines, qui influencent les distances de dispersion. L'endozoochorie modifie la composition de l'assemblage d'espèces dispersé par rapport à la flore régionale en imposant un filtre fonction de l'habitat dans lequel se nourrit le vecteur animal, mais indépendant des traits morphologiques des graines. A échelle des communautés, l'effet de la zoochorie est cependant réduit relativement aux autres processus abiotiques et biotiques tels que les filtres liés à l'habitat ou l'herbivorie. Compte tenu de ces résultats, je propose de prendre en compte l'influence de la dispersion dans les modèles prédictifs de distributions des plantes, afin d'améliorer notre compréhension des dynamiques d'aires et leur prédiction en lien avec les scénarios de changements climatiques. Il apparaît en particulier nécessaire de mieux quantifier la contribution de la dispersion zoochore aux patrons de diversité et de composition des communautés végétales, relativement aux autres processus qui résultent d'interactions plantes-animaux et aux autres modes de dispersion des graines.

Mots clés : Dispersion, Ongulés, Zoochorie, Communautés, Traits.

Influence of endozoochorous dispersal on the composition of plant communities: a functional approach based on three wild ungulates

Dispersal is a key process shaping population dynamics. In passive dispersers like plants, the dispersal of the seed bank relies on biotic or abiotic vectors. Among the wide range of passive dispersal, zoochory influences spatial plant diversity and distribution patterns through an interaction between the ecological traits of dispersed plants and their animal vectors. In this work, I investigate the outcomes of this interaction on the taxonomic and functional composition of plant communities. I address three main questions: (1) How do the ecological traits of dispersed plants and their vectors influence the dynamics of endozoochorous dispersal? ; (2) Does zoochory affect the functional traits of dispersed species as a community assembly filter? ; (3) What is the imprint of zoochory on spatial patterns of plant diversity? I frame my work within an experimental approach focused on the West-European flora and on the three most common wild ungulates in this area: red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and wild boar (Sus scrofa). I show that interactions between plant and vector traits influence dispersal distances by modulating seed retention times. Endozoochory modifies the composition of dispersed plant assemblages as compared with that of the regional pool by filtering species according to the feeding habitats of the vectors. At a community level, zoochory has a limited influence relative to other abiotic or biotic processes including habitat and herbivory. On the basis of these results, I suggest to include dispersal in predictive models of plant distributions to improve our understanding of range dynamics and their prediction especially within the framework of current global changes. My results further suggest that the contribution of zoochory to plant diversity and community composition patterns needs to be better quantified and compared with other plant-animal interactions and other dispersal modes.

Keywords: Dispersal, Ungulates, Zoochory, Communities, Traits.

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« Pour bien connaître la nature, il faut l'avoir admirée.

C'est alors qu'on a le goût d'en chercher les merveilleux secrets. »

Gaston Bachelard

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J'ai mené mon travail au centre Irstea de Nogent-sur-Vernisson, dans l'Unité de Recherche « Ecosystèmes forestiers », au sein de l'équipe « Interactions Forêt-Ongulés-Activités humaines ». J'ai également été accueillie ponctuellement par l'équipe « Comportement et Ecologie de la Faune Sauvage » de l'INRA de Toulouse, par l'Ecole Nationale Vétérinaire d'Alfort (ENVA) et par la Réserve de la Haute-Touche (MNHN).

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En introduction, il m'a semblé important de donner une définition de la dispersion, de développer ses causes évolutives, son déclenchement et ses conséquences, puis de détailler la zoochorie, le processus de dispersion des graines par les animaux, avant de présenter mes objectifs et justifier ma démarche. Le premier chapitre est consacré à l'étude des multiples étapes qui composent le processus d'endozoochorie. Le deuxième chapitre vise à rechercher un éventuel effet de filtre de la zoochorie sur l'assemblage régional d'espèces végétales. Le troisième chapitre concerne les conséquences de la zoochorie sur la composition fonctionnelle des communautés végétales. Enfin, la discussion générale établit un bilan des résultats et propose quelques perspectives pour les recherches futures.

J'ai ajouté en annexes six documents périphériques à ma thèse :

- un article traitant de la dispersion épizoochore (Annexe 1 : Article 6),
- un deuxième article concernant la zoochorie et reliant les traits des plantes dispersées aux traits des vecteurs animaux (Annexe 2 : Article 7),
- la liste des communications autres que les articles scientifiques que j'ai réalisées pendant ma thèse (Annexe 3),
- et enfin la liste des affiliations des différents co-auteurs de mes manuscrits (Annexe 4).

SOMMAIRE

GLOSSAIRE

Adaptation : propriété fonctionnelle d'un organisme, favorisée par la sélection naturelle, qui lui permet de survivre et de se reproduire (Howe and Smallwood, 1982).

Dispersion : mouvement spatial conduisant à un flux de gènes, quel que soit le comportement ou le mouvement en question (Clobert et al., 2012).

Dispersion primaire : dispersion par un premier vecteur de dispersion.

Dispersion secondaire : dispersion par un second vecteur de dispersion, après dispersion primaire.

Syndrome de dispersion : phénotype de dispersion multivarié, constitué par plusieurs traits qui co-varient (Clobert et al., 2012).

Propagule : unité végétale dispersée. Il peut s'agir d'une graine, d'une graine et des structures qui l'entourent (ailes, crochets), d'un fruit, d'un fragment végétatif, d'une entité génétiquement identique au parent comme un bulbe, ou même d'une plante entière (Cousens et al., 2008).

Plante parent -ou- plante mère : plante individuelle dont sont issues les graines dont il est question.

Etablissement : processus par lequel une graine germe, développe des racines, utilise les ressources parentales et acquiert une croissance indépendante en tant que plantule (Howe and Smallwood, 1982).

Phénologie : cycles saisonniers des phénomènes biologiques, comme la floraison ou la fructification périodique d'une plante par exemple.

Environnement : ensemble des conditions biotiques et abiotiques dans l'entourage immédiat d'un individu.

Trait : propriété d’un individu comparable entre espèces (McGill et al., 2006). On parle de « trait fonctionnel » quand le trait influence indirectement la fitness de l’individu à travers ses effets sur la croissance, la reproduction et la survie (Violle et al., 2007). Les traits associés à la dispersion peuvent être considérés comme tels, car ils impactent la survie des individus qui dispersent, et par conséquent leur succès de reproduction. La diversité fonctionnelle est la diversité des traits fonctionnels. La composition fonctionnelle est la composition en traits fonctionnels.

Population : ensemble d’individus appartenant à une même espèce.

Métapopulation : population spatialement structurée, constituée d’un groupe de populations dans un espace discret, liées entre elles par la dispersion, à travers des dynamiques de colonisation/extinction (Clobert et al., 2012; Lowe and McPeek, 2014).

INTRODUCTION

I. La dispersion, un processus clé

Au cours de l'histoire du vivant, l'évolution a conduit à l'apparition de stratégies d'histoire de vie qui permettent aux organismes de persister et se reproduire dans un environnement dynamique et spatialement hétérogène. Le développement d'une plasticité phénotypique ou l'adaptation locale figurent parmi les processus évolutifs qui permettent la persistance d'une espèce face aux fluctuations de l'environnement (Ackerly, 2003; Cody and Mooney, 1978; Kawecki and Ebert, 2004; Sultan, 1995). Toutefois, ces processus ne permettent pas de répondre à des changements de l'environnement brutaux ou de grande amplitude (Both et al., 2006; Parmesan, 2006). Une réponse individuelle fréquente à de tels changements consiste à changer de localité pour s'établir dans un lieu plus favorable, c'est-à-dire à disperser (Clobert et al., 2012; Parmesan and Yohe, 2003).

I. 1. Définition

La définition la plus générale de la dispersion fait référence à tout mouvement spatial qui conduit à un flux de gènes (Ronce, 2007). Il s'agit d'un processus en trois étapes successives: le départ de l'environnement local (émigration), le mouvement à travers une matrice plus ou moins hostile (transfert) et l'arrivée dans un nouvel habitat (immigration) (Baguette and Van Dyck, 2007; Figure 1). Chez les animaux territoriaux, l'émigration fait référence à l'acte de quitter le territoire parental, tandis que chez les plantes, elle correspond au moment où la propagule quitte l'organisme parent. L'immigration correspond quant à elle à l'arrivée de l'animal dans un nouvel environnement, ou à l'arrivée de la graine sur un microsite où elle donnera naissance à une nouvelle plante adulte. La définition de la dispersion est donc variable et dépend du mode de dispersion de l'organisme considéré, de son cycle de vie et de ses traits d'histoire de vie.

On distingue usuellement deux modes de dispersion. La dispersion passive domine chez les plantes, les organismes unicellulaires (bactéries, algues, protozoaires) et les petits vertébrés peu mobiles (plancton). Elle nécessite un vecteur de dispersion, c’est-à-dire un facteur biotique ou abiotique permettant le mouvement (Matthysen, 2012). Il peut s’agir du vent (anémochorie), des courants d’eau (hydrochorie), des animaux (zoochorie) ou de l’Homme (anthropochorie) (Cousens et al., 2008). La dispersion passive a lieu, par définition, lorsque l’individu qui disperse ne contrôle pas son mouvement. A l’inverse, la dispersion active, qui domine chez la plupart des animaux terrestres, implique que l’individu contrôle sa propre mobilité, à travers des prises de décision complexes en relation avec les signaux de l’environnement physique et social (Matthysen, 2012). Les causes et les conséquences de la dispersion diffèrent donc selon le mode de dispersion considéré.

La mobilité d’un individu varie au cours de son cycle de vie. Chez les plantes, qui sont le plus souvent fixées par des racines, le mouvement est procuré par la dispersion de la propagule. Selon l’identité de l’espèce végétale, cet événement de dispersion a lieu une ou plusieurs fois au cours du cycle de vie (plantes annuelles ou bisannuelles *versus* plantes pérennes). Comme pour les animaux, la dispersion est considérée comme efficace si elle est suivie par la reproduction de l’individu (Greenwood, 1980; Schupp, 1993; Schupp et al., 2010). Chez les plantes, cela implique que la propagule dispersée donne naissance à une nouvelle plante adulte. Chez les animaux, on distingue usuellement la dispersion juvénile (ou dispersion natale) de la dispersion de reproduction (Matthysen, 2012). La dispersion juvénile a lieu quand un jeune individu quitte son site ou son groupe social de naissance, pour rejoindre un nouveau site ou groupe où il pourra se reproduire. La dispersion de reproduction a lieu quand un individu adulte se déplace entre des sites ou des groupes dans le but de se reproduire (Greenwood and Harvey, 1982). Les implications individuelles ou populationnelles de la dispersion dépendent donc (1) du nombre d’événements de dispersion et (2) de leur place dans le cycle de vie d’un organisme.

La dispersion peut s’envisager à de multiples échelles écologiques. Il s’agit à la fois d’un processus individuel et d’un processus populationnel, car la résultante des mouvements des individus crée des flux, à travers l’émigration et l’immigration (Levin, 1992; Figure 1). Ces deux processus sont liés, mais sont déterminés par des facteurs différents : le choix de disperser ou non est un trait d’histoire de vie individuel qui dépend d’interactions entre l'individu et son environnement, alors que les flux d'individus répondent à des processus à plus long terme qui contribuent à l'histoire évolutive d'une espèce. L'évolution étant la résultante de processus qui conduisent à la survie, la mortalité et la reproduction des individus, comprendre les implications évolutives de la dispersion implique d'en examiner les déclencheurs proximaux à échelle individuelle.

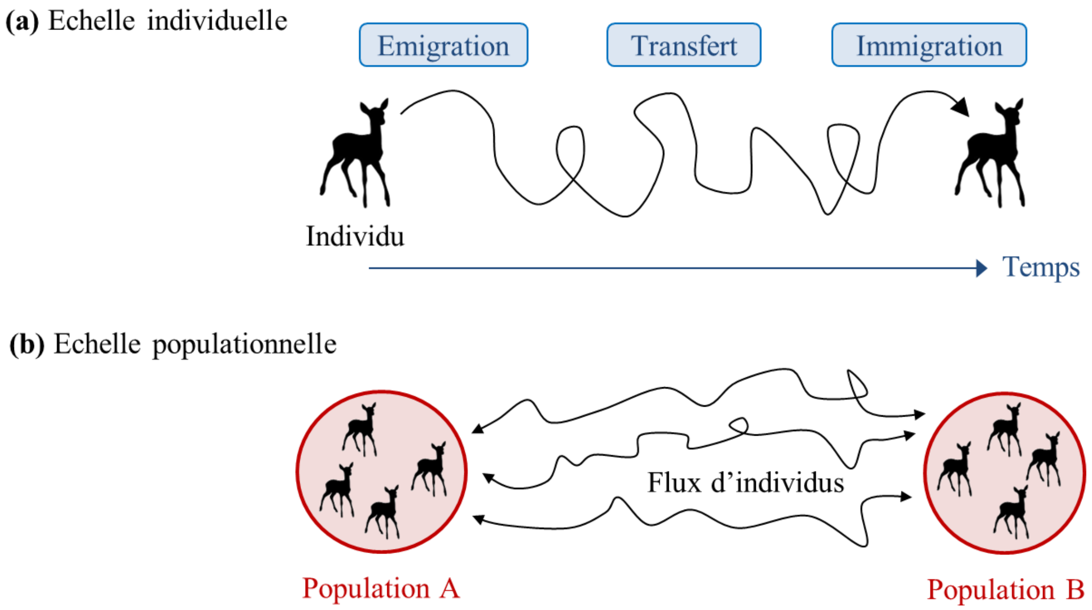


Figure 1 : Schéma du processus de dispersion. **(a)** Pour chaque individu qui disperse, le processus de dispersion est composé de trois étapes successives : l'émigration, le transfert et l'immigration. **(b)** La dispersion individuelle a des conséquences populationnelles à travers les flux d'individus.

I. 2. Déclenchement de la dispersion

A échelle individuelle, le déclenchement de la dispersion dépend du mode de dispersion. Dans le cas d'une dispersion active, le déclenchement est souvent associé à des pressions environnementales locales. La dispersion est le plus souvent une réponse à un changement dans la qualité de l'habitat, la disponibilité des ressources ou la pression de compétition, en particulier intraspécifique. De nombreuses études ont montré que le nombre d'individus qui dispersent est plus élevé dans les habitats dégradés, par exemple en cas de diminution des ressources (Bonte et al., 2008; Mathieu et al., 2010), de fortes densités de prédateurs ou de parasites (McIntosh et al., 2002; Sorci et al., 1994) ou de perturbations physiques de l'environnement (inondation de l'habitat par exemple ; Bates et al., 2006). Il a aussi été démontré qu'une forte densité de population, qui tend à limiter l'accès aux ressources et accentuer la compétition, incite les individus, en particulier juvéniles, à émigrer (Matthysen, 2005; Figure 2).

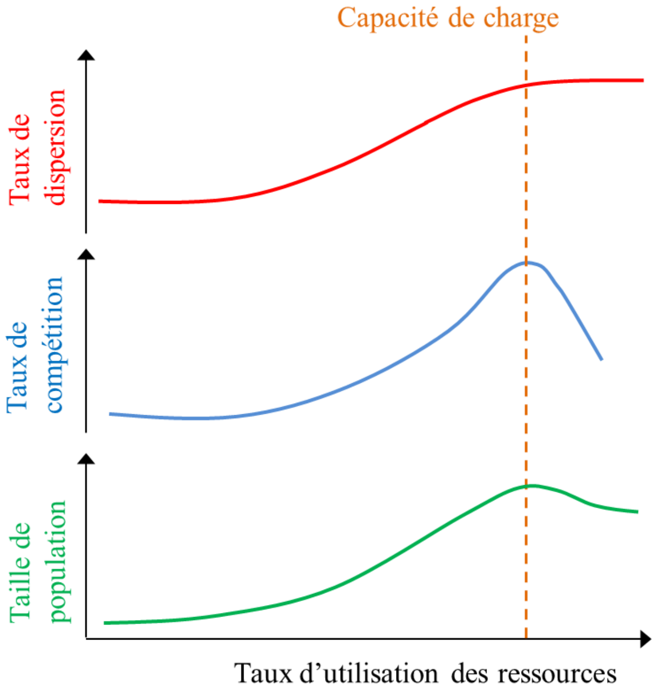


Figure 2 : Représentation schématique de dispersion densité-dépendante. Si la densité locale de population est telle que les ressources locales ne permettent pas à tous les individus de subvenir à leurs besoins (capacité de charge atteinte et compétition élevée), les individus peuvent augmenter leur fitness en dispersant vers d'autres lieux où ils pourront accéder à des ressources.

Les variations de la qualité de l'habitat et la densité de population sur le lieu d'arrivée des propagules ont aussi des effets sur l'immigration. Que la dispersion soit active ou passive, la probabilité qu'un individu s'établisse et se reproduise est maximum dans un habitat de bonne qualité, mais décroit si la compétition pour les ressources y est forte. La taille de la population influe donc négativement sur la probabilité d'immigration si la compétition intraspécifique est forte, ou positivement en cas d'attraction conspécifique, par exemple dans le cas d'espèces sociales (Kim et al., 2009).

Les processus qui déclenchent la dispersion de reproduction et la dispersion juvénile diffèrent. Chez les individus adultes, la recherche d'un partenaire non apparenté et un échec de reproduction ou la perte du partenaire sexuel l'année passée favorisent la dispersion de reproduction (Forero et al., 1999). La dispersion juvénile est influencée par le comportement des parents et la présence d'individus apparentés. En effet, les parents peuvent agresser leurs descendants ou les déplacer pendant les soins parentaux (Bonte et al., 2007; Perrin and Mazalov, 2000; Figure 3). Il a aussi été montré que les descendants augmentent leur dispersion en réponse à la présence d'individus apparentés (Moore et al., 2006). Les agressions du parent envers les descendants de même sexe sont fréquentes et sont considérées comme un contrôle parental permettant d'éviter les appariements consanguins (Handley and Perrin, 2007). De tels comportements d'agression conduisent à une dispersion sexe-dépendante. Par exemple, chez les lions, les jeunes femelles ayant atteint la maturité sexuelle restent dans le groupe social, alors que les jeunes mâles sont chassés par le mâle dominant.

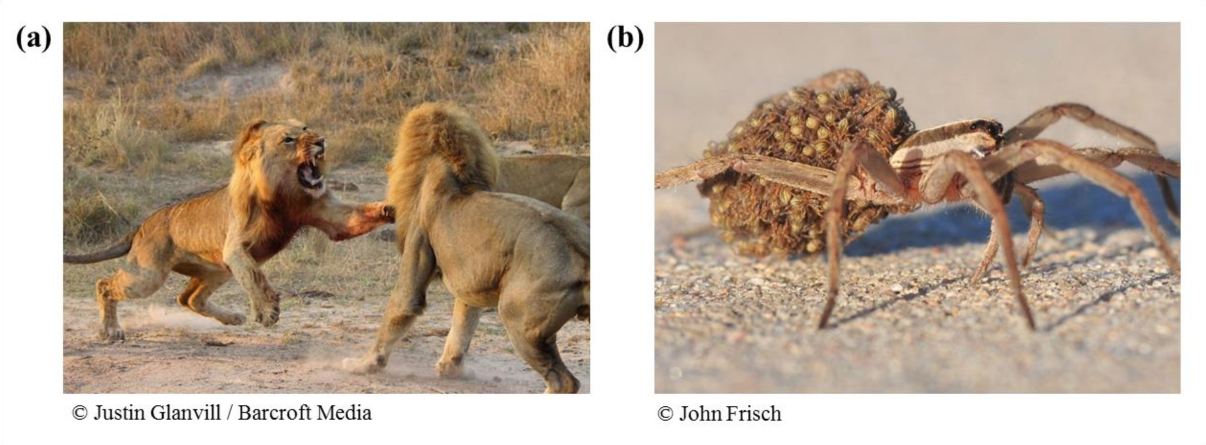


Figure 3 : **(a)** Un combat entre un père et un descendant mâle, chez les lions, et **(b)** une araignée-loup femelle (famille des Lycosidae) transportant ses jeunes sur son abdomen.

Chez les plantes, le déclenchement de la dispersion n'est pas sous le contrôle de l'individu disperseur lui-même. La dispersion peut être initiée par la plante parent, si celle-ci disperse elle-même ses graines (autochorie), *via* l'explosion d'une capsule par exemple (Narbona et al., 2005). Dans les autres cas, l'émigration est fonction de l'interaction entre l'architecture de la plante parent (qui reflète les conditions environnementales), la quantité de graines qu'elle produit, la taille et la morphologie des graines et la densité de vecteurs dans l'environnement (Cousens et al., 2008). Je reviendrai plus en détail sur le cas des plantes. La dispersion en tant que trait d'histoire de vie est donc mise en œuvre à travers une interaction entre les traits de l'individu disperseur ou de la plante parent et les conditions environnementales (Benard and McCauley, 2008).

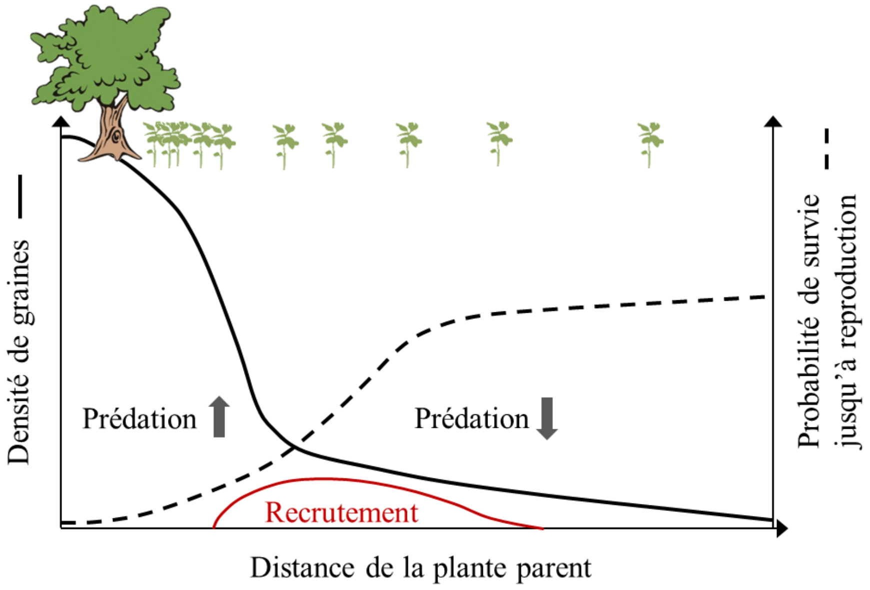


Figure 4 : L'hypothèse de Janzen-Connell prédit que la probabilité d'établissement des plantules est fonction de la distance à la plante parent. La densité des prédateurs est élevée près de la plante parent, et peu de graines sont dispersées loin de celle-ci. La probabilité maximale de recrutement des plantules se situe donc à des distances intermédiaires à la plante parent (Connell, 1971; Janzen, 1970).

I. 3. Evolution de la dispersion

Comme pour tous les traits soumis à la sélection naturelle, la dispersion évolue en fonction de l'avantage sélectif qu'elle procure aux individus qui dispersent dans un contexte environnemental et biotique donné (Bowler and Benton, 2005). En limitant la densité d'individus qui s'agrègent autour des parents, la dispersion réduit la compétition entre apparentés (Hamilton and May, 1977). Comme je l'ai évoqué précédemment, la dispersion des jeunes animaux pourrait avoir évolué parce qu'elle limite la compétition avec les parents ou les individus apparentés. Toutefois, la dispersion peut aussi procurer un désavantage sélectif si la présence d'apparentés a un effet positif sur la valeur adaptative des individus, par exemple à travers les reproductions coopératives (Baglione et al., 2003). Chez les plantes, la majorité des graines tombent ou sont dispersées à proximité de la plante parent, créant des agrégats de propagules où la prédation, la prévalence de pathogènes et la compétition sont accrues (Connell, 1971; Janzen, 1970). De plus, quitter la proximité immédiate et l'influence chimique de la plante parent (allélopathie) peut aussi être avantageux pour la germination des graines et la survie des plantules (Herrera and Pellmyr, 2002). Ainsi, la probabilité de survie des plantules est positivement corrélée à la distance à la plante mère, et le recrutement des plantules se situe généralement à des distances intermédiaires (Figure 4).

A échelle populationnelle, la dispersion est souvent associée à la réponse aux variations environnementales. La variabilité temporelle de l'environnement augmente la probabilité de dispersion, alors que la variabilité spatiale seule tend à la diminuer (Johnson and Gaines, 1990). En effet, si la variabilité temporelle est forte, le risque de disperser est réduit relativement à celui de rester dans un environnement qui risque de changer brutalement. En revanche, dans un paysage diversifié, un individu qui disperse risque de ne pas trouver d'habitat favorable ou d'immigrer dans un habitat sub-optimal qui aura pour conséquence de diminuer sa valeur adaptative. Si un trait héritable est associé à la capacité de dispersion, sa fréquence dans la population varie en fonction de la valeur adaptative des individus qui dispersent. Plusieurs études ont mis en évidence de telles variations de fréquences en utilisant des traits polymorphiques héritables dont les différentes modalités ne confèrent pas la même capacité de dispersion. Chez les insectes, la taille des ailes est un trait fortement héritable. Il existe deux morphes chez la plupart des espèces : un avec de longues ailes qui est capable de voler, et un avec de petites ailes qui ne vole pas (Roff and Fairbairn, 1991). Denno et al. (1996) ont montré que chez les sauterelles, la fréquence du morphe à longues ailes est plus élevée dans les habitats éphémères que dans les habitats à forte stabilité temporelle. De la même manière, chez des criquets, Simmons et Thomas (2004) ont montré que la fréquence du morphe volant est plus élevée dans les habitats en marge d'aire de répartition, récemment colonisés, qu'au cœur de l'aire de répartition. De manière similaire, le polymorphisme des graines est lié à la dispersion chez certaines espèces de plantes. Par exemple, l'astéracée *Crepis sancta* possède deux types d'akènes (fruit sec contenant une graine), dont la proportion de chaque type est héritable : l'un porte une aigrette et est typiquement dispersé par le vent ; l'autre est plus lourd, dépourvu d'aigrette et tombe au pied de la plante mère. Dans un habitat urbain très fragmenté, où les akènes volants subissent une forte mortalité, Cheptou et al. (2008) ont observé qu'en une douzaine de générations, la proportion d'akènes non volants est passée de 10 % en campagne à 15 % dans les patchs urbains. La proportion relative de graines qui dispersent répond donc rapidement à la sélection naturelle. Ces trois études mettent en évidence les processus adaptatifs de la dispersion, qui interviennent en réponse aux contraintes environnementales. La dispersion est sélectionnée en réponse aux fluctuations de l'environnement, *via* la probabilité de reproduction et de mortalité, c'est-à-dire le rapport coût-bénéfice associé à la dispersion (Johnson and Gaines, 1990).

I. 4. Conséquences individuelles

La probabilité de dispersion est influencée par un compromis entre coûts et bénéfices pour la valeur adaptative d'un individu. Comme nous l'avons vu précédemment, un avantage majeur de la dispersion est qu'elle permet d'éviter la compétition avec les individus apparentés, la mortalité près des parents et la reproduction consanguine. Toutefois, la perte de coopération entre apparentés peut constituer un coût à disperser, qui favorise la philopatrie et influence la décision d'émigrer (Starrfelt and Kokko, 2012). La dispersion augmente par ailleurs le coût potentiel de dépression hybride, c'est-à-dire de produire des descendants ayant une valeur adaptative plus faible que celle des parents (Matthysen, 2012). La dispersion est aussi une réponse à la baisse de la qualité de l'habitat ou de la disponibilité des ressources ; mais des coûts peuvent s'appliquer à chacune de ses étapes. L'émigration implique un coût énergétique et physiologique pour un phénotype disperseur et le développement de structures de locomotion permettant le mouvement (Matthysen, 2012). Il existe un compromis entre la capacité de dispersion et la survie ou la fécondité (Starrfelt and Kokko, 2012). Les exemples les plus connus concernent le compromis entre dispersion et germination des graines chez les plantes, et entre vol et fécondité chez les insectes. Chez les plantes, la production de nombreuses graines augmente la probabilité de dispersion, mais est associée à la réduction de la taille des graines, qui a pour conséquence de réduire les capacités d'établissement des plantules (Eriksson and Jakobsson, 1999). Chez les insectes, le développement des muscles permettant le vol et donc la dispersion induit un retard de l'âge de première reproduction et réduit la fécondité, en raison d'un déficit d'allocation d'énergie pour le développement de l'appareil reproducteur et/ou parce que l'efficacité du vol est corrélée négativement au nombre d'œufs transportés (Roff and Fairbairn, 1991). Pendant la phase de transfert, un individu qui disperse est exposé à un risque direct de mortalité, notamment quand il traverse une matrice d'habitats non-familiers ou peu favorables, où il peut par exemple faire l'objet de prédation ou être sujet à la famine (Matthysen, 2012). Le succès de l'individu en tant qu'immigrant dépend de ses capacités à trouver un habitat favorable (Starrfelt and Kokko, 2012). Les difficultés rencontrées pour trouver un habitat où immigrer interagissent fortement avec le risque de mortalité et peuvent prolonger la phase de transfert (McCarthy, 1999). Finalement, la dispersion est la résultante d'un compromis entre les pressions locales poussant à la dispersion (qualité de l'habitat, disponibilité des ressources, densité de population, compétition, incitation parentale, caractéristiques de la plante mère, morphologie des graines) et le coût à disperser.

I. 5. Conséquences populationnelles

Une espèce est rarement distribuée de façon homogène dans l'espace, mais est plutôt structurée en populations locales, connectées par la dispersion (Husband and Barrett, 1996). Un tel patron se théorise par le concept de métapopulation, définie comme un assemblage régional de populations, dont la dynamique dépend de la résultante de processus d'extinction locale et de colonisation (Hanski, 1998; Harrison, 1991). A l'échelle locale, les populations diffèrent en termes de taille et de qualité de l'habitat ; leurs dynamiques sont asynchrones et leur extinction peut être causée par la stochasticité démographique (variabilité des taux de naissance et de mortalité), génétique (diminution de l'hétérozygotie et augmentation des appariements consanguins) ou environnementale (variation temporelle des conditions météorologiques ou de la disponibilité des ressources) (Hanski, 1991; Harrison, 1991). Le risque d'extinction est plus élevé quand la population est de petite taille, présente un taux élevé de consanguinité et est isolée des autres populations (Hanski, 1991; Saccheri et al., 1998; Trakhtenbrot et al., 2005). A travers l'émigration et l'immigration, la dispersion conduit à des flux d'individus et de gènes dans et entre les populations (Levin, 1992; Ronce, 2007). L'émigration peut réduire la croissance des populations locales, et avec la stochasticité démographique, induire un risque élevé d'extinction (Hanski, 1998). A l'inverse, l'immigration peut réduire le risque d'extinction dans les petites populations, en augmentant la taille de la population et sa diversité génétique (effet de sauvetage ; Brown and Kodric-Brown, 1977; Hanski, 1998). A travers les flux d'émigration et d'immigration, la dispersion connecte les populations locales, permet de coloniser ou recoloniser des environnements vacants et maintien les populations puits (Harrison, 1991; Murphy and Lovett-Doust, 2004; Figure 5). La persistance de la métapopulation à l'échelle régionale dépend donc des taux de dispersion entre les populations locales. La dispersion peut avoir lieu entre toutes les populations, ou seulement depuis une ou plusieurs population(s) résistante(s) à l'extinction

(Hanski, 1991; Harrison, 1991; Figure 5). La dispersion est donc le principal processus qui permet de connecter les populations et de coloniser de nouveaux environnements.

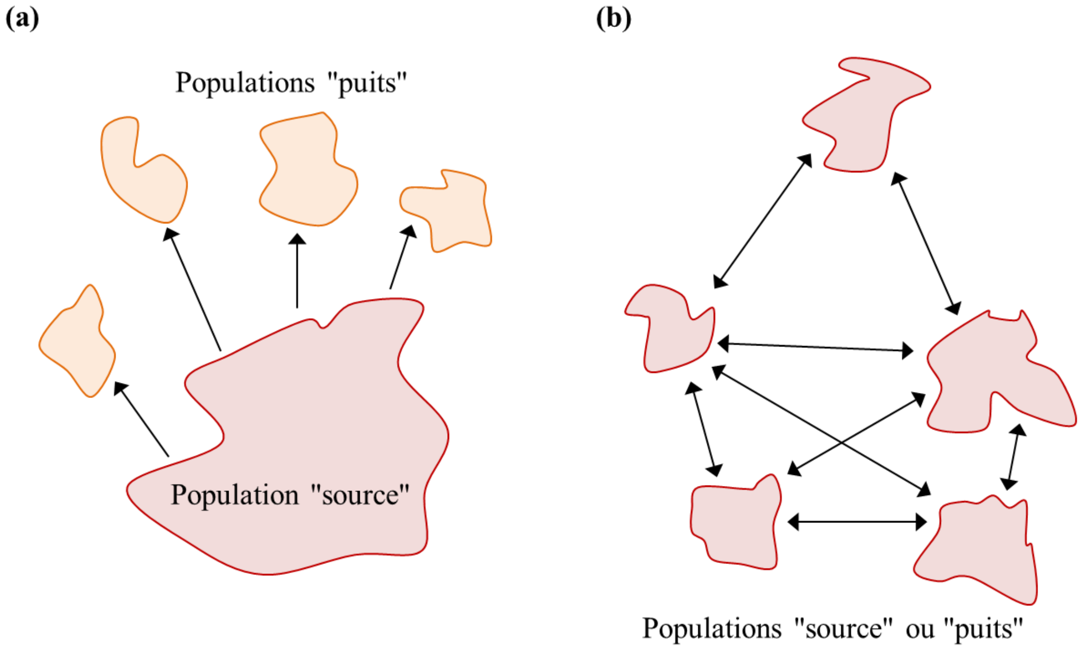


Figure 5 : Exemples de métapopulations. **(a)** Une dynamique de métapopulation dite "île-continent" ou "source-puits" : une seule population, souvent celle à la plus forte densité, joue le rôle de "source" (d'où les individus émigrent). **(b)** Une dynamique de métapopulation où chaque population locale peut être à la fois "source" ou "puits" (où les individus immigrent).

Toutes les populations ne sont pas également connectées et la connectivité ne dépend pas que des capacités de dispersion des individus, mais aussi des caractéristiques du paysage, qui peuvent empêcher la dispersion ou augmenter la mortalité qui lui est associée (Goodwin and Fahrig, 2002; Hanski, 1998). La connectivité n'est donc pas une simple fonction de la distance entre les populations. Il s'agit d'une mesure fonctionnelle de la structure du paysage, qui est souvent exprimée en termes de résistivité ; laquelle représente le degré avec lequel les différents types d'habitats qui composent le paysage facilitent ou empêchent le mouvement des individus entre les populations (Ricketts, 2001; Taylor et al., 1993). Les mouvements entre les populations dépendent en effet de la composition et de la structure des habitats rencontrés (Murphy and Lovett-Doust, 2004). L'environnement dans lequel s'insèrent les populations (la matrice) peut procurer des habitats alternatifs sub-optimaux ou agir comme une barrière ou comme un conduit pour le mouvement (Murphy and Lovett-Doust, 2004). Des îlots d'habitats peuvent par exemple faciliter le mouvement des individus et augmenter de ce fait les flux de gènes (Murphy and Lovett-Doust, 2004). En revanche, d'autres habitats peuvent représenter une barrière à la dispersion, comme par exemple un massif montagneux ou une zone urbaine. Il peut aussi exister un *effet bordure*, s'il existe un fort contraste entre l'habitat où la population se situe et l'habitat aux alentours. Un fort contraste tend à diminuer l'émigration et à augmenter l'immigration, car le contraste d'habitat rend l'habitat occupé plus facilement détectable par les immigrants (Englund and Hambäck, 2007). Chez les espèces à dispersion passive, la structure du paysage a aussi un effet sur la connectivité des populations. La hauteur de la végétation influe par exemple sur la force et la direction du vent, tandis que les conditions météorologiques (pluies) influent sur le volume et la vitesse des courants d'eau (Cousens et al., 2008). La structure du paysage peut aussi influencer la présence et/ou les mouvements des vecteurs animaux (zoochorie) (Matthysen, 2012). La composition de la mosaïque paysagère a donc un effet sur le comportement des individus et des vecteurs abiotiques de dispersion, avec des effets en termes de trajectoire et de distance de dispersion.

Dans un paysage spatialement hétérogène et/ou fragmenté, les événements rares de dispersion à longue distance peuvent être le seul processus qui permette la connectivité entre populations (Ozinga et al., 2004; Trakhtenbrot et al., 2005). Les distances de dispersion des individus issus d'une même source sont habituellement représentées par un *kernel de distance de dispersion*, c'est-à-dire une fonction qui décrit la forme de la densité de probabilité liée à la distribution des distances de dispersion (Figure 6). Chez les espèces animales et végétales, cette courbe possède une longue queue de distribution ; ce qui signifie que la dispersion s'effectue le plus souvent à de relativement courtes distances, et que les événements de dispersion à longue distance sont rares (Nathan et al., 2008, 2012). En raison de leur faible fréquence, les événements de dispersion à longue distance sont difficiles à quantifier (Trakhtenbrot et al., 2005). On les considère comme étant soit une faible proportion des distances de dispersion (par exemple 1%), soit au-delà de la distance moyenne entre les populations, soit au-delà d'une distance prédéterminée (Nathan et al., 2008). Chez les plantes, la dispersion à longue distance est souvent définie comme étant supérieure à 100 mètres (Cain et al., 2000). Les vecteurs de dispersion ou animaux connus pour être impliqués dans la dispersion à longue distance incluent les tempêtes et ouragans, les oiseaux frugivores (endozoochorie) et les grands mammifères qui peuvent transporter des graines dans leur pelage et sous leurs sabots (épizoochorie) ou dans leur tube digestif (endozoochorie) (Cain et al., 2000; Ozinga et al., 2004; Vellend et al., 2003). A échelle régionale, la distribution des distances de dispersion détermine la probabilité de connexion entre populations distantes et la probabilité de colonisation de nouveaux sites. La dispersion à longue distance influence donc la persistance de la structure de la métapopulation, et donc la survie à long terme des espèces dans un paysage fragmenté (Ouborg et al., 1999; Trakhtenbrot et al., 2005).

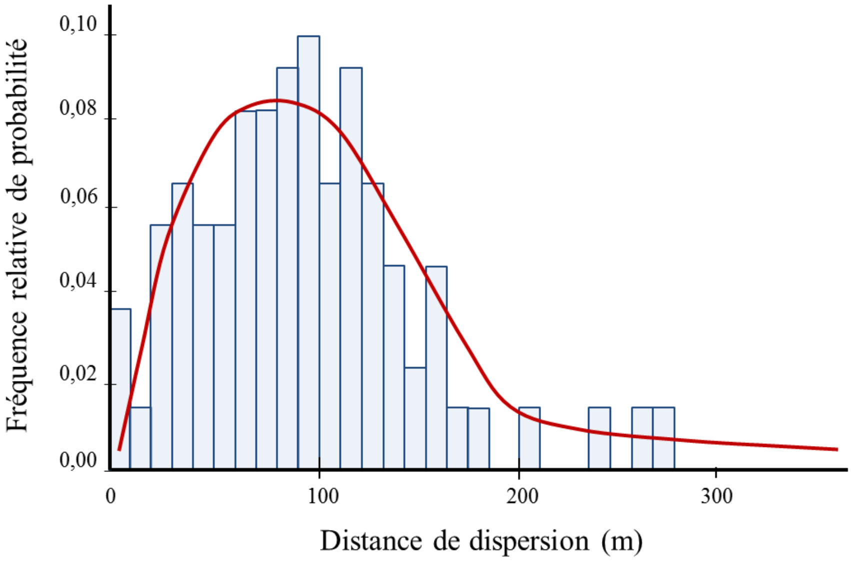


Figure 6 : Histogramme représentant la distribution des fréquences des distances de dispersion, sur laquelle est modélisée la courbe de densité de probabilité des distances de dispersion.

I. 6. Impact biogéographique

La capacité des espèces à suivre un changement climatique rapide et à persister dans des paysages fragmentés dépend de façon critique de la dispersion dans des habitats favorables (Vittoz and Engler, 2007). Un changement climatique, en particulier s'il est rapide, modifie la répartition spatiale de l'enveloppe thermique et indirectement des habitats d'une espèce, dont la persistance nécessite soit une plasticité phénotypique suffisante, soit un déplacement de son aire de distribution (Vittoz and Engler, 2007). Par exemple, les études paléobotaniques ont révélé une alternance, par le passé, entre des phases de rétraction des aires de distribution des espèces, qui ont conduit à la formation de refuges glaciaires, et des phases d'expansion durant les périodes interglaciaires (Cain et al., 1998; Parmesan, 2006). Sur le court terme, entre 1990 et 2008 et en réponse au réchauffement climatique actuel, les communautés d'oiseaux et de papillons ont migré respectivement de 37 et 114 km vers le Nord (Devictor et al., 2012). Un des processus qui expliquent ces changements d'aire de répartition est la dispersion asymétrique entre marge Sud et Nord d'aire de distribution (Hampe and Petit, 2005).

Prédire la capacité d'une espèce à coloniser de nouveaux environnement favorables nécessite par conséquent une compréhension approfondie des processus de dispersion (Higgins and Richardson, 1999). Les modèles prédictifs de distributions utilisaient jusqu'à récemment des fonctions kernel avec des queues courtes de distribution pour paramétrer le processus de dispersion (Higgins and Richardson, 1999). Or, chez les plantes de milieux tempérés, ces modèles prédisaient des taux de migration de 1 à 50 mètres par an (Higgins et al., 1996; Skellam, 1991), alors que les taux de migrations rapides des arbres après la dernière période glaciaire sont estimés comme étant de 50 à 1000 mètres par an (Delcourt and Delcourt, 1987; Mack, 1981) et les taux actuels sont de 5 à 13 kilomètres par an (Mack, 1981; Plummer and Keever, 1963). Ce paradoxe entre les prédictions et l'observé a été nommé paradoxe de Reid (Clark, 1998). Les modèles récents, qui modélisent la dispersion avec des fonctions à longue queue de distribution semblent avoir résolu ce paradoxe (Boulangeat et al., 2012; Clark, 1998; Higgins and Richardson, 1999; Kot et al., 1996). Cela suggère que les événements de dispersion à longue distance sont clés pour comprendre les dynamiques d'aires de distribution des plantes, et qu'ils ne peuvent pas être ignorés (Cain et al., 2000; Higgins and Richardson, 1999).

Des individus pionniers peuvent franchir les limites de l'aire de répartition de leur espèce, et former de nouvelles populations en marge d'aire de répartition si les conditions environnementales sont favorables et si aucun événement stochastique ne conduit à une extinction locale rapide (Sexton et al., 2009). Quand la capacité de dispersion est héritable (longues ailes chez les insectes, graines à aigrette chez les plantes, par exemple), ces nouvelles populations contiennent des individus disperseurs, conduisant ainsi à des hauts taux de dispersion qui évoluent rapidement sur le front d'expansion (Ibrahim et al., 1996). L'augmentation de la dispersion en marge d'aire de distribution a été observée chez de nombreuses espèces (Travis et al., 2013). Ainsi, l'émergence de phénotypes dispersifs peut augmenter la vitesse à laquelle les espèces colonisent de nouveaux environnements (Parmesan, 2006; Thomas et al., 2001). De plus, si les nouveaux immigrants ont une reproduction rapide (cycle de vie court), ils peuvent permettre un effet fondation et une adaptation locale rapide (Ibrahim et al., 1996; Travis et al., 2013). Toutefois, toutes les espèces ne sont pas capables de modifier leur aire de répartition rapidement. En particulier, les espèces philopatriques, sédentaires et spécialistes risquent d'échouer à initier une expansion (Parmesan, 2006).

I. 7. Influence sur les communautés

Au sein d'une communauté locale, les espèces interagissent, notamment à travers la compétition, la prédation et le mutualisme, et ces interactions influent sur la démographie et donc la taille de population de chacune des espèces qui compose la communauté (Leibold et al., 2004; Ricklefs, 2004). Ces interactions biotiques tendent à limiter la similarité des espèces qui coexistent au sein de la communauté, tandis que les conditions environnementales filtrent les espèces en fonction de leur niche écologique, car elles ne permettent l'établissement local que des espèces pour lesquelles elles sont favorables (Keddy, 1992; Pavoine et al., 2011). Toutefois, la dynamique et la diversité de la communauté locale ne dépendent pas seulement des interactions entre espèces et des conditions environnementales, mais aussi de la dispersion des individus entre les communautés (Leibold et al., 2004; Tilman, 1994). Par exemple, une espèce peut être absente d'une localité, non pas parce qu'elle en a été exclue par les autres espèces, mais parce qu'aucun individu de l'espèce n'est encore arrivé dans la localité (Tilman, 1994). Les communautés locales peuvent donc se structurer en métacommunautés (Ozinga et al., 2004), c'est-à-dire comme des ensembles de communautés locales dont la dynamique est influencée par la démographie et les capacités de dispersion des espèces qui les composent (Leibold et al., 2004; Wilson, 1992). Lorsque des individus immigrent au sein d'une communauté, les interactions entre espèces de la communauté sont affectées par les traits des immigrants (Lowe and McPeek, 2014). Il existe un compromis entre la compétition et la colonisation qui implique qu'une espèce peu compétitive peut subsister au sein d'une communauté si elle possède une capacité de dispersion et donc d'immigration élevée ; favorisant ainsi la coexistence des espèces (Lowe and McPeek, 2014; Tilman, 1994). Les processus qui déclenchent et modulent la dispersion des espèces entre les communautés locales peuvent donc affecter les dynamiques régionales des métacommunautés (Lowe and McPeek, 2014).

Une question majeure de l'écologie concerne la compréhension des processus qui sous-tendent la composition des communautés (Cody and Diamond, 1975; Pavoine and Bonsall, 2011). Historiquement, la composition d'une communauté était décrite par le nombre d’espèces (diversité spécifique) qui la compose ; mais on la décrit désormais plus fréquemment par sa diversité fonctionnelle et/ou phylogénétique afin de mieux refléter la complexité des réseaux locaux d’interactions entre espèces aux degrés d’apparentements variables (Pavoine et al., 2011; Violle et al., 2007). Les traits fonctionnels reflètent la réponse des espèces aux conditions environnementales, leur capacité compétitive ou encore leur capacité de dispersion, et sont donc des proxies de leur niche écologique (McGill et al., 2006). L’utilisation des traits permet d’aller au-delà de l’explication de la présence d’une ou quelques espèce(s) dans une communauté, et permet de généraliser et prédire la réponse de groupes fonctionnels d’espèces (qui partagent les mêmes traits) aux conditions biotiques et abiotiques (McGill et al., 2006). L’association entre les traits et la phylogénie permet de tenir compte du fait que les espèces proches génétiquement sont susceptibles de partager les mêmes traits, et permet de déterminer si les traits impliqués dans la réponse aux conditions environnementales, dans les interactions biotiques ou dans la dispersion sont des traits conservés par l’évolution ou ayant convergés (Pavoine et al., 2011).

On simplifie souvent la multiplicité des échelles spatiales de la diversité en trois niveaux : la diversité locale (diversité alpha), la diversité entre les communautés (diversité beta) et la diversité régionale (diversité gamma) (Ackerly and Cornwell, 2007; De Bello et al., 2010). La diversité locale est souvent corrélée positivement à la diversité régionale, tandis que la disparité entre la diversité locale et régionale (diversité beta) est due à la variation dans le turnover des espèces entre les communautés locales (Ricklefs, 2004). Ainsi, les échelles locales et régionales sont intrinsèquement connectées, car la composition locale est une réalisation plus ou moins déterministe de l’assemblage régional, influencée par les gradients biotiques et abiotiques locaux, les niches et les dynamiques populationnelles des espèces. En effet, les variations dans la configuration du paysage et du climat à échelle régionale altèrent les interactions entre espèces et entre populations et communautés (Ricklefs, 2004). Il existe des filtres écologiques à chaque niveau d’assemblage. Les grands gradients climatiques filtrent les espèces au niveau régional, tandis que les gradients d’habitat et les interactions biotiques structurent les communautés (Pearson and Dawson, 2003; Figure 7). La dispersion joue un rôle majeur dans la connexion entre populations et communautés distinctes, et participe donc à la formation des gradients de diversité beta en structurant les assemblages régionaux à échelle locale.

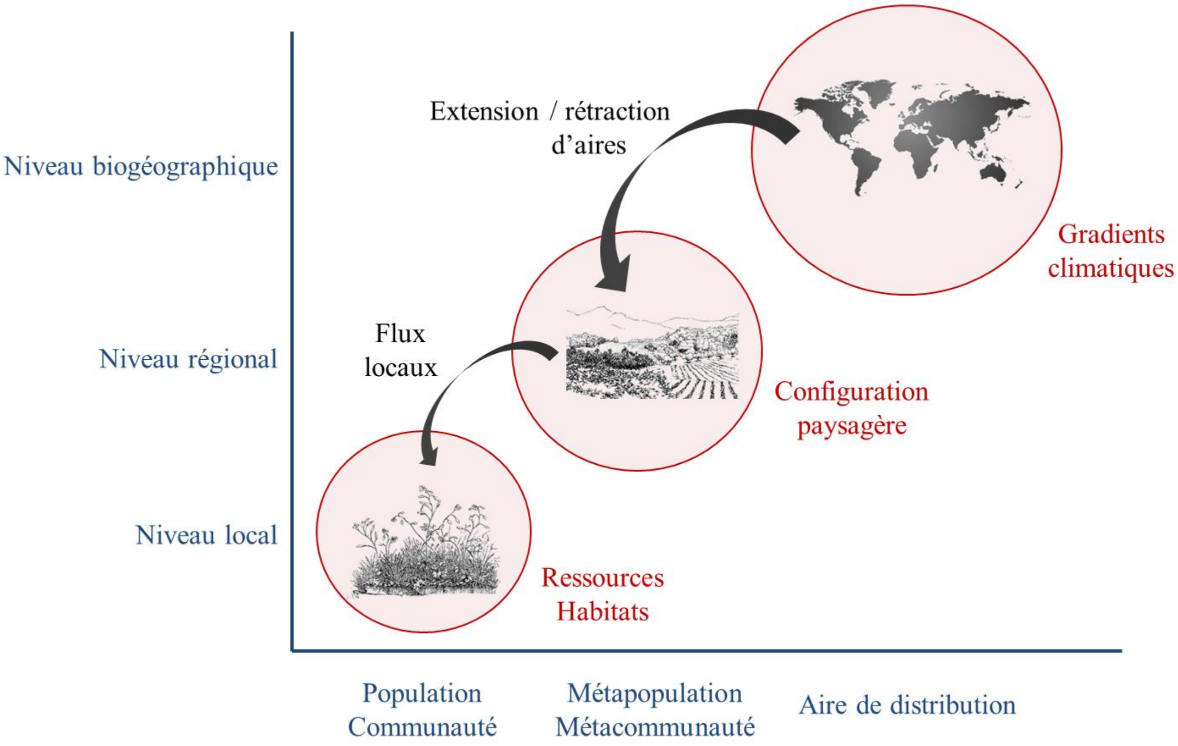


Figure 7 : Représentation schématique des différentes échelles spatiales (locale, régionale, biogéographique) et des différents niveaux d'organisation (communauté, métacommunauté, aire de distribution) dans lesquels la dispersion intervient.

II. La dispersion des plantes

Chez les plantes, les propagules de dispersion incluent des fragments végétatifs, des stolons ou des rhizomes, ainsi que des éléments de reproduction sexuée, comme les graines et le pollen. Ma thèse se concentre sur la dispersion de la banque de graines, qui est la plus susceptible d'impliquer des vecteurs animaux mais aussi et surtout celle dont l'impact sur les patrons de diversité des plantes est le mieux documenté (Figure 8).

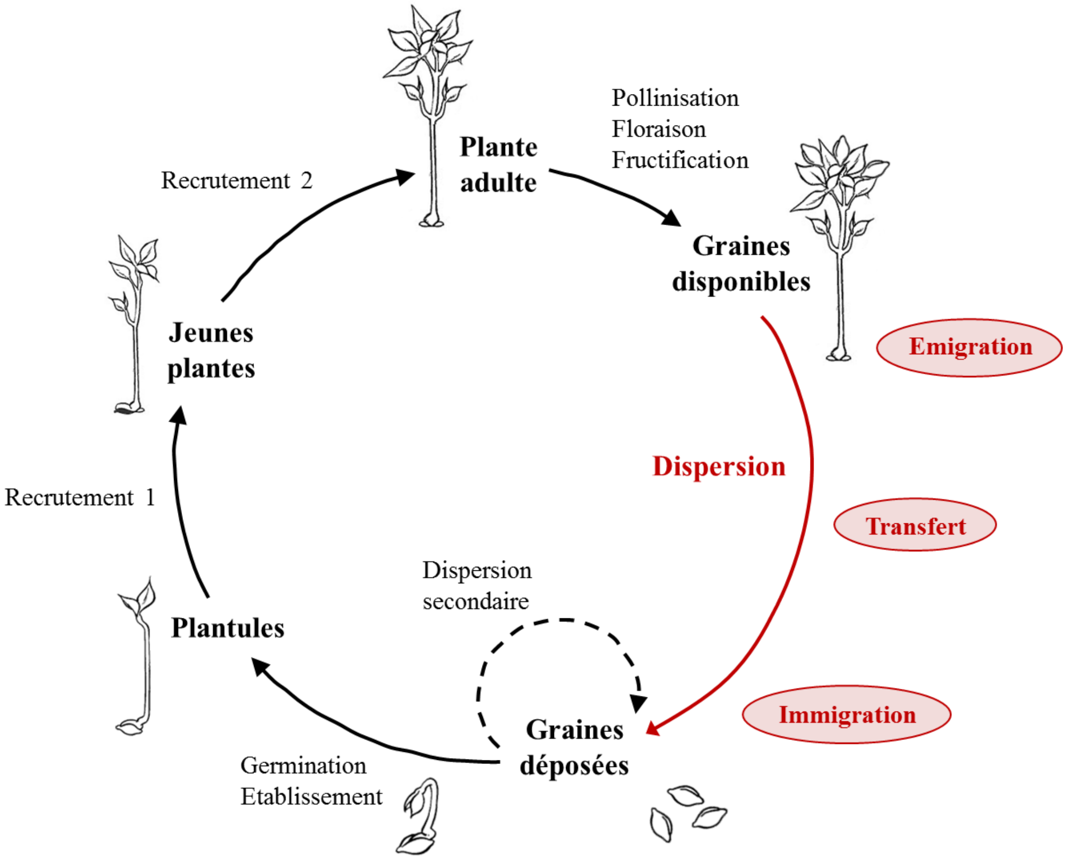


Figure 8 : Cycle de vie d'une plante, dont le processus de dispersion fait partie. Le processus de dispersion lui-même est composé de trois étapes successives : l'émigration, le transfert et l'immigration. (Schéma d'après Wang and Smith, 2002).

Il existe une grande diversité de vecteurs de dispersion des graines. Certaines plantes pratiquent l'autochorie en dispersant elles-mêmes leurs graines, par exemple en les éjectant (autochorie balistique) (Narbona et al., 2005). De nombreuses herbacées annuelles dispersent ainsi leurs graines, mais les distances effectuées par ce biais atteignent rarement plus de sept mètres (Malo, 2004; Vaughn et al., 2011). Les distances sont plus grandes chez les arbres : le record est d'environ 45 mètres pour l'arbre tropical *Hura crepitans* qui mesure 11 mètres de haut (Swaine and Beer, 1977). Les vecteurs de dispersion des graines sont le vent (anémochorie), les courants d'eau (hydrochorie), les animaux (zoochorie) et l'Homme (anthropochorie) (Vittoz and Engler, 2007). Les distances de dispersion par anémochorie et hydrochorie varient dans une large gamme selon les obstacles rencontrés et la vitesse et la direction des courants d'air ou d'eau (Cousens et al., 2008) (voir Tableau 1 pour les distances de dispersion associées à chaque vecteur). La dispersion zoochore implique une large diversité de taxa terrestres ou aquatiques, couvrant la quasi-totalité des groupes animaux (Cousens et al., 2008). Par conséquent, les distances de dispersion associées à la zoochorie varient fortement (Vittoz and Engler, 2007). Elles dépendent surtout de l'espèce animale considérée et de la façon dont les graines sont dispersées. Les graines peuvent être dispersées par ingestion puis défécation ou régurgitation (endozoochorie) ; par adhésion au pelage, aux plumes ou aux pattes des animaux (épizoochorie) ; ou *via* leur stockage par les animaux en vue d'une consommation ultérieure (dyszoochorie). Les distances de dispersion sont habituellement plus importantes pour les vecteurs animaux de grande taille (Vittoz and Engler, 2007; Tableau 1).

Mode de dispersion	**Distance de dispersion (m)**	
	50 %	**90 %**
Autochorie avec rhizome ou bulbe, anémochorie dans des capsules (plantes < 30m), hydrochorie par chute des graines	0.1	1
Autochorie balistique (éjection des graines), anémochorie pour les fruits dans les prairies et pour les plantes > 30m	1	5
Anémochorie pour les herbacées, myrmécochorie (dispersion par les fourmis), anémochorie en forêt, épizoochorie par les petits mammifères	2	15
Anémochorie sur la neige, pour les inflorescences sèches ou pour les arbres, dyszoochorie par les petits animaux	40	150
Anémochorie dans les milieux ouverts et pour les fougères et les orchidées	10	500
Dyszoochorie par les grands animaux, endozoochorie par les oiseaux et les grands vertébrés, épizoochorie par les grands mammifères	400	1500
Anthropochorie	500	5000

Tableau 1 : Distances de dispersion maximales pour lesquelles entre 50 et 99 % des graines d'une population sont dispersées. D'après Vittoz et Engler (2007).

III. La zoochorie

« This is the fascination of plant and animal relationships: the richness of species, the spectacular variety and complexity of interactions, the beguiling loveliness of evolutionary creations, dynamic evolutionary processes and the quest for understanding. We hardly require more justification to study plant-animal interactions, yet there are many other reasons. »

Herrera et Pellmyr (2002)

III. 1. L'endozoochorie

III. 1. A. La phase d'émigration

Pendant la formation des graines, la paroi ovarienne ou d'autres tissus se développent et forment la pulpe ou le tégument. Ensuite, pendant la maturation des graines, ces différentes structures peuvent développer des appendices (crochets, ailes). La division cellulaire dans les tissus qui relient la graine à la plante, ou la dessiccation de ceux-ci, conduit généralement à l'abscission : la séparation entre la graine mature et sa plante parent. Cette étape correspond au début de la dispersion, c'est-à-dire à l'émigration. L'architecture de la plante mère détermine le point d'où débute la trajectoire de dispersion des graines (Cousens et al., 2008). Ainsi, la hauteur et le port (dressé, prostré) de la plante, la localisation des graines (en bout de branches ou tiges, au ras du sol) déterminent à la fois la hauteur de libération des graines et leur accessibilité pour les vecteurs de dispersion. Toutefois, les graines ne peuvent être dispersées que si leur disponibilité coïncide avec la présence et/ou l'activité des vecteurs. Par exemple, les oiseaux migrateurs ne sont présents sur leur aire de nidification qu'à une période donnée de l'année. Les fruits charnus (contenant une ou plusieurs graines) qui composent leur régime alimentaire ne sont alors consommés que pendant cette période, qui peut tout de même durer plusieurs mois. En milieu tempéré, la période de production des graines couvre au minimum deux mois (observation personnelle d'après les bases de traits existantes). La fenêtre de dispersion est donc relativement large, d'autant plus que certaines graines conservent leur intégrité longtemps après maturité ou peuvent finir leur maturation sur l'animal (*Geum urbanum* par exemple ; communication personnelle : Christophe Baltzinger).

Ainsi, la plante parent joue un rôle prédominant dans l'émigration, à travers son architecture et sa phénologie (Cousens et al., 2008).

La prise en charge des graines par le vecteur animal ne dépend pas seulement de leur accessibilité, mais aussi de leur intérêt pour le vecteur, qui est procuré par la taille du lot de graines et/ou la valeur nutritive des graines ou des structures qui les portent ou les entourent (Herrera, 2002; Jordano, 1987). Il existe une corrélation positive entre la biomasse de la plante et le nombre de graines produites (Niklas, 1994; Watkinson and White, 1986). Par ailleurs, un compromis existe entre le nombre de graines produites et la taille de ces dernières (Eriksson and Jakobsson, 1999). L'adaptation morphologique la plus évidente à l'endozoochorie est la production d'un fruit charnu, particulièrement fréquente en milieu tropical (Howe and Smallwood, 1982). Les fruits à pulpe sont consommés par les animaux frugivores comme les chauves-souris, les singes, les mustélidés ou les oiseaux. La composition des fruits est très variable. L'eau est le composant essentiel, auquel peuvent s'ajouter des sucres, des lipides ou des protéines (Cousens et al., 2008; Herrera, 2002). Les fruits peuvent aussi contenir des substances toxiques (alcaloïdes, glucosides), contre lesquels seuls certains vecteurs sont immunisés. Dans ce cas, la dispersion est restreinte à ces vecteurs en particulier (Schaefer et al., 2003). Selon leur composition, les fruits peuvent donc agir comme attractifs ou répulsifs pour les animaux. Les graines peuvent être ingérées sans pour autant être contenues dans un fruit. Janzen (1984) postule que le feuillage de la plante est fonctionnellement équivalent au fruit (« *folliage is the fruit* »), dans le sens où il a aussi un intérêt nutritif pour les vecteurs, notamment pour les mammifères herbivores. Les petites graines, qui passent facilement inaperçues au sein du feuillage, sont souvent retrouvées dans les fèces des herbivores (Couvreur et al., 2005; Mouissie et al., 2005; Pakeman et al., 2002). Ainsi, que ce soit par l'intermédiaire d'un fruit charnu ou d'un feuillage riche en éléments nutritifs (azote, phosphore, potassium), les plantes apportent aux animaux une ressource alimentaire, en contrepartie du bénéfice procuré par le service de dispersion.

La couleur et l'odeur des fruits ou du feuillage agissent souvent comme des signaux. Par exemple, chez beaucoup d'espèces, les fruits changent de couleur quand ils murissent, les rendant ainsi visibles à maturité (Cousens et al., 2008). La taille du fruit joue aussi un rôle, puisque plus le fruit est gros, plus il est détectable. Toutefois, la taille des fruits ingérés est contrainte par la morphologie de l'animal vecteur, et notamment par le diamètre de son tube digestif ou la capacité d'ouverture de son bec ou de sa mâchoire (exemple chez les oiseaux:

Herrera, 1984). Au contraire, un très petit fruit risque d'être ignoré. La couleur, l'odeur et la taille des fruits sont donc des stimuli qui guident les animaux jusqu'aux fruits ou graines matures.

III. 1. B. La phase de transfert

Une fois que la graine est ingérée par un vecteur, la distance qu'elle parcourt depuis sa source dépend (1) du temps qui s'écoule jusqu'à sa défécation ou régurgitation et (2) des mouvements effectués par le vecteur animal pendant ce temps.

III. 1. B. 1. Temps de rétention des graines

Le temps entre l'ingestion et la régurgitation est plus court que le temps de transit à travers l'appareil digestif (Levey, 1986), qui lui dépendent surtout de la longueur de l'intestin et du fonctionnement du système digestif du vecteur. En général, plus l'animal est grand et lourd, plus son intestin est long et large, et plus le temps de rétention des graines est long (exemple chez les primates: Milton, 1984). Typiquement, les temps de rétention des graines sont courts chez les oiseaux, puisqu'ils possèdent un intestin très court (Levey, 1986) ; alors que ceux observés chez les ruminants sont beaucoup plus longs, car ceux-ci possèdent des systèmes intestinaux relativement complexes et pratiquent la rumination, c'est-à-dire qu'ils remâchent plusieurs fois les gros éléments ingérés (Hofmann, 1989; Illius and Gordon, 1992; Figure 9). Le fonctionnement du système digestif de nombreux animaux varie en fonction de leur régime alimentaire et/ou de leurs activités. Les oiseaux migrateurs accélèrent par exemple leur digestion avant et pendant la migration (Figuerola and Green, 2002). De la même manière, le fonctionnement du système digestif des ruminants varie d'une saison à l'autre, en réponse aux modifications de leur régime alimentaire (Hofmann, 1989; Holand, 1994). La qualité (digestibilité), mais aussi la quantité de nourriture ingérée peuvent aussi affecter le temps de rétention. Plus la quantité ingérée est importante, plus le temps nécessaire à la digestion est long (French, 1996). Ainsi, la taille et le fonctionnement du système digestif du vecteur animal influencent le temps de rétention des graines. Le temps de rétention varie donc d'une espèce animale à l'autre, d'une saison à l'autre, et même d'un individu à l'autre (voir Tableau 2 pour les temps de rétention estimés pour différentes espèces animales).

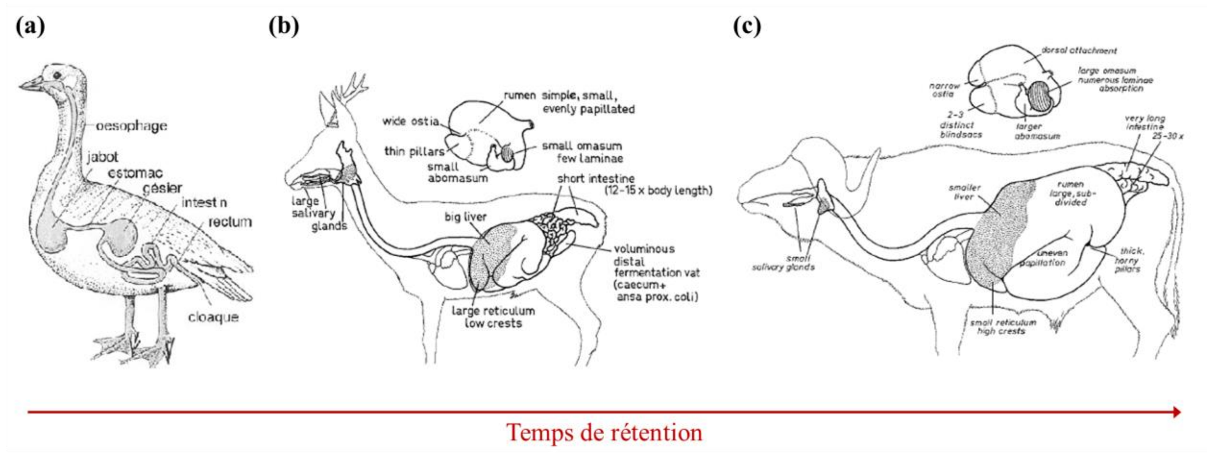


Figure 9 : Exemple d'appareils digestifs. **(a)** Un oiseau : l'oie, **(b)** un petit ruminant : le chevreuil, et **(c)** un grand ruminant : le bœuf. (Schémas extraits de Hofmann (1989) et http://ethologie.unige.ch/). Voir Tableau 2 pour les temps de rétention correspondants.

Les traits morphologiques et chimiques des propagules ingérées affectent également le temps de rétention. Par exemple, chez des bovins, Gardener et al. (1993) ont observé un transit plus rapide pour les grosses graines à tégument fin. Certaines graines contiennent aussi des composés chimiques qui peuvent avoir un effet laxatif ou astringent (Wahaj et al., 1998). Ainsi, la durée de rétention des graines n'est pas simplement fonction des caractéristiques physiologiques du vecteur animal, mais dépend aussi des traits des graines ingérées, et donc de l'interaction entre les traits du vecteur et des graines. Le temps de rétention influe sur les distances de dispersion, car un animal parcourt potentiellement une plus longue distance pendant un long temps de rétention. Cependant, la relation entre temps de rétention et distance de dispersion n'est pas linéaire, car elle dépend du comportement du vecteur, et en particulier de son parcours et de ses déplacements entre l'ingestion et l'excrétion.

Espèce animale	**Minimum**	**Moyenne**	**Médiane**	**Mode**	**Maximum**	**Source**
Oiseaux (9 espèces)	9-43 min			13-54 min	28-348 min	Levey (1986)
Oiseaux (3 espèces)	4-15 min		13-33 min	5-35 min	28-81 min	Murray (1988)
Oiseaux (Calao)		2.6-5.8 h				Hollbrook et Smith (2000)
Oiseaux (Casoar)	0.9-7.7 h	3.3-27 h	2.9-30 h		10-40 h	Westcott et al. (2005)
Renard		6.8-7.7 h				Varela et Bucher (2006)
Primates (4 espèces)		21-25 h				Poulsen et al. (2001)
Primates (14 espèces)	2.75-38 h				84 h (une espèce)	Milton (1984)
Cochon				1 jour	9 jours	Setter et al. (2002)
Mouton		44.8 h		1-4 jours	8-31 jours	Piggin (1978) ; Cosyns et al. (2005)
Cheval		54.7 h				Cosyns et al. (2005)
Ane		70.2 h				Cosyns et al. (2005)
Vache		49.1 h				Cosyns et al. (2005)
Daim	13 h	25 h			38 h	Mouissie et al. (2005)
Chevreuil		27 h				Holand (1994)

Tableau 2 : Exemples de temps de rétention des graines dans le tube digestif des animaux. Différentes statistiques sont présentées, en fonction de celles qui étaient données par les articles cités. (Tableau tiré de Cousens et al. (2008) et complété).

III. 1. B. 2. Mouvements du vecteur animal

La mobilité du vecteur et les directions qu'il prend changent fréquemment et déterminent la trajectoire de la graine. Le rythme d'activité des animaux comprend différentes phases (repos/rumination, déplacement, alimentation). De nombreux animaux possèdent un pic d'activité à l'aube ou au crépuscule, et une longue période d'inactivité la nuit ou en journée (Cousens et al., 2008). La mobilité du vecteur varie donc d'une période à l'autre, et de telles variations peuvent résulter en des distances de dispersion très différentes selon le moment où les graines sont ingérées et/ou déféquées. De plus, le trajet effectué par l'animal vecteur dépend de la composition de la mosaïque paysagère. Pour une même durée de trajet, un animal qui se déplace en ligne droite parcourt potentiellement une plus longue distance qu'un individu qui effectue des détours et d'éventuels retours sur ses pas. En effet, bien qu'un animal puisse parcourir plusieurs kilomètres par jour dans un enclos, la distance de dispersion (entre le point d'émigration et le point d'immigration), ne dépassera pas la dimension maximale de l'enclos. La trajectoire d'un animal est donc rarement en ligne droite, en raison de facteurs tels que la répartition spatiale des ressources et des types d'habitat, ou de la présence éventuelle d'obstacles (clôtures, routes). La présence de compétiteurs ou de prédateurs impacte également les mouvements de l'animal. Ainsi, la distance de dispersion varie en fonction de l'activité et des décisions prises par le vecteur, elles-mêmes dépendantes des conditions biotiques et abiotiques rencontrées par ce dernier. La dispersion n'est donc pas un processus unique mais une succession de choix/événements dont la résultante définit la distance entre la source et le lieu d'arrivée.

III. 1. C. La phase d'immigration

La dispersion se termine quand la graine est déféquée ou régurgitée, et n'est efficace que si la graine est encore viable, c'est-à-dire capable de germer, de s'établir et de donner naissance à une nouvelle plante adulte (Schupp, 1993; Schupp et al., 2010). Or, de nombreux facteurs influent sur la viabilité des graines. La mastication par les animaux pendant la phase de transfert, notamment par les ruminants, ainsi que leurs enzymes digestives peuvent détruire ou endommager les graines. Toutefois, la fréquence élevée du transport endozoochore dans de nombreux groupes de plantes suggère qu'une proportion suffisante de graines survit au passage par le tractus digestif (Cousens et al., 2008). Les traits des graines associés à une meilleure survie après défécation sont une petite taille, une forme arrondie et un tégument épais, dur ou imperméable (Cosyns et al., 2005; Gardener et al., 1993; Mouissie et al., 2005; Pakeman et al., 2002). En effet, les petites graines échappent plus facilement à la mastication, tandis qu'un tégument résistant à la salive ou aux enzymes digestives permet de conserver l'intégrité des graines. La probabilité de germination de la graine ne dépend pas seulement de sa viabilité une fois déféquée, mais aussi des conditions biotiques et abiotiques sur le microsite d'immigration. En effet, une graine viable peut ne pas germer, ou la jeune plantule peut ne pas réussir à s'établir, si par exemple les prédateurs ou les pathogènes sont nombreux, ou si la compétition avec d'autres plantules ou des plantes adultes est trop forte (Howe and Smallwood, 1982; Janzen, 1984). La graine déféquée peut également faire l'objet d'une dispersion secondaire, par un second agent de dispersion, comme des coléoptères coprophages ou des rongeurs par exemple (Forget and Milleron, 1991; Shepherd and Chapman, 1998). Les conditions biotiques telles que la température, le pH, la luminosité ou la quantité de nutriments (azote, phosphore, potassium) influent également sur la probabilité de germination et d'établissement de la plantule. Ainsi, l'établissement d'une nouvelle plante adulte à partir d'une graine dispersée dépend d'interactions complexes entre les traits de la graine et du vecteur dans un premier temps, et entre la graine et son environnement biotique et abiotique dans un second temps.

III. 2. L'épizoochorie

L'épizoochorie est similaire à l'endozoochorie dans le sens où l'architecture de la plante mère, sa phénologie et la taille du lot de graines influent sur la probabilité d'émigration. En revanche, les traits morphologiques des graines qui favorisent l'émigration par épizoochorie diffèrent de ceux associés à l'endozoochorie. Les graines munies de crochets, d'épines ou de soies sont souvent transportées sur le corps des animaux (Heinken et al., 2002). En effet, ces traits morphologiques facilitent l'adhésion au pelage ou aux plumes des vecteurs. Il a d'ailleurs été montré que beaucoup d'espèces végétales possédant de telles adaptations ne dépassent pas 2 mètres de hauteur ; ce qui leur confère sans doute une plus grande probabilité de contact avec les vecteurs animaux (Fischer et al., 1996; Hughes et al., 1994; Sorensen, 1986). D'autres graines peuvent adhérer à différentes surfaces parce qu'elles sont entourées d'une substance collante, le mucilage. De la même manière, des graines de petite taille peuvent facilement coller à une surface, par exemple les pattes des animaux, si elles sont mouillées. La valeur adaptative des traits morphologiques des graines supposés influencer la dispersion dépend aussi des traits des vecteurs animaux. Par exemple, beaucoup de graines peuvent s'accrocher à un pelage épais et/ou frisé, alors que seules les plus adaptées adhérent à un pelage lisse (Heinken and Raudnitschka, 2002). Des animaux comme le sanglier pratiquent la bauge et peuvent ainsi prendre en charge une grande diversité de graines par l'intermédiaire de la terre qui colle à leur corps (Heinken and Raudnitschka, 2002; Picard and Baltzinger, 2012).

Les distances de dispersion épizoochores dépendent aussi du temps de rétention des graines et des mouvements et comportements de l'animal pendant ce temps. Si l'animal se nettoie, heurte ou se frotte contre un buisson ou un arbre, les graines risquent de se décrocher, mettant ainsi fin au processus de dispersion. Quand l'animal mue, il est probable que les graines soient libérées par la chute du pelage ou des plumes. Le temps de rétention des graines sur l'animal dépend donc d'une interaction entre les traits morphologiques des graines et les traits morphologiques et comportementaux de l'animal vecteur. Les petites graines, qu'elles aient des adaptations ou non, sont retenues plus longtemps, car leur présence passe inaperçue pour l'animal qui, quand il se nettoie, retire plutôt les graines de grande taille (Römermann et al., 2005; Tackenberg et al., 2006). Similairement à l'endozoochorie, les mouvements du vecteur sont influencés par la configuration du paysage.

A la différence de l'endozoochorie, les graines dispersées par épizoochorie ne subissent pas l'action des enzymes digestives ou la mastication. Leur probabilité de germination dépend donc plus des conditions biotiques et abiotiques sur le microsite d'immigration, que des contraintes subies lors de l'événement de dispersion.

III. 3. Les syndromes de dispersion

Comme nous l'avons vu précédemment, certains traits des graines sont directement impliqués dans la dispersion, puisqu'ils influent sur l'attractivité et/ou la probabilité de prise en charge par les animaux ou sur le temps de rétention. Une graine et sa plante mère possèdent souvent un complexe de traits qui sont usuellement associés à la dispersion par un vecteur particulier (Moles and Westoby, 2006). Ces complexes de traits déterminent le syndrome de dispersion, défini comme un phénotype de dispersion multivarié, constitué par plusieurs traits qui co-varient (Hughes et al., 1994) (voir le Tableau 3 pour les syndromes de dispersion des différents modes de dispersion). Le syndrome de dispersion est souvent utilisé pour prédire les vecteurs principaux de dispersion, sur la base de la morphologie de la plante mère (hauteur, port) ou des graines (masse, taille, forme, présence ou non d'appendices, de pulpe, etc.) (Thomson et al., 2010). Toutefois, les syndromes de dispersion constituent une vision réductrice des possibilités de dispersion. En effet, rares sont les cas où une espèce végétale est dispersée par une seule espèce animale. Une plante attire généralement plusieurs vecteurs, tout comme un vecteur animal consomme une grande diversité d'espèces végétales (Cousens et al., 2008). Les syndromes de dispersion sont par exemple considérés comme peu informatifs concernant les vecteurs de dispersion à longue distance, car la dispersion à longue distance est souvent le fait de vecteurs de dispersion inhabituels (Higgins et al., 2003).

Mode de dispersion	**Syndrome de dispersion**	
	Traits des graines	**Milieu**
Autochorie balistique	Forme arrondie et surface lisse	
Anémochorie	Présence d'une ou plusieurs aile(s), plume(s) ou structure laineuse	Milieux ouverts, végétation basse, plaines herbeuses, landes, dunes et déserts
Hydrochorie	Faible densité, présence d'aérenchyme, de tissu spongieux	Bords de cours d'eau, zones inondables
Endozoochorie	Présence de pulpe, petite taille, forme arrondie, tégument épais	Milieu forestier et buissonnant
Epizoochorie	Présence de crochets, mucrons, poils, soies	Milieux ouverts
Myrmécochorie	Présence d'un élaiosome (structure lipidique)	

Tableau 3 : Modes de dispersion et syndromes associés. D'après Ozinga et al. (2004) et Cousens et al. (2008).

IV. Influences de la zoochorie sur la dynamique des populations et des communautés végétales

IV. 1. Influences de la zoochorie sur les populations de plantes

Le plus souvent lors d'un événement de dispersion endozoochore, de nombreuses graines sont ingérées puis libérées simultanément. Si le nombre de graines déposées est élevé, une compétition locale pour l'accès à l'espace et aux ressources peut se mettre en place sur le microsite d'immigration, ajoutant un nouveau coût à celui de la dispersion proprement dite (Potthoff et al., 2006). Les grands mammifères herbivores, en raison de leur grande taille et grande capacité de prise alimentaire, peuvent ingérer de grandes quantités de graines d'une même espèce. Les espèces animales qui possèdent un régime alimentaire généraliste ingèrent quant à elles une grande diversité d'espèces, résultant en une compétition interspécifique accrue sur le site de libération. L'endozoochorie peut donc imposer un coût, mais elle apporte aussi un substrat à haute teneur en nitrates *via* les fèces des animaux, et peut donc permettre à un grand nombre de plantules de subvenir à leurs besoins et de s'établir (Mouissie, 2004). En revanche, par épizoochorie, la probabilité pour que des graines prises en charge au même moment soient toutes libérées au même endroit est faible. De plus, il n'y a pas d'apport de nutriments pour la germination.

Les animaux, de par leurs activités, orientent le mouvement des graines de manière non aléatoire et pratiquent de ce fait une dispersion orientée (Wenny, 2001). En effet, un grand nombre d'animaux sont fidèles à leurs sites d'alimentation, de parade ou de repos, et peuvent ainsi visiter fréquemment quelques plantes ou se rendre fréquemment dans des sites particuliers (Cousens et al., 2008). Par exemple, beaucoup d'oiseaux fréquentent régulièrement les mêmes perchoirs, qu'ils utilisent à la fois pour parader, manger ou dormir. C'est le cas d'un oiseau tropical, l'Araponga tricaronculé (*Procnias tricarunculata*) qui disperse les graines de l'arbre *Ocotea endresiana* de façon prédominante sous ses perchoirs, situés dans des trouées forestières où les pathogènes fongiques sont peu abondants : le taux de survie des plantules est ainsi augmenté (Wenny and Levey, 1998). La distance de dispersion est non seulement fonction de la fréquentation d'un site d'alimentation, mais aussi du temps passé sur ce site ; les graines ingérées au début de visites longues ayant une probabilité plus élevée d'être libérées sur leur site de départ (Cousens et al., 2008). De nombreux animaux paradent dans des sites particuliers (arènes des Tétras-lyres) ou possèdent des sites habituels de repos (gorilles, chauves-souris) où la probabilité qu'une graine y soit déposée est grande. Lors d'événements climatiques extrêmes, les vecteurs tendent à s'immobiliser ou réduire leurs déplacements, limitant la distance de dispersion des graines ingérées. A l'échelle d'une population, si la dispersion orientée est influente, la plante dispersée peut coloniser les habitats les plus fréquentés par ses vecteurs animaux, car des graines y sont libérées régulièrement. De plus, si un animal fait des allers retours réguliers entre le patch d'habitat où il se nourrit et l'endroit où il passe le reste de son temps (pour le repos ou la parade par exemple), cela entraine des flux préférentiels d'individus et de gènes, et donc une connectivité accrue entre certains sites en particulier.

IV. 2. Influences de la zoochorie sur les communautés de plantes

Les processus qui opèrent à l'échelle des individus et des populations ont des conséquences à plus large échelle, sur les communautés végétales. La dispersion agit comme un filtre d'assemblage des communautés, car seule une proportion restreinte des espèces et individus dispersés s'établit effectivement sur le site de destination. De plus, les kernels de dispersion qui résultent de la dispersion ont des effets sur la diversité taxonomique et fonctionnelle des communautés. Ces kernels de dispersion sont spécifiques à un mode de dispersion donné, à une plante et un vecteur donné. Un même animal peut produire des distributions spatiales différentes pour une même plante dispersée soit par endozoochorie, soit par épizoochorie. De nombreux processus agissent entre la dispersion des graines et l'établissement de nouvelles plantes adultes. En effet, la résultante de la dispersion, la pluie de graines, est modulée par les interactions spécifiques et les facteurs environnementaux, qui peuvent fortement modifier le patron laissé par la pluie de graines (Levine and Murrell, 2003; Figure 10).

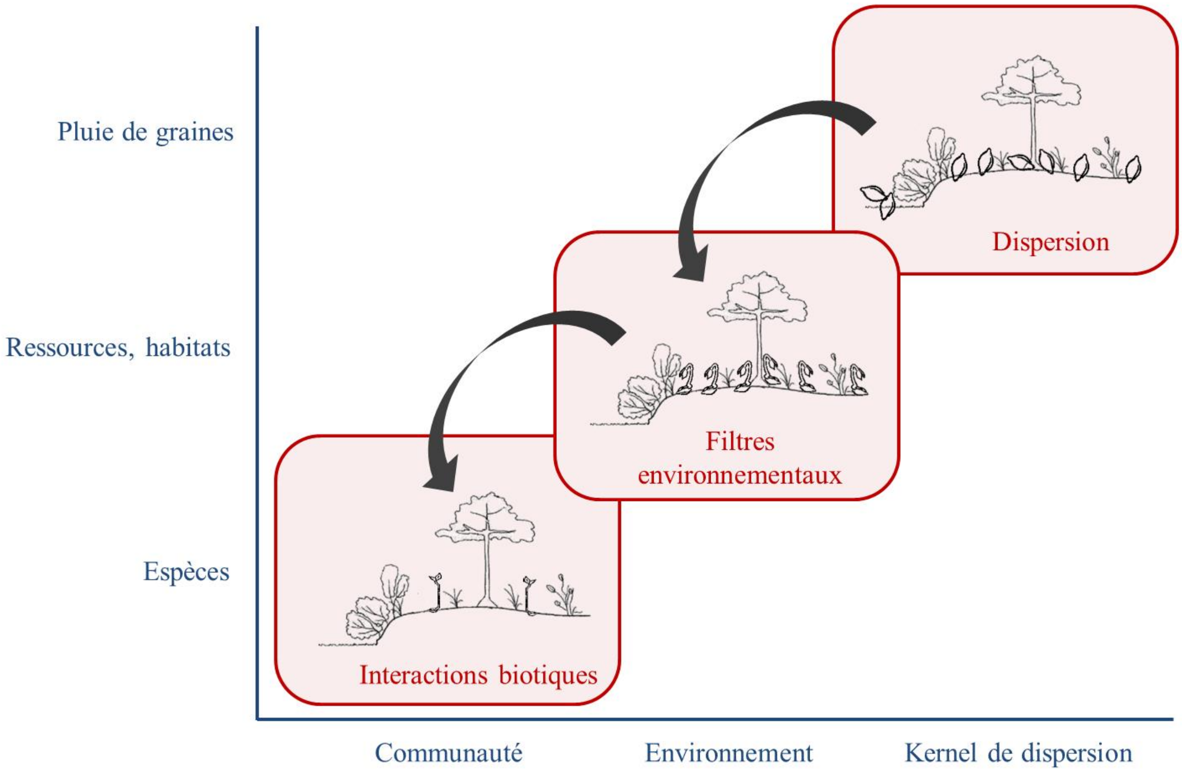


Figure 10 : Représentation schématique des différents filtres qui interviennent dans la composition taxonomique, fonctionnelle et la structuration des communautés végétales.

OBJECTIFS DES TRAVAUX

I. Problématique

Mes travaux visent à tester l'influence de la zoochorie, et plus particulièrement de l'endozoochorie, sur la composition des communautés végétales. Pour cela, j'ai cherché à comprendre expérimentalement l'influence de l'identité des espèces et de leurs caractéristiques fonctionnelles dans l'interaction plante-animal que constitue l'endozoochorie, et ses conséquences sur les patrons de composition des communautés végétales.

II. Modèles d'étude : les ongulés sauvages

Les fortes abondances des ongulés sauvages communs tels que le le cerf élaphe (*Cervus elaphus*), le chevreuil (*Capreolus capreolus*) et le sanglier (*Sus scrofa*), observées depuis les années 1970 en France (ONCFS CNERA Cervidés-Sanglier, Figure 11), ainsi que la capacité de ces animaux à parcourir rapidement de longues distances au sein d'habitats diversifiés (forêt, prairie, culture, etc.), en font des modèles biologiques pertinents pour étudier la dispersion des plantes dans le cadre des changements globaux.

De nombreuses études montrent que ces trois espèces dispersent des graines dans leur pelage ou leur fèces (Heinken and Raudnitschka, 2002; Heinken et al., 2002; Malo and Suárez, 1995; von Oheimb et al., 2005; Schmidt et al., 2004). De plus, les grands mammifères herbivores sont souvent cités comme vecteurs potentiels de dispersion à longue distance, notamment pour expliquer les migrations rapides suite à la dernière période glaciaire (Cain et al., 1998; Pakeman, 2001; Vellend et al., 2003). Cependant, peu de preuves existent sur leur rôle dans la dispersion à longue distance et leur implication dans l'expansion des aires de répartition des espèces végétales. Dans des fèces de cervidés, Vickery et al. (1986) ont toutefois identifié des marqueurs génétiques provenant d'une population de *Mimulus guttatus* située à plus d'un kilomètre du lieu de défécation. Vellend et al. (2003) ont modélisé la dispersion de *Trillium grandiflorum* par le Cerf de Virginie et ont montré que ce dernier dispersait les graines sur quelques centaines de mètres, et occasionnellement à plus de 3 kilomètres. De plus, Boulanger et al. (2011) ont mis en évidence le rôle du cerf et du chevreuil dans la colonisation d'un massif forestier par le cynoglosse d'Allemagne (*Cynoglossum germanicum*), une plante dont les graines possèdent des crochets. En effet, la répartition de la plante au sein d'un massif forestier de 11000 ha a progressée de manière synchrone avec les densités de populations des deux ongulés.

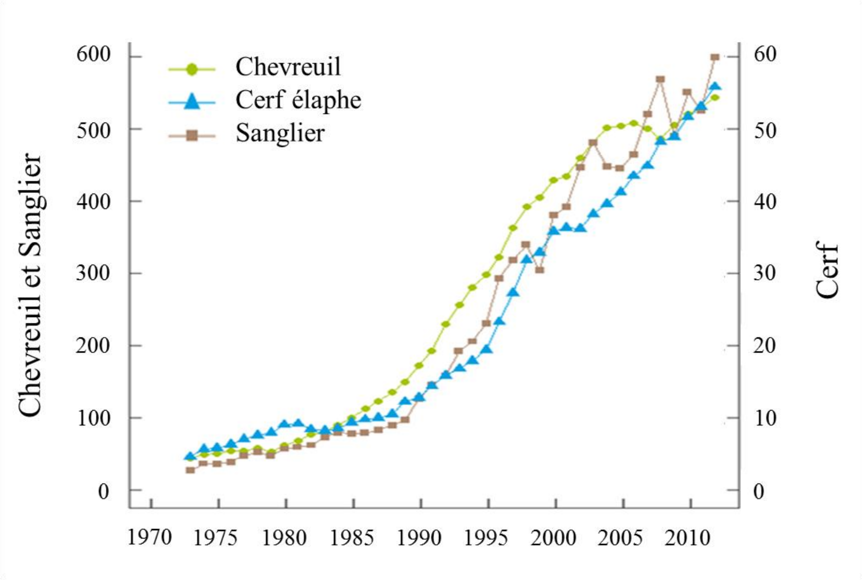


Figure 11 : Evolution des niveaux de populations des trois espèces animales : cerf (*Cervus elaphus*), chevreuil (*Capreolus capreolus*) et sanglier (*Sus scrofa*). Les niveaux de population sont exprimés en 1000 animaux tués, sur la période 1970 à 2013. Les données sont issues du Réseau Ongulés sauvages, ONCFS, CNERA Cervidés-Sanglier.

Les grands mammifères herbivores sont surtout connus pour leurs effets sur la composition des communautés végétales à travers l'herbivorie (Augustine and McNaughton, 1998; Kuijper et al., 2010; Mysterud and Østbye, 2004). En revanche, on ne sait pas si la dispersion peut compenser la perte liée à l'herbivorie. A ma connaissance, seuls Vellend et al. (2006) ont modélisé conjointement les deux processus antagonistes. Ils ont montré que la dispersion de *Trillium grandiflorum* était maximale à des taux relativement faibles d'herbivorie (< 15 %). Une meilleure quantification de la dispersion est nécessaire afin de mieux comprendre comment ces deux processus interfèrent dans la démographie des plantes. A noter qu'en plus de leurs effets directs sur la végétation, à travers l'herbivorie et la dispersion, les ongulés ont aussi un effet indirect *via* leurs fèces qui apportent des nutriments (processus chimique) et les perturbations du sol qu'ils provoquent en formant leurs couchettes ou pendant leur recherche de nourriture (processus physique), et qui peuvent favoriser le recrutement des plantules (Klinkhamer and Jong, 1988; Mysterud, 2006).

Effet de l'interaction entre les plantes et les vecteurs animaux sur la composition taxonomique et fonctionnelle des communautés floristiques

III. Démarche générale

Afin de tester l'influence de la zoochorie, et plus particulièrement de l'endozoochorie, sur la composition des communautés végétales, j'ai choisi d'adopter une approche expérimentale à travers laquelle j'ai suivi le destin des graines, depuis leur émigration par ingestion par les vecteurs animaux, jusqu'à leur immigration et leur germination. J'ai ensuite étudié la composition fonctionnelle de l'assemblage d'espèces dispersé à la fin du processus. Enfin, j'ai étudié la résultante de la zoochorie en termes de patrons de diversité des communautés de plantes, à large échelle. Je me suis concentrée sur la flore d'Europe de l'Ouest et sur les trois ongulés sauvages les plus communs dans cette région : le cerf élaphe, le chevreuil et le sanglier.

- **La première étape (Chapitre 1) vise à décrire les facteurs influant sur le processus de dispersion endozoochore, et plus particulièrement la phase de transfert** (Figure 12). De nombreux travaux se sont d'ores et déjà attachés à caractériser la flore dispersée par endozoochorie par les ongulés sauvages, en termes de richesse spécifique et de composition fonctionnelle (Couvreur et al., 2005; Eycott et al., 2007; Heinken et al., 2002; Jaroszewicz et al., 2013; Malo and Suárez, 1995; Myers et al., 2004; von Oheimb et al., 2005; Schmidt et al., 2004). Ces études informent sur la probabilité d'émigration des graines par ingestion en fonction de leurs traits, et ont servi à définir le syndrome de dispersion endozoochore (voir Tableau 3). En revanche, peu d'entre elles se sont intéressées à la phase de transfert, et notamment au temps de rétention des graines (Cosyns et al., 2005; Mouissie et al., 2005). Ces études n'ont par ailleurs pas différencié les temps de rétention des différentes espèces végétales, et n'ont donc pas considéré les traits des plantes et les traits des animaux, et leurs interactions. Dans un premier temps, j'ai donc cherché à étudier l'effet de l'interaction entre les traits des graines et des vecteurs sur le temps de rétention. J'ai à cette fin mené un suivi individuel de l'excrétion des graines par des animaux captifs en conditions contrôlées, qui m'a permis de modéliser la dynamique d'excrétion des graines au cours du temps, en fonction de l'espèce animal et végétale (Article 1). Puisque la dispersion n'est efficace que si les graines dispersées sont capables de germer et de s'établir, j'ai également testé le coût lié à la dispersion en termes de survie des graines après défécation. Pour cela, j'ai testé la capacité de germination des graines lors du suivi individuel précédemment cité.

J'ai ensuite couplé les distances parcourues par des animaux de chacune des trois espèces animales aux durées de rétention estimées, et ainsi obtenu les distances potentielles de dispersion des graines (Article 2).

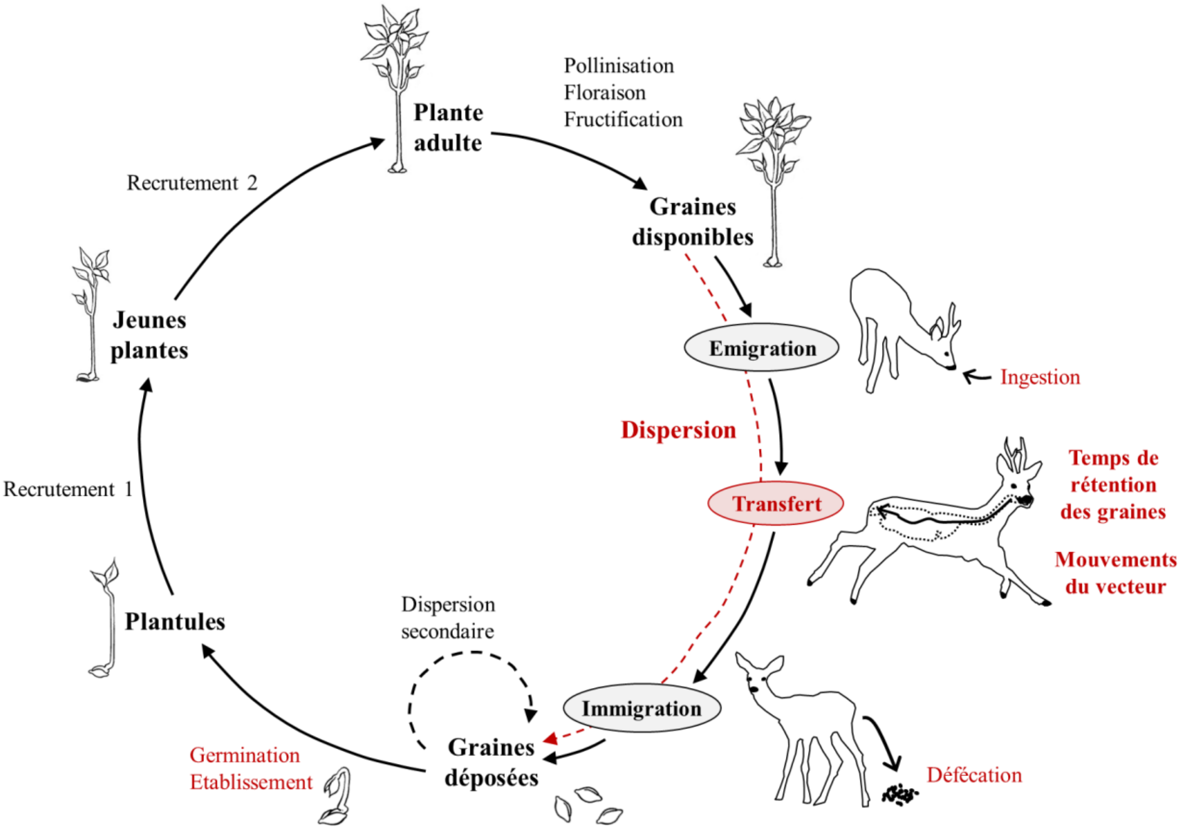


Figure 12 : Cycle de vie d'une plante, dont fait partie le processus de dispersion, lui-même composé de trois étapes : l'émigration, qui correspond à l'ingestion des graines par l'animal vecteur ; le transfert, pendant lequel les graines sont déplacées par l'intermédiaire du vecteur ; et l'immigration, qui correspond à l'excrétion des graines. Les composants signalés en rouge correspondent à ceux traités dans mon travail de thèse.

- **Dans un deuxième temps (<u>Chapitre 2</u>), j'ai testé la prédiction que la composition taxonomique et fonctionnelle des assemblages dispersés par zoochorie diffère de celle de la flore régionale.** Les études antérieures ont décrit les traits de la flore dispersée dans les fèces des ongulés sauvages, mais rares sont celles qui ont testé si ces traits étaient bel et bien sélectionnés (filtrés positivement) par le processus de dispersion, ou s'il ne s'agissait en fait que des traits les plus représentés dans la flore régionale (Eycott et al., 2007; Heinken et al., 2002). De plus, ces études ont considéré chacun des traits végétaux séparément, alors que des études récentes ont suggéré que ce sont des combinaisons de traits, et non certains traits isolés, qui expliquent la survie des graines après défécation (Couvreur et al., 2005; D'hondt and Hoffmann, 2011). Pour savoir si les ongulés sauvages dispersent préférentiellement un assemblage d'espèces défini par des traits écologiques distincts de ceux de la flore régionale, j'ai placé des fèces récoltées dans deux forêts du Loiret sous conditions contrôlées afin de forcer la germination des graines qu'elles contiennent. J'ai ensuite comparé l'assemblage des espèces végétales transporté à la flore régionale, dans un espace fonctionnel multivarié formé par les traits des espèces végétales (<u>Article 3</u>).

J'ai ensuite contribué à tester cette même prédiction à échelle Européenne, en considérant à la fois l'épizoochorie et l'endozoochorie, et à la fois des ongulés sauvages et des ongulés domestiques. Nous avons réalisé une méta-analyse basée sur 52 études Européennes. Nous avons défini deux assemblages d'espèces, dispersés et non dispersés, que nous avons comparés dans un espace fonctionnel multivarié. De plus, pour chaque trait végétal considéré, nous avons calculé un pourcentage de variation entre les espèces dispersées et les non dispersées, pour tester si cette variation pouvait être expliquée par l'effet du mode de dispersion. Nous avons également testé si la magnitude de l'effet variait entre épizoochorie et endozoochorie (<u>Article 4</u>).

- **Enfin, j'ai cherché à savoir si l'influence de la zoochorie (épizoochorie et endozoochorie) pouvait être décelée dans les patrons de composition des communautés végétales (<u>Chapitre 3</u>).** Pour cela, j'ai mis en relation les densités de populations d'ongulés et certaines variables paysagères avec les traits observés dans la flore locale, à l'échelle du quart nord-est français (<u>Article 5</u>).

Trois espèces animales

Le fait de prendre en compte trois espèces animales dont les traits diffèrent permet d'étudier l'influence du vecteur et donc de ses traits sur le temps de rétention et les distances de dispersion, mais aussi d'étudier la façon dont les traits des vecteurs interagissent avec les traits des espèces végétales.

Chaque espèce animale est décrite ci-après par une figure qui résume les principaux traits qui interviennent dans la dispersion des plantes (données provenant de l'ONCFS, CNERA Cervidés-Sanglier) :

- le régime alimentaire et le mode de consommation (selon Hofmann, 1989), qui déterminent quelles graines et quelles quantités de graines sont susceptibles d'être ingérées par l'espèce animale,

- le mode de digestion, qui influe sur le temps de rétention et la survie des graines,

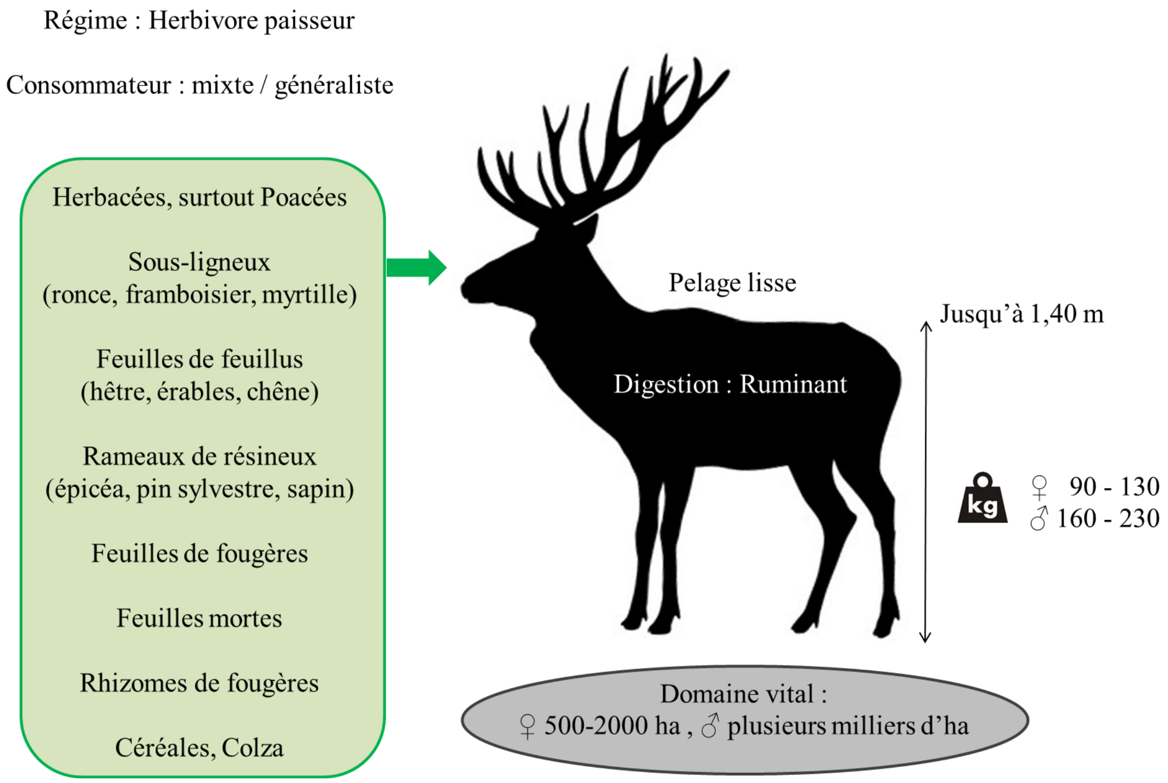
- la masse corporelle, qui renseigne sur la longueur de l'intestin et donc le temps de rétention,

- la hauteur au garrot, qui informe sur la taille de l'animal et les espèces végétales auxquelles il peut accéder (sachant que le Cerf élaphe consomme principalement des plantes de la strate herbacée),

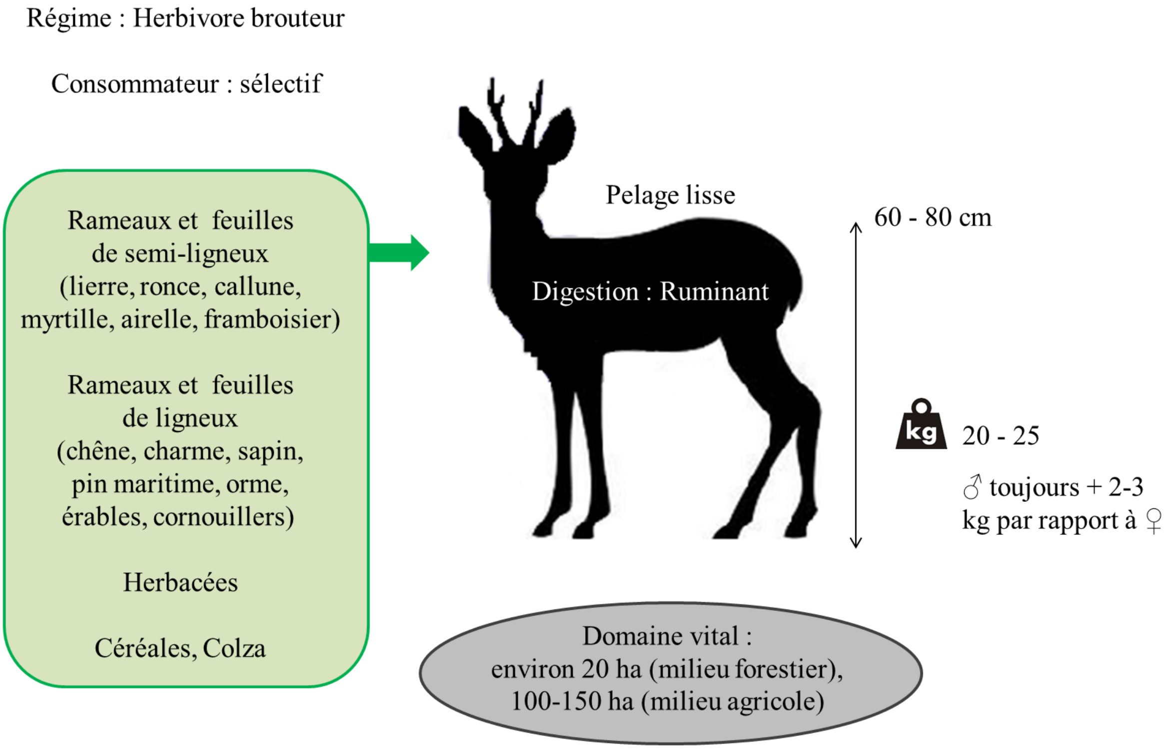
- le type de pelage, qui renseigne sur les possibilités d'adhésion des graines à celui-ci,

- le domaine vital, qui influe sur les distances potentielles de dispersion, car il est probable qu'un animal ayant un grand domaine vital parcourt de grandes distances journalières. La taille du domaine vitale est souvent fonction de la masse corporelle de l'animal (Ottaviani et al., 2006).

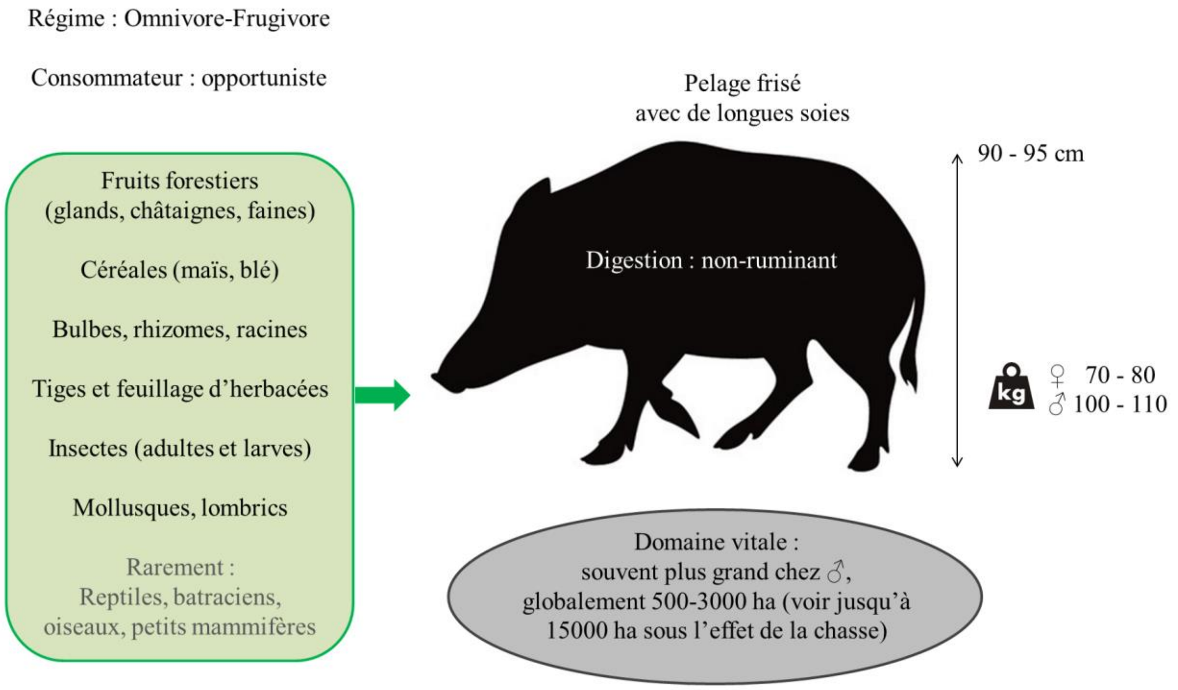
Le cerf (*Cervus elaphus*) est un artiodactyle de la famille des cervidés. Il possède un rythme d’activité polyphasique, avec 4 à 6 périodes d’alimentation quotidienne, dont les plus importantes sont à l’aube et au crépuscule, entrecoupées de phases de rumination (ONCFS, CNERA Cervidés-Sanglier).



Le chevreuil (*Capreolus capreolus*) est un artiodactyle de la famille des cervidés. Il possède un rythme d'activité polyphasique, avec 6 à 12 périodes d'alimentation quotidienne, dont les plus importantes sont à l'aube et au crépuscule, entrecoupées de phases de rumination (ONCFS, CNERA Cervidés-Sanglier).



Le sanglier (*Sus scrofa*) est un artiodactyle de la famille des suidés. Il possède un rythme d'activité cyclique avec une phase de repos pendant la journée, et une phase d'activité, essentiellement à vocation alimentaire, pendant la nuit (cas des populations chassées ; ONCFS, CNERA Cervidés-Sanglier).



Approche par traits

L'utilisation des traits fonctionnels permet de généraliser et prédire la réponse de groupes fonctionnels d'espèces aux conditions biotiques et abiotiques (McGill et al., 2006). Les traits écologiques utilisés dans mon travail concernent ceux usuellement associés à la dispersion zoochore :

- hauteur de la plante mère,
- forme de croissance de la plante mère (selon la classification de Raunkiær),
- indice L d'Ellenberg (besoins en lumière) associé à l'espèce végétale,
- indice N d'Ellenberg (besoins en azote) associé à l'espèce végétale,
- hauteur de présentation des graines,
- nombre de graines produites,
- présence ou non d'appendices sur les graines,
- type d'appendices,
- présence ou non d'aérenchyme,
- présence ou non de mucilage,
- présence ou non d'élaiosome,
- dimensions des graines (longueur, largeur, épaisseur),
- masse des graines,
- forme des graines (arrondie ou allongée/aplatie),
- longévité de la banque de graines,
- mode de dispersion associé au syndrome de traits,
- vecteurs de dispersion répertoriés,
- habitat préférentiel de l'espèce.

La proximité phylogénétique des espèces végétales étudiées n'a pas été prise en compte, car comme souvent pour les données expérimentales, l'échantillon d'espèces et la quantité de données ne permettaient pas ce niveau de complexité.

Deux modes de dispersion

Le fait de considérer à la fois l'épizoochorie et l'endozoochorie permet d'avoir une approche complémentaire du rôle des ongulés sauvages dans la dispersion des plantes. Un même individu peut disperser des graines dans son pelage, sous ses sabots, mais aussi par ingestion puis excrétion, simultanément. Par ailleurs, cette comparaison permet de mettre en évidence la diversité des traits impliqués dans la zoochorie. En effet, alors que pour l'épizoochorie c'est par exemple la présence de structures adhérentes sur les graines qui compte, pour l'endozoochorie, c'est plutôt la taille et la forme des graines ou des propagules.

Différents niveaux d'organisation : individus, populations, communautés.

Différentes échelles spatiales : département du Loiret, quart Nord-Est français, Europe, Europe et Amérique du Nord.

RAPPEL DE LA DEMARCHE

La dispersion structure les métapopulations et les métacommunautés.

La dispersion peut prendre la forme d’une interaction plante-animal : la zoochorie.

Le mode de dispersion, les traits des graines et des vecteurs influent sur le processus de dispersion zoochore.

Question : Quel est l’effet de l’interaction entre les traits des graines et des vecteurs sur la composition taxonomique et fonctionnelle des communautés floristiques ?

Modèles d’études : Les ongulés sauvages.

Chapitre 1 : Le processus de dispersion endozoochore

Chapitre 2 : La zoochorie : un filtre d’assemblage des communautés floristiques ?

Chapitre 3 : Conséquences de la dispersion zoochore sur la composition fonctionnelle des communautés végétales

CHAPITRE 1

Le processus de dispersion endozoochore

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I. Influence des interactions entre les traits des graines et des vecteurs sur le temps de rétention et la probabilité de germination des graines

J'ai testé ici l'hypothèse que les traits des graines et des vecteurs animaux influent conjointement sur le temps de rétention endozoochore des graines. J'ai eu recours à des suivis individuels d'animaux captifs, puisqu'il est impossible de réaliser des observations directes sur des animaux sauvages. J'ai quantifié le temps de rétention grâce à des suivis individuels d'excrétion des graines menés sur 48h en conditions contrôlées, sur des animaux de chacune des trois espèces cibles : cerf, chevreuil et sanglier. Ces trois espèces animales diffèrent de par leur régime alimentaire, masse corporelle et stratégie de digestion. Six espèces végétales, choisies pour représenter un gradient de taille et de forme des graines, ont été présentées à chaque animal. Afin d'estimer le coût associé à l'endozoochorie, j'ai également quantifié la probabilité de germination des graines excrétées. A l'aide d'un modèle dynamique bayésien, j'ai modélisé de façon conjointe l'excrétion des graines au cours du temps et leur probabilité de germination en fonction de l'espèce animale et végétale.

Le temps de rétention est plus long chez le sanglier (> 36h) que chez les deux ruminants : cerf (de 3h à 36h) et chevreuil (de 18h à 36h), pour lesquels le temps de rétention dépend des traits des graines. En effet, chez les ruminants, les graines rondes et de petite taille sont excrétées plus rapidement que les graines plus grosses et allongées. Ce patron semble inversé chez le sanglier, même si l'excrétion des graines se poursuit après la fin de l'expérience au bout 48h. La probabilité de germination des graines est faible (entre 0.07 et 0.39) et une corrélation négative existe entre le temps de rétention et la probabilité de germination des graines, mettant en évidence le coût élevé imposé par l'endozoochorie.

Les traits des graines, des vecteurs et leurs interactions modulent donc les durées de rétention et les probabilités de germination des graines. Les variations du temps de rétention influencent donc non seulement les distances de dispersion et le microsite d'immigration des graines, mais aussi leur viabilité et donc l'efficacité de la dispersion. La probabilité de germination des graines et l'établissement de la plantule dépendent de plus des conditions biotiques et abiotiques rencontrées une fois la graine excrétée. L'endozoochorie est susceptible de modifier les patrons spatiaux de diversité végétale en fonction d'une interaction entre l'assemblage d'espèces susceptible d'être dispersées et les vecteurs localement dominants.

Article 1

Temporal dynamics of seed excretion by wild ungulates: implications for plant dispersal

Picard M., Papaïx J., Gosselin F., Picot D., Bideau E. and Baltzinger C.

Resoumis après révision majeure à *Ecology and Evolution*

Abstract

Dispersal is a key process in metapopulation dynamics as it conditions species' spatial responses to gradients of abiotic and biotic conditions, and triggers individual and gene flows. In the numerous plants that are dispersed through seed consumption by herbivores (endozoochory), the distance and effectiveness of dispersal is determined by the combined effects of seed retention time in the vector's digestive system, the spatial extent of its movements and the ability of the seeds to germinate once released. Estimating these three parameters from experimental data is therefore crucial to calibrate mechanistic metacommunity models of plant-herbivore interactions. In this study, we jointly estimated the retention time and germination probability of six herbaceous plants transported by roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), and wild boar (*Sus scrofa*) through feeding experiments and a Bayesian dynamic model. Retention time was longer in the non-ruminant wild boar (> 36h) than in the two ruminant species (roe deer: 18h - 36h, red deer: 3h - 36h). In the two ruminants, but not in wild boar, small and round seeds were excreted faster than large ones. Low germination probabilities of the excreted seeds reflected the high cost imposed by endozoochory on plant survival. Trait-mediated variations in retention time and germination probability among animal and plant species may impact plant dispersal distances and interact with biotic and abiotic conditions at the release site to shape the spatial patterns of dispersed plant species.

Keywords: endozoochory, metacommunity dynamics, retention time, digestion mode, ruminants, Bayesian dynamic model.

INTRODUCTION

Habitat loss and fragmentation may disrupt metapopulation dynamics by isolating populations in space, thus impairing local and regional species persistence (Cain et al., 2000; Fahrig, 2003; Soons et al., 2005). In island-based formulations of the metapopulation theory, connectivity among distant populations mainly depends on spatial patterns of suitable habitat patches and on species' ability to reach these habitats through unsuitable matrices (Soons et al., 2005). Quantifying dispersal processes is therefore crucial to explain spatial patterns of species occurrence and abundance dynamics, as well as community assembly processes.

In zoochory, dispersal distances are the product of the probability of encroachment or consumption of a seed on/by its vector, the duration of the seed retention by the vector (retention time), and the distance covered by the vector during this time. These three parameters are influenced by the ecological characteristics of both the transported plants and the vector. In the case of endozoochory (dispersal following plant consumption by an animal), fruit releasing height, its colour, and animal habitat and feeding preferences influence probability of being swallowed. In herbaceous plant species, foliage attracts the vector with its palatability and high nutrient contents, thus acting as a fruit (Janzen, 1984). Digestion time mainly depends on animal physiology and food quality (Elston and Hewitt, 2010; Holand, 1994; Jiang and Hudson, 1996), while the distance covered by the vector is influenced by its habitat preferences, the extant and habitat composition of its home range and the landscape configuration.

Endozoochory has been studied for a diversity of vectors including birds (Murray, 1988), bats (Muscarella and Fleming, 2007), rodents (Forget and Milleron, 1991) and large mammals (Couvreur et al., 2005; Eycott et al., 2007; Jaroszewicz et al., 2013; Malo and Suárez, 1995). Among these, species with large home range and large intake capacities, including ungulates, are potentially effective vectors for long distance dispersal in herbaceous plants (Will and Tackenberg, 2008).While ungulate movements and the distances they cover are easily accessible through GPS monitoring, experimental assessments of retention time remain rare because they rely on individual monitoring in controlled conditions with heavy logistic constraints and associated small sample sizes. Endozoochorous seed retention time has rarely been quantified, but mostly for livestock (sheep, cattle, horse and donkey, by Cosyns et al., 2005), with the exception of single studies on fallow deer (Mouissie et al., 2005) and moose (Seefeldt et al., 2010). As an illustration of the weaknesses of existing data, Will and Tackenberg (2008) calibrated a model of endozoochorous plant dispersal based on a single study with data from feeding experiments involving sheep and cattle (Bonn, 2005), while D'hondt et al. (2012) assumed a theoretical retention-time distribution in order to model endozoochory by cattle. Furthermore, the parameters of endozoochory mediated by wild ungulates and livestock may differ due to differences in species' feeding preferences, movements and digestion strategy. Hence, calibrating dispersal model with experiments on livestock may not reflect the actual dynamics of endozoochory in plant communities that primarily interact with wild ungulates.

Food retention time increases with the vector's body mass (Illius and Gordon, 1992), but also depends on its digestion mode (ruminant or not, Elston and Hewitt, 2010) and feeding preferences (browser or grazer). In ruminants, the fine fraction of ingested plants (including small seeds) is passed onwards in the digestive tract, while larger particles (including large seeds) are selectively retained to be chewed twice and further broken down (Clauss et al., 2009). Schwarm et al. (2008) showed that in non-ruminants, this particle sorting mechanism is reversed. Thus, retention time probably differs as a function of seed size and the vector's digestion mode. Furthermore, among ruminants, seed retention time is expected to be longer in grazers (grass and roughage eaters) than in browsers (concentrate selectors feeding on forbs, shrub, leaves and stems) due to the low digestibility of fibers present in high quantities in grasses (Behrend et al., 2004; Hofmann, 1989). Mixed feeders like red deer are either browser or grazer according to seasonal vegetation availability, which implies that their influence as dispersal vectors changes with time. Consistent variations in retention time according to food quality were observed in red deer and roe deer (Holand, 1994; Jiang and Hudson, 1996).

Dispersal is only effective if a sufficient number of seeds germinate once released (Schupp et al., 2010), but endozoochory imposes high costs on seeds due to mastication and exposure to digestive enzymes, such that the survival percentage of defecated seeds is low (Cosyns et al., 2005; Mouissie et al., 2005). Seed morphology influences seed survival after their passage through the digestive system. Seeds that germinate after defecation by ruminant species often share a suite of physical characteristics that enhance germination probability, including a small size, round shape, low mass and a hard seed coat (Couvreur et al., 2005; Mouissie et al., 2005; Pakeman et al., 2002), although smaller proportions of virtually any seeds have been found in animal faeces. Pakeman et al. (2002) suggested that the characteristics that allow seed survival in a soil seedbank, including small size and round seeds (Thompson et al., 1993), may also enhance seed survival after excretion. Furthermore, small and round seeds probably have shorter retention times (Lauper et al., 2013) that limit their exposure to digestive enzymes and may thus increase post-release survival probability. However, these trait-germination relationships have received mixed support. For instance, Mouissie et al. (2005) found no relation between mean seed retention time and seed shape, mass and longevity, while D'hondt and Hoffmann (2011) failed to explain post-release seed mortality with seed size and shape. They proposed instead that seed coat impermeability to water (i.e. physical dormancy) could increase seed survival. The ecological significance of endozoochory for plant dispersal therefore probably differs among seeds with differing morphologies and compositions, although this remains to be experimentally tested.

Using a comparative experimental approach, we quantified endozoochorous seed retention times and germination rates for six plant species abundant in Western Europe and frequently consumed by wild ungulates (*Calluna vulgaris* L., *Juncus effusus* L., *Plantago media* L., *Prunella vulgaris* L., *Rubus fruticosus* L. and *Trifolium pratense* L.). We tested differences in retention times among three vectors: roe deer (*Capreolus capreolus*: a small browser ruminant), red deer (*Cervus elaphus*: a large intermediate mixed-feeder ruminant), and wild boar (*Sus scrofa*: an omnivore-frugivore non-ruminant) (Clauss et al., 2008; Hofmann, 1989). These three vectors are assumed to differ in their retention times because of their differences in digestion modes, feeding preferences and body masses. Contrary to domesticated ungulates, they occupy large home ranges not limited by human confinement, and should as a result disperse seeds over longer distances. However, data on seed retention time by these wild animals are still needed, to calibrate mechanistic models on seed dispersal. We tested four predictions:

- (1) Seed retention time is shorter in a small-bodied browser ruminant (roe deer) than in a larger mixed-feeder ruminant (red deer).

- (2) For the roe and red deer ruminants, median retention time is shorter for plant species bearing small, round, light and/or long-lived seeds with a hard coat than for plant species with opposite traits.
- (3) For the non-ruminant wild boar, the reverse pattern should be found: plant species with small seeds (*Juncus effusus* and *Calluna vulgaris*) should have longer median retention times than large seeds.
- (4) A shorter median retention time should increase median germination probability.

From (2) to (4), we thus expected higher germination rates for *Juncus effusus* and *Calluna vulgaris*, whose seeds share all the characteristics associated with short retention times in (2) than for other seeds for the two ruminant species, and the reverse trend for wild boar.

MATERIALS AND METHODS

Feeding experiments

We conducted feeding experiments on captive animals in three experimental platforms used to work with wild animals (see more details in Appendix 1). All experiments complied with the ethical standards of animal manipulation as defined by the French laws on animal welfare (Décret n°2013-118, see Appendix 1 for the licenses numbers). We monitored eleven individual animals of the three species (Figure 1): five young roe deer (four females and one male), four young female red deer and two adult wild boars (one female and one male). Body mass per species respectively averaged 21.2 ± 4.6 kg, 53.3 ± 5.2 kg and 100 kg (hereafter ± Standard Deviation unless otherwise specified). Retention time can vary between sexes due to sexual size dimorphism, but this was not the case in our experiment, since both sexes weighed roughly the same in roe deer and wild boar. We replicated the monitoring six times for each animal species; some individuals were thus used in several replicates.

Estimating retention time critically requires that the initiation of the individual monitoring corresponds precisely to the time at which all the seeds are ingested. We therefore adapted seed quantities to the intake capacity of our animal vectors (Table 1), which is lower than that of livestock (in particular, roe deer cannot ingest large seed quantities over a short timelag). We limited our study to six plant species, to ensure sufficient seed sample sizes, and mixed controlled seed quantities to constitute seed mixtures in which seed proportions reflected the relative natural seed production of each plant species (Table 1). We measured several seed traits in the initial pure seed samples from commercial suppliers to serve as a quantitative support to the interpretation of our results (see Table 1).

Feeding experiments were conducted from June 2009 to November 2010. Each animal was isolated in a cleaned enclosure (roe deer and wild boar) or box (red deer). Each individual was then fed with a seed mixture mixed with its usual food in a bucket to facilitate ingestion: granules (roe deer), Triticale (mixed with hay during the experiment; red deer), and pears (wild boar). Since the animals were fed with their usual food, no adaptation period was needed before the experiments. Prior to feeding animals, we checked that seeds present in the hay were absent from the seed mixtures. Additionally, all faeces found in the enclosures and boxes were removed before the onset of the monitoring, and kept to serve as controls for possible seed contamination. We began the experiments in the morning, ensuring that each animal ingested as many seeds as possible. We rubbed the animal muzzle above the bucket and added food so that it swallowed seeds while eating anew. We interrupted the feeding phase whether all seeds appeared to be ingested or the animal refused to eat. It took as long as 20 minutes for roe deer. We fixed t=0 as the time of the last ingestion. After the feeding phase, we collected unconsumed seeds that remained in buckets and counted them under stereo microscope to estimate the percentage of ingested seeds by every animal, which ranged from 87.3 % to 100 % (mean = 95.8 ± 3.0 %). Note that some seeds may have fallen unnoticed on the soil during the experiment, in quantities likely too small to affect the results of our experiment. During the experiments, the animals had free access to fresh water and received their usual food every day.

We used Illius and Gordon’s equations (1992) for ruminants and hindgut fermenters relating mean retention time to animal body mass to determine the maximum duration of individual monitoring necessary according to the body mass values of our animal species. For ruminants, we predicted a longer mean retention time (42.8 hours) for red deer, with a maximum weight of 60 kg, than for roe deer (34.3 h for 25 kg), while mean retention time should be lower for the hindgut fermenter wild boar (30.4 h for 100 kg). To ensure that we covered the estimated maximum retention duration, we collected all fresh faeces for 54 hours, from seed ingestion (t=0), every 3 hours during the first 24 hours and every 6 hours thereafter.

Seed release and germination

Dissecting entirely all the collected faeces for seed extraction revealed intractable. Hence, we extracted and dissected two random samples of 4.0 g for roe deer or 8.0 g for red deer and wild boar from each faeces. Sampled weight reflected the average faeces weight of each species, which was lower for roe deer (24.1 ± 17.7 g) than for wild boar (42.6 ± 23.2 g) and red deer (61.9 ± 32.9 g). We dissected the first sample ("dissected sample") under stereo microscope, to visually identify and count the seeds that passed animal guts. We used the second sample ("germination sample") to assess post-release seed germination after a one month vernalisation period in a cold chamber (4°C). We washed each germination sample through sieves of 2 mm, 800 µm, 400 µm and 200 µm stacked on top of each other, which respectively retained large components, large seeds (*Plantago media*, *Prunella vulgaris*, *Trifolium pratense* and *Rubus fruticosus*), medium components, and small seeds (*Calluna vulgaris* and *Juncus effusus*). This process also removed fungi spores. We placed the contents of the 800 µm and 200 µm sieves together on wet blotting paper as a 3-mm-thick layer in germination boxes. For each plant species, we also prepared a control box equally divided in four replicates of 100 non-ingested seeds. We monitored all the germination boxes under controlled conditions in a growth chamber, with daily cycles of 16 hours of light at 25°C and 8 hours of darkness at 15°C, and water supply when necessary. These conditions are supposed to allow germination of a large range of plant species. We counted and identified seedlings twice a week for two months. We thus obtained standardized seed and seedling counts for each dissected and germination sample, for a total of 154 faeces (roe deer: 53, red deer: 64 and wild boar: 37 faeces). We calculated the germination percentage for the non-ingested seeds by averaging the number of seedlings in each of the four replicates of 100 non-ingested seeds.

Statistical analyses

We modelled the dynamics of seed excretion and seed germination together, which, instead of all previous similar studies, allowed us to estimate jointly retention time and its cost on seed viability. A Bayesian state/space formulation allowed us to represent both the observation process through observation variables (seed and seedling counts) and the system process through unobserved latent variables. The model is composed of three sub-models (Figure 2). The excretion sub-model describes the process of defecation and seed excretion, the dissection sub-model describes the seed count experiment and the germination sub-model describes the germination of excreted seeds in the germination sample.

Excretion sub-model – At the beginning of the experiment (t=0), the number of ingested seeds of plant species j by animal i ($Nt_{i,j,0}$) was modelled as a Poisson distribution with mean $Ntot_{i,j}$:

$$Nt_{i,j,0} \sim \text{Poisson}\,(Ntot_{i,j}).$$

$Ntot_{i,j}$ corresponds to the observed number of seeds of plant j ingested by animal i. After seed ingestion, the number of seeds in the digestive system at a given t ($Nt_{i,j,t}$) is given by:

$$Nt_{i,j,t} = Nt_{i,j,t\text{-}1} - Nf_{i,j,t}$$

where $Nf_{i,j,t}$ is the number of seeds that are excreted during the time interval between t and $t\text{-}1$. $Nf_{i,j,t}$ is drawn from $Nt_{i,j,t\text{-}1}$ in a binomial distribution with a probability $pexeff_{i,j,t}$ (excretion probability):

$$Nf_{i,j,t} \sim \text{Binomial}\,(pexeff_{i,j,t}\,,\, Nt_{i,j,t\text{-}1}).$$

The excretion probability was defined as $pexeff_{i,j,t} = defec_{i,t} \times pex_{i,j,t} \times \Delta_t$. The binary variable $defec_{i,t}$ represents the defecation by animal i at time t (1 for excretion, 0 otherwise), modelled as a Bernoulli distribution with probability $pdef_{i,t}$ (defecation probability) :

$$defec_{i,t} \sim \text{Bernoulli}\,(pdef_{i,t}).$$

The defecation probability was then related to the time lag between two observation times (Δt) and was allowed to vary among animal species $s(i)$:

$$\text{logit}\,(pdef_{i,t}) = \alpha^{d}_{s(i)} + \beta^{d}_{s(i)} \times \Delta_t.$$

The potential excretion probability per time step $pex_{i,j,t}$ was related through a logit link to a quadratic function of time (which permits $pex_{i,j,t}$ to have a maximum) and was allowed to vary among animal species $s(i)$ and plant species j :

$$\text{logit}\,(pex_{i,j,t}) = \alpha^{e}_{s(i),j} + \beta^{e}_{s(i),j} \times \mathrm{t} + \gamma^{e}_{s(i),j} \times \mathrm{t}^2 + \varepsilon^{e}_{i,j,t}$$

where $\varepsilon^{e}_{i,j,t}$ is a normally distributed random effect, which variance τ^{e} varied among animal species:

$$\varepsilon^{e}_{i,j,t} \sim \text{Normal}\,(0,\tau^{e}_{s(i)}).$$

Dissection sub-model – The actual number of seeds in the dissected sample ($Nfd_{i,j,t}$) was sampled in the total number of seeds in the whole faeces ($Nf_{i,j,\mathrm{t}}$) proportionally to the weight of the dissected sample ($Wd_{i,t}$) relative to the weight of the whole faeces ($W_{i,t}$), $WD_{i,t} = Wd_{i,t} / W_{i,t}$, as a binomial distribution:

$$Nfd_{i,j,t} \sim \text{Binomial}\,(WD_{i,t},\, Nf_{i,j,t}).$$

The number of seeds counted in the dissected sample ($Y_{i,j,t}$) was then drawn from $Nfd_{i,j,t}$ in a binomial distribution with a probability $\lambda_{i,j,t}$, representing imperfect seed detection:

$$Y_{i,j,t} \sim \text{Binomial}\ (\lambda_{i,j,t}\,,\ Nfd_{i,j,t}).$$

$\lambda_{i,j,t}$ was related to seed detection probability ($pviz_{s(i),j}$), with a normally distributed random effect ($\varepsilon_{i,j,t} \sim \text{Normal}\ (0,\tau_{s(i)})$):

$$\text{logit}\ (\lambda_{i,j,t}) = \text{logit}\ (pviz_{s(i),j}) + \varepsilon_{i,j,t}$$

Germination sub-model – The number of seedlings counted in the germination sample ($G_{i,j,t}$) was a sub-sample of the number of seeds in the non-dissected part of the faeces ($restNf_{i,j,t} = Nf_{i,j,t} - Nfd_{i,j,t}$) and depended on the relative weight of the germination sample: $\text{WG}_{i,t} = (Wg_{i,t}\ /\ W_{i,t})\ /\ (1 - WD_{i,t})$, where $Wg_{i,t}$ is the absolute weight of the germination sample. Thus, $G_{i,j,t}$ was modelled so as to be drawn from $restNf_{i,j,t}$ in a binomial distribution with a probability $pg_{i,j,t}$:

$$G_{i,j,t} \sim \text{Binomial}\ (pg_{i,j,t}\,,\ restNf_{i,j,t}).$$

$\text{pg}_{i,t}$ was related through a logit link function to germination probability ($pgerm_{i,j,t}$) for the given relative weight of the germination sample ($\text{WG}_{i,t}$) and to a normally distributed random effect ($\varepsilon^{g}_{i,j,t} \sim \text{Normal}\ (\mu,\tau^{g}_{s(i)})$):

$$\text{logit}\ (pg_{i,j,t}) = \text{logit}\ (WG_{i,t} \times pgerm_{i,j,t}) + \varepsilon^{g}_{i,j,t}$$

$pgerm_{i,j,t}$ was linearly related to time, with variations among animal and plant species:

$$\text{logit}\ (pgerm_{i,j,t}) = \alpha^{g}_{s(i),j} + \beta^{g}_{s(i),j} \times \text{t}.$$

Run – Non informative priors were specified for all parameters (Kéry, 2010). Three Monte Carlo Markov chains (MCMC) were run under JAGS 3.3.0 (Plummer, 2003), on one million iterations of burn-in and an additional million iterations, thinned by 500.

Analyses

Chain mixing and convergence were assessed with the Gelman and Rubin statistic (Rhat), and was considered acceptable when Rhat < 1.2 (Gelman et al., 2004). Model fit was assessed through a posterior predictive check based on the posterior distributions of replicated data ($Y.rep_{i,j,t}$ and $G.rep_{i,j,t}$) (Gelman et al., 2004). The posterior distributions of the replicated data showed an adequate fit (see Appendix 2).

We calculated the mean percentage of seeds excreted during 54 hours by each animal species. We then compared defecation, excretion and germination probabilities between animal and plant species by computing the percentage of overlap in their posterior distributions, for each plant pair and animal species pair. We further computed median defecation probability

($pdef_{i,t}$) and its associated 95% credibility interval for each animal species and the median maximal $pgerm_{i,j,t}$ for each plant-animal species pair. We compared retention times across plant-animal species pairs by calculating the time associated with the maximum excretion probability ($pex_{i,j,t}$).

RESULTS

Experimental results

No seeds of the experimental plant species were found in any of the faeces collected from the enclosures and boxes just before seed ingestion, indicating that our experiment was not polluted by the intrusion of external seeds. Roe deer, red deer and wild boar respectively defecated 6.3 ± 1.5, 5.4 ± 1.4 and 4.0 ± 1.4 faeces per day, on average 152.8 ± 62.7, 334.4 ± 87.9 and 172.4 ± 65.5 grams of faeces per day.

Bayesian model results

Defecation – Defecation probability ($pdef_{s(i),t}$) was lower in wild boar (0.38 [0.21 ; 0.61]; hereafter median [2.5 ; 97.5 % quantiles] unless otherwise specified) than in roe deer (0.70 [0.42 ; 0.94]) and red deer (0.74 [0.59 ; 0.87], posterior probability that $pdef_{i,t\ \text{wild boar}} < pdef_{i,t\ \text{ruminants}}$ was 99.5 ± 0.3 %), and similar in roe deer and red deer ($pdef_{i,t\ \text{red deer}} > pdef_{i,t\ \text{roe deer}}$: 55.3 %, Figure 3).

Seed excretion and retention time – Roe deer, red deer and wild boar excreted respectively 3.6 ± 4.9, 7.8 ± 4.9 and 34.7 ± 17.2 % of the seeds ingested. As a result, excretion probability was higher in wild boar than in the two ruminant species (posterior probability that $pex_{i,j,t\ \text{wild boar}} > pex_{i,j,t\ \text{ruminants}}$ was 98.7 ± 1.8 % for all plant species, Figure 4A). Median retention times (MRT) did not differ between the two ruminant species, although red deer exhibited a wider range of MRT than roe deer (roe deer: 25.5 ± 7.8 h, red deer: 22.5 ± 11.9 h, Table 2). Wild boar had a longer retention time, irrespective to the plant species (42 ± 4.1 h). In roe deer, seeds of *Juncus effusus*, *Calluna vulgaris* and *Trifolium pratense* were excreted faster than other seeds (Figure 4B and Table 2). In red deer, we observed roughly the same pattern. The seeds of *Trifolium pratense* and *Calluna vulgaris* were excreted first (posterior probability that $\text{MRT}_{\text{Trifolium pratense, Calluna vulgaris}} < \text{MRT}_{\text{other species}}$ was > 82.4 %), followed by *Juncus effusus* and *Plantago media* (posterior probability that MRT $_{\text{Juncus effusus,}}$

$_{\text{Plantago media}} < \text{MRT}_{\text{Rubus fruticosus, Prunella vulgaris}}$ was > 83.0 %) and then *Rubus fruticosus* and *Prunella vulgaris*. In wild boar, retention times were globally homogenous, although *Juncus effusus* and *Trifolium pratense* tended to be excreted later than the other species (posterior probability that $\text{MRT}_{\text{Juncus effusus}} > \text{MRT}_{\text{other four species}}$ was > 63.2 % and that $\text{MRT}_{\textit{Trifolium pratense}} > \text{MRT}_{\text{other four species}}$ was > 61.2 %). Nevertheless, in wild boar, the excretion probability of *Juncus effusus* had only begun to decrease 54 hours after ingestion and it was still increasing for *Trifolium pratense*, suggesting that seed release continued after the experiment (Figure 4A).

Germination – In controls, the germination percentage of non-ingested seeds of *Plantago media* (91 ± 2 %, n = 4 × 100), *Prunella vulgaris* (75 ± 2 %) and *Trifolium pratense* (70 ± 6 %) were all higher than 70 %. Germination was lower for *Juncus effusus* (23 ± 3 %) and *Calluna vulgaris* (8 ± 2 %), while *Rubus fruticosus* did not germinate at all. Considering all the faecal samples, all the six plant species germinated at least once. Per 100 grams of faeces, 26.94 (± 36.11) seedlings germinated from red deer, whereas only 5.40 (± 13.34) and 4.71 (± 9.86) germinated respectively from wild boar and roe deer. All vectors taken together, we observed seedlings in only 53 out of 154 faeces. In roe deer, isolated seedlings of *Calluna vulgaris*, *Plantago media* and *Prunella vulgaris* germinated in 10 faeces. In red deer, we observed up to 9 seedlings of *Juncus effusus* in all but one faeces; up to 4 seedlings of *Calluna vulgaris* per faeces, in 11 faeces; up to 2 seedlings of *Plantago media* per faeces, in 7 faeces; and up to 2 seedlings of *Trifolium pratense* per faeces, in 3 faeces. In wild boar, only *Plantago media* and *Rubus fruticosus* germinated in small numbers (respectively up to 2 seedlings per faeces, in 2 faeces; and up to 4 seedlings per faeces, in 4 faeces), while *Rubus fruticosus* did not germinate at all in controls. As a consequence of the rarity of germination events, median germination probabilities were misestimated to either zero or 1, except for *Calluna vulgaris* (maximal $pgerm_{s(i),j,t}$: 0.058 [0.013 ; 0.243]), *Juncus effusus* (0.388 [0.136 ; 0.787]) and *Plantago media* (0.071 [0.001 ; 0.508]) in red deer. For these three plant-animal pairs, germination probabilities decreased rapidly with retention time (Figure 5).

DISCUSSION

We showed that seed retention time varied among plant-animal species pairs chosen for their contrasting morphological and physiological traits, and that germination probability was low and tended to decrease with retention time. Animal and seed characteristics probably interact through the endozoochorous process, with consequences on the spatial structure of the seed shadow as well as the resulting plant distribution and community patterns.

Our model is the first to quantify jointly retention time and post-dispersal germination probability in an explicit dynamic framework. Our experiment also represents the first attempt to estimate seed retention time by a small browser ruminant species (roe deer) and a relatively small hindgut fermenter (wild boar). So-doing, we provide experimental-based data suitable to calibrate mechanistic models of zoochorous plant dispersal similar to those of Will and Tackenberg (2008) or D'hondt et al. (2012). These innovations come with some limitations imposed by the usual constraints of experimental monitoring of captive animals of wild origin, the first one being small sample size. The limited availability of captive ungulates in experimental platforms and the difficulty of controlling animal behaviour during the experiments are particularly restrictive when studying wild species. Nevertheless, our sample size (six replicates per animal species) was higher than in previous studies (four replicates for fallow deer or moose, and five for rabbit, cattle, sheep, donkey and horse, by Cosyns et al., 2005; Mouissie et al., 2005; Seefeldt et al., 2010). Furthermore, the small size of the plant species assemblage and the limited number of animal individuals limited the extent of interspecific variability in seed retention time, thus making it difficult to disentangle the effects of vector and plant traits in a quantitative way. In the prospect of improving the empirical validation of these models, we strongly encourage the replication of our data to fit our model over longer study periods and with larger animal and plant species samples.

Seed retention times

Our seed retention times are consistent with those obtained for particles or food in previous experiments (Behrend et al., 2004; Elston and Hewitt, 2010; Holand, 1994; Jiang and Hudson, 1996). Yet, contrary to our initial hypotheses, differences in feeding preferences and body mass did not translate into shorter retention times in roe deer than in red deer. Wild boar exhibited longer retention times (> 36h) than the two ruminant species for all the plant species concerned, contrary to what we expected following Illius and Gordon's equations. Separating the effects of body mass from those of digestion strategy would require intraspecific replication (in red deer for example, because of its high sexual dimorphism and large range of body masses among individuals). In our case, this was not feasible due to the difficulty of finding adequate wild animals available for experimentation. However, our results are unlikely to be solely attributable to differences in body mass as the mass difference between wild boar and red deer equaled that between red deer and roe deer. Additionally, body mass appeared unrelated to retention time in previous studies (Schwarm et al., 2008; Steuer et al., 2011), which suggests that the effects of digestion strategy may dominate those of body mass on seed retention time.

Our results showed that seeds may be sorted according to their size and shape, as was previously shown for other digested particles (Clauss et al., 2009). As predicted, small and light seeds (*Juncus effusus* and *Calluna vulgaris*) and round seeds (*Calluna vulgaris* and *Trifolium pratense*) were excreted faster than other seeds by the two ruminant species. In wild boar, small and round seeds seemed to be excreted later than others, suggesting that particles are sorted through different processes in non-ruminants compared to ruminants. Hence, animal and seed characteristics interact and influence seed retention time. We further noticed that the differentiation between seeds was more marked in red deer, which exhibited a wider range of retention times (from 3h to 36h: *Trifolium pratense* and *Calluna vulgaris* first, followed by *Juncus effusus* and *Plantago media*, and then *Prunella vulgaris* and *Rubus fruticosus*) than roe deer (from 18h to 36h). Clauss et al. (2009) also found that browsers tend to stratify the gut content less than mixed-feeders and grazers, suggesting that red deer may increase heterogeneity in dispersal distances among plant species, which could increase spatial heterogeneity among plant communities, while roe deer would rather increase local heterogeneity and spatial homogeneity. Hence, each vector is likely to affect plant community at different spatial scales.

The GPS monitoring of wild animals revealed that red deer covered longer distances in a straight line (2.6 km in average, and up to 3.5 km) than wild boar (2.2 km and up to 3.1 km) than roe deer (1.7 km and up to 2.0 km) in 48 hours (unpublished data). Moreover, Adrados (2002) showed that a male red deer can cover up to 10.3 km in 24 hours between two seasonal parts of its annual home range, and female roe deer can cover up to 1.4 km in 6 hours during the rut (Richard et al., 2008). The distances covered by the three animal species are longer than one kilometer, which correspond to long dispersal distances (Cain et al., 1998; Higgins and Richardson, 1999). Thus, the three ungulates would induce long-distance dispersal rather than short-distance dispersal, suggesting that they could impact connectivity among distant populations and colonisation processes.

Seed survival

As we expected, germination probability decreased with retention time in all plant-animal pairs. We were only able to estimate germination probability for three plant-animal pairs. Since all the six plant species germinated either in faeces or controls, low germination probabilities unlikely result from the controlled conditions in the germination chamber. Hence, the main possible experimental limitation that could have contributed to our results is the limited time allowed to the germination tests, which could have been too short for some dormant seeds. Indeed, some studies have shown that a considerable number of seeds migrate from decomposing faeces to deeper soil layers instead of germinating (Jaroszewicz, 2013; J. e. Malo and Suárez, 1995; Pakeman et al., 1999). We therefore suggest replicating our germination data allowing for longer experimental durations and conditions closer to the natural context to strengthen our conclusions.

Although wild boar excreted more seeds than the other two species, fewer seeds germinated in its faeces. Hence, longer retention time and the resulting long dispersal distances associated with this vector come at the cost of the mortality of most seeds. Contrastingly, the fact that fruit seeds (*Rubus fruticosus*) only germinated in wild boar faeces (and not in controls) suggests that endozoochory may not systematically be costly to seeds and can even favour germination. *Rubus* seeds are enclosed by a hard endocarp that impedes water imbibition (Wada et al., 2011), which increases seed survival but impair germination in the absence of aggressive physical conditions such as digestive enzymes. Our results therefore suggest that slow-digesting animals are more effective to disperse resistant seeds over longer distances than ruminants.

Conclusion

Our study focused on an individual process limited in space and time. However, we have to keep in mind that endozoochory is a spatially and temporally continuous process, involving a wider range of plants consumed at different times in different places, as long as the animal is feeding. Endozoochory by large ungulates may allow long-distance seed dispersal, favouring connectivity among distant populations within metapopulations or the colonization of unoccupied suitable patches. Our experimental findings and the associated modelling framework have key implications for understanding the role of zoochorous dispersal in shaping plant communities. Different vectors are likely to impact the dynamics of plant species at different spatial scales, not only according to their daily movements within their home ranges, but also according to their life history traits and those of the dispersed plants. Therefore, spatial patterns of plant distributions and community composition are likely to depend in a predictable way on the composition and relative abundance of herbivores, not only through grazing, but also as connectivity agents. Comparing the relative influence of endozoochory to other plant dispersal modes will require extensive experimentation combining animal displacement tracking and seed retention-time estimations similar to ours. Our results support a more extensive assessment of the influence of wild ungulates as vectors of plant dispersal and their impact on spatial patterns of community composition and connectivity.

Acknowledgements

We thank the Behaviour and Ecology of Wildlife unit (C.E.F.S – Comportement et Ecologie de la Faune Sauvage, Toulouse, France), the Alfort Veterinary School (E.N.V.A – Ecole Nationale Vétérinaire d'Alfort, Champignelles, France) and Animal Contact studio (Ladon, France) which respectively provided roe deer, red deer and wild boar. We thank Jean-Luc Rames, Nicolas Cebe, Hélène Verheyden, Hélène Benoît-Valiergue, Claire Debulois, Muriel Bec and Yves Boscardin for their help in collecting faeces. We also thank Victoria Moore for her English proofread.

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FIGURES

Figure 1. Captive roe deer (*Capreolus capreolus*) used in the feeding experiments, in Gardouch, France. Photography © Mélanie Picard.

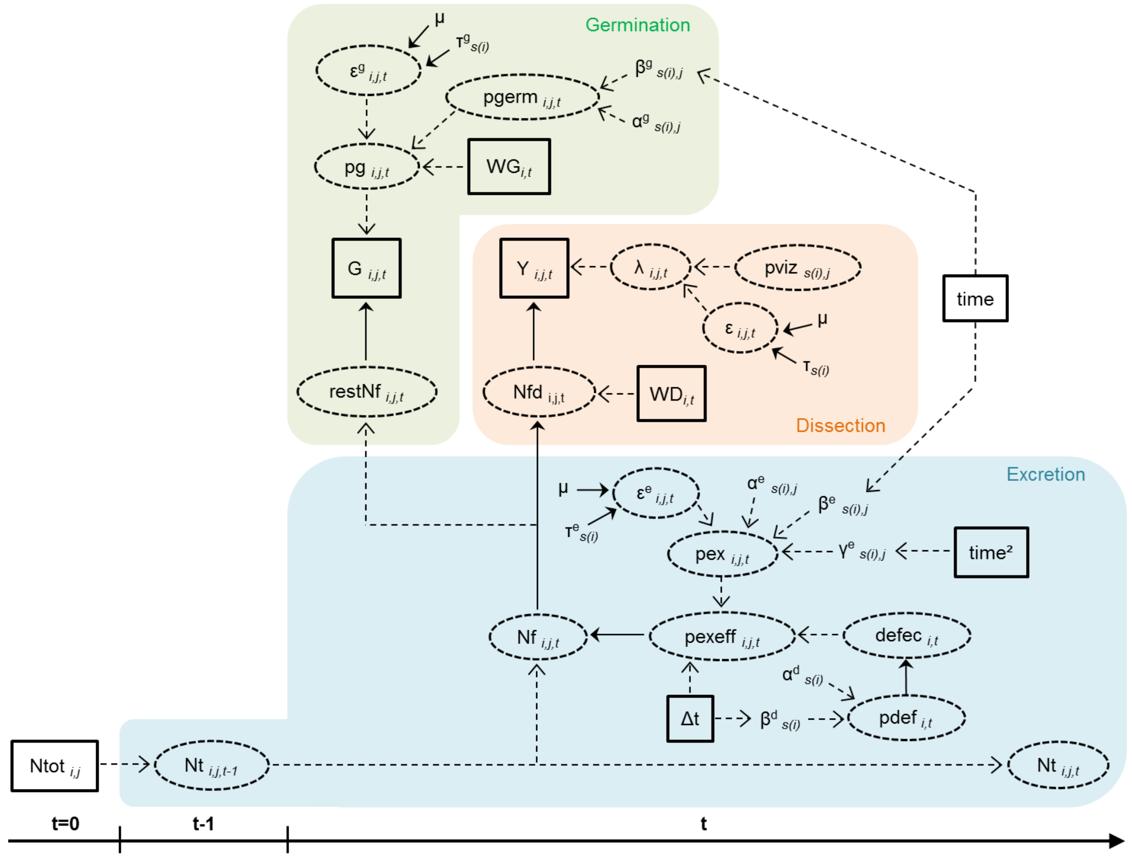


Figure 2. Schematic representation of the Bayesian model. Subscripts correspond to individual *i*, animal species *s(i)*, plant species *j* and time *t*. Δ*t* is the time lag between *t* and *t-1*. The notations for the different sub-models are as follow. Excretion sub-model: observed number of seeds ingested ($Ntot_{i,j}$), number of seeds in the digestive system at *t-1* ($Nt_{i,j,t-1}$) and *t* ($Nt_{i,j,t}$), number of seeds excreted in a whole faeces ($Nf_{i,j,t}$, with $Nt_{i,j,t} = Nt_{i,j,t-1} - Nf_{i,j,t}$), excretion probability ($pexeff_{i,j,t}$), defecation occurrence (0 or 1: $defec_{i,t}$), potential excretion probability ($pex_{i,j,t}$) and defecation probability ($pdef_{i,t}$). Dissection sub-model: number of seeds in the dissected sample ($Nfd_{i,j,t}$), relative weight of the dissected sample ($WD_{i,t}$), seeds counted in the dissected sample ($Y_{i,j,t}$), probability of being counted ($\lambda_{i,j,t}$) and seed detection probability ($pviz_{s(i),j}$). Germination sub-model: number of seeds in the non-dissected part of a faeces ($restNf_{i,j,t}$), seedlings counted in the germination sample ($G_{i,j,t}$), relative weight of the germination sample ($WG_{i,t}$), probability of occurrence in the germination sample ($pg_{i,j,t}$) and germination probability ($pgerm_{i,j,t}$). $\varepsilon_{i,j,t}$, $\varepsilon^{e}_{i,j,t}$, and $\varepsilon^{g}_{i,j,t}$ are random effects. $\alpha^{d}_{s(i),j}$, $\beta^{d}_{s(i),j}$, $\alpha^{e}_{s(i),j}$, $\beta^{e}_{s(i),j}$, $\gamma^{e}_{s(i),j}$, $\alpha^{g}_{s(i),j}$, $\beta^{g}_{s(i),j}$ are the different probability distribution parameters. Solid squares and dashed circles respectively represent observed and latent variables. Solid and dashed arrows respectively represent stochastic and deterministic relationships. The detailed relationships among these variables can be found in the text.

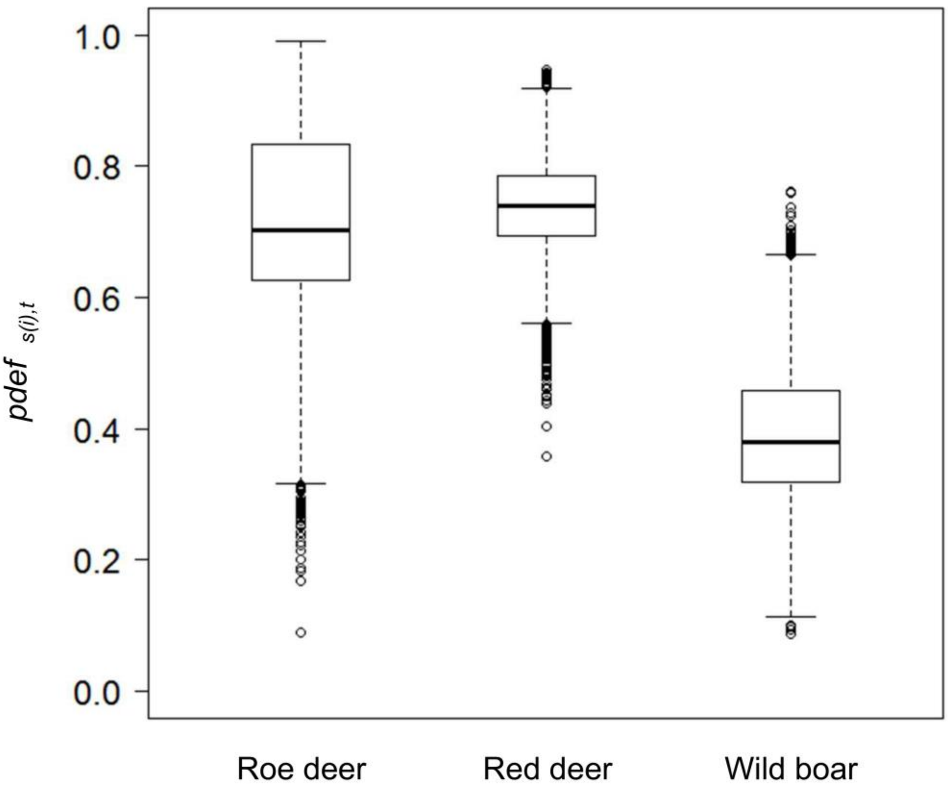


Figure 3. Defecation probability. Defecation probability ($pdef_{s(i),t}$) by roe deer, red deer and wild boar, from left to right. Boxplots show the median, 25th and 75th percentile.

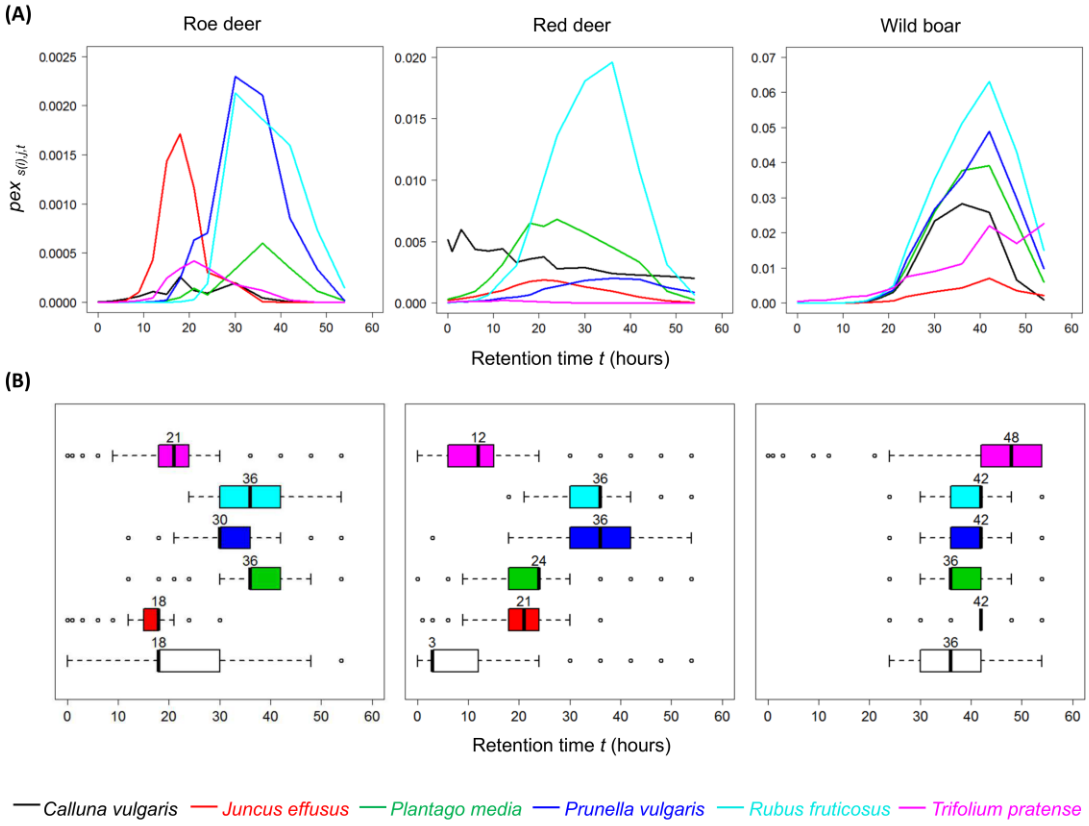


Figure 4. Excretion probability and time associated with maximum excretion probability. (A) Median excretion probability ($pex_{s(i),j,t}$) through time, represented with a different scale for each animal species and without its credibility intervals (which were large) for better readability. **(B)** Time associated with the maximum $pex_{s(i),j,t}$ (boxplots with median, 25th and 75th percentile).

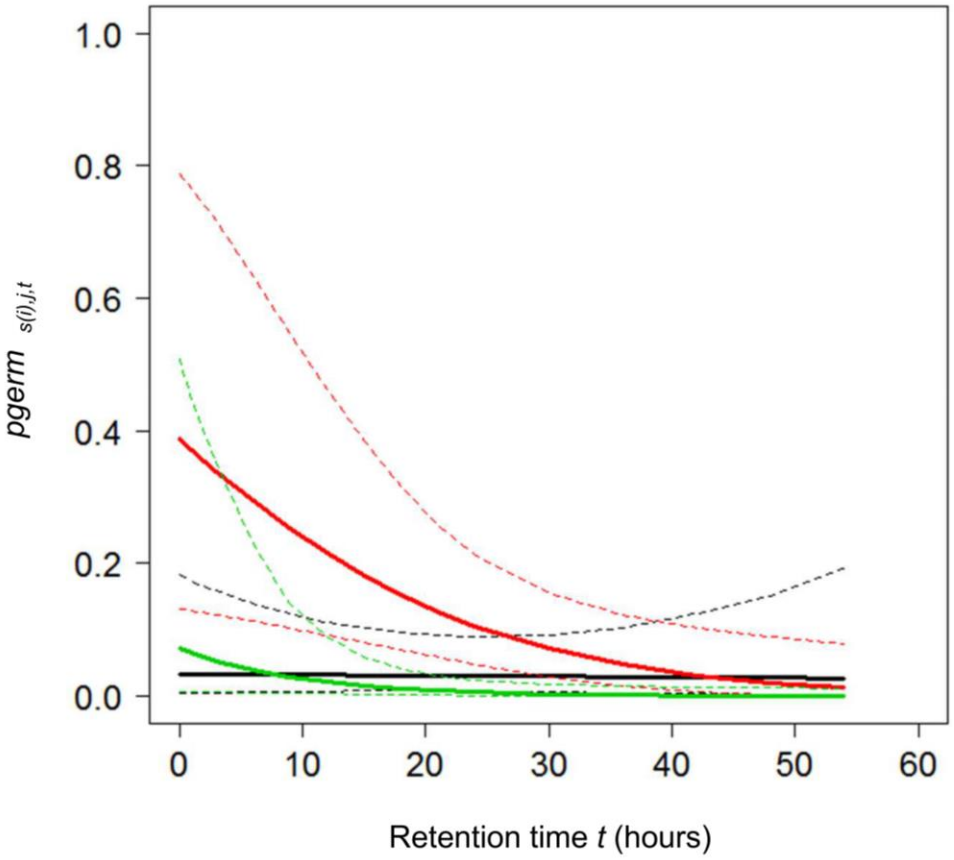


Figure 5. Germination probability. Variation of germination probability ($pgerm_{s(i),j,t}$) with seed retention time, in red deer, for *Calluna vulgaris* (in black), *Juncus effusus* (in red) and *Plantago media* (in green). Plant-animal pairs which were misestimated due to low sample size are excluded. Bold and dashed curves respectively represent the median and its 95% credibility interval.

TABLES

Table 1. Plant species used in the feeding experiments and their corresponding seed characteristics.

Plant species	Seed size (mm)	Seed mass (mg)	Seed shape	Seed longevity index	Seed number per flower // plant	Seed quantity in a seed mixture:	
						Roe deer	**Red deer** and **Wild boar**
Calluna vulgaris L.	0.5 × 0.4 (small)	0.05 ± 0.04 (light)	0.03 (round)	0.81	10-100 // >10000	11000	15000
Juncus effusus L.	0.5 × 0.2 (small)	0.01 ± 0.01 (light)	0.08 (rather round)	0.93	10-100 // >10000	11000	15000
Plantago media L.	2.0 × 1.0 (large)	0.44 ± 0.01 (medium)	0.14 (rather flat or elongated)	0.29	<10 // 1000-10000	1500	2000
Prunella vulgaris L.	1.9 × 1.1 (large)	0.73 ± 0.06 (medium)	0.05 (rather round)	0.20	<10 // 100-1000	1500	2000
Rubus fruticosus L.	3.0 × 2.0 (large)	3.53 ± 0.08 (heavy)	0.07 (rather round)	0.11	10-100 // NA	1500	2000
Trifolium pratense L.	2.0 × 1.4 (large)	1.51 ± 0.01 (heavy)	0.04 (round)	0.24	<10 // NA	1500	2000

Seed size is expressed as length × width (in millimetres, measured in a random sample of 50 seeds per species). Mean mass ± s.d (in milligrams) was measured in a random sample of 100 air-dried seeds per species. Seed shape corresponds to variance in dimensions *Vs*, calculated following Bekker et al. (1998), ranking from 0: perfectly spherical, to 0.2: flat or elongated. Seed longevity index ranks from 0: no persistent records, to 1: all records persistent in Thompson et al.'s database (1997) or in the LEDA Traitbase (Kleyer et al. 2008) for *Rubus fruticosus*. Seed numbers are from Ecoflora database (Fitter and Peat 1994). NA indicates "no data".

Table 2. Maximum excretion probability and its associated retention time.

Plant species		***Calluna vulgaris***	***Juncus effusus***	***Plantago media***	***Prunella vulgaris***	***Rubus fruticosus***	***Trifolium pratense***
Roe deer	***Max $pex_{s(i),j,t}$***	0.0004 [1^{E}-4 ; 0.005]	0.0023 [9^{E}-4 ; 0.014]	0.0009 [1^{E}-4 ; 0.009]	0.0032 [9^{E}-4 ; 0.017]	0.0034 [0.001 ; 0.019]	0.0008 [1^{E}-4 ; 0.007]
	MRT	18h [1 ; 36h]	18h [12 ; 24h]	36h [21 ; 54h]	30h [21 ; 42h]	36h [30 ; 54h]	21h [15 ; 36h]
Red deer	***Max $pex_{s(i),j,t}$***	0.0075 [0.003 ; 0.026]	0.0022 [0.001 ; 0.004]	0.0086 [0.004 ; 0.026]	0.0026 [0.001 ; 0.007]	0.0223 [0.012 ; 0.052]	0.0003 [1^{E}-4 ; 7^{E}-4]
	MRT	3h [0 ; 54h]	21h [15 ; 30h]	24h [15 ; 36h]	36h [24 ; 54h]	36h [24 ; 42h]	12h [0 ; 21h]
Wild boar	***Max $pex_{s(i),j,t}$***	0.0360 [0.013 ; 0.103]	0.0083 [0.004 ; 0.041]	0.0472 [0.026 ; 0.104]	0.0536 [0.033 ; 0.100]	0.0714 [0.045 ; 0.148]	0.0331 [0.013 ; 0.202]
	MRT	36h [30 ; 42h]	42h [30 ; 54h]	36h [30 ; 48h]	42h [30 ; 54h]	42h [30 ; 54h]	48h [30 ; 54h]

Median maximum excretion probability (*Max* $pex_{s(i),j,t}$) and its associated median retention time (MRT), with their 95% credibility interval [2.5 ; 97.5% quantiles].

APPENDICES

Appendix 1 - Description and location of experimental platforms.

All experiments were conducted in agreement with the ethical standards of animal manipulation as defined by the French laws on animal welfare (see Décret n° 2013-118), in three platforms with relevant licenses for the capture, care and use of non-protected wild animal species (see the licenses numbers, issued by the French Government, hereafter). These permits also cover our study. Indeed, additional ethical approval was not required for our kind of non-intrusive experimental protocol (without injection). Animals were used directly on site, in each of the three platforms, under the supervision of veterinarians who also contributed to the experimental design (within a partnership: animal and staff rental). All efforts were made to minimize animal stress due to confinement and human proximity, especially by choosing the most impregnated animals. Enclosures and boxes were from 10 to 15 m², side by side and separated by an open wall, so that each animal could see its congeners. Animals in enclosures had free access to a covered area. Boxes were illuminated by windows. During the experiments, the animals had free access to fresh water and received their usual food every day. After the experiments, animals were released within their usual enclosure.

Décret n° 2013-118 du 1er février 2013 relatif à la protection des animaux utilisés à des fins scientifiques. Article 1, Section 6:
- Sous-section 1, Article R. 214-88, 7° ;
- Sous-section 2, Paragraphe 2 ;
- Sous-section 3, Paragraphe 1 and 2.

http://www.legifrance.gouv.fr/affichTexte.do?cidTexte=JORFTEXT000027037840&dateTexte=&categorieLien=id

- *Roe deer*

Roe deer were provided by the I.N.R.A (French National Institute for Agricultural Research) “Behaviour and Ecology of Wildlife” unit (C.E.F.S). I.N.R.A is a public research institution under the joint authority of the French Ministry of Higher Education and Research and the French Ministry of Agriculture, Food Industry and Forests. C.E.F.S unit works on natural and captive populations of ungulates and possesses an experimental enclosure of about 20

hectares, comprising 7 sub-enclosures (from 0.5 to 1 hectare), with 18 roe deer (14 females and 4 males), in Gardouch (see location in the figure hereafter).
C.E.F.S website: http://www6.toulouse.inra.fr/cefs/

C.E.F.S has relevant authorizations for the care and use of roe deer.
Name: I.N.R.A's experimental platform 0035 in Gardouch
Approval number: A-31-210-001, by the French Government
Date of issue: 21 July 2011
Person in charge: Michèle Marin, president of the I.N.R.A regional center of Toulouse.
E-mail: Michele.Marin@toulouse.inra.fr
Address: I.N.R.A – C.E.F.S, Chemin de Borde Rouge, Auzeville, BP 52627, 31326 Castanet-Tolosan Cedex, France.
On-site delegate: Hélène Verheyden, C.E.F.S unit manager
E-mail: Helene.Verheyden@toulouse.inra.fr

- Red deer

Red deer were provided by the Alfort Veterinary School (E.N.V.A), a higher education and research establishment under the authority of the French Ministry of Agriculture, Food Industry and Forest. E.N.V.A possesses a field station of about 100 hectares of agricultural land and an experimental deer unit, with 40 red deer (all females but 2 males), in Champignelles (see location in the figure hereafter).
E.N.V.A website: http://www.vet-alfort.fr/web/en/291-champignelles.php

E.N.V.A has relevant authorizations for the use of deer.
Name: Deer program
Approval number: 89129, by the French Government
Type: B category, meat and reproduction
Person in charge: Hélène Benoît
E-mail: hbenoit@vet-alfort.fr
Address: Centre d'application de l'E.N.V.A, domaine de Croisil, 89350 Champignelles, France.

- *Wild boar*

Wild boars were provided by Animal Contact studio, specialized in animal training for cinema, television, publicity, photography and events, in Ladon, France (see location in the figure hereafter). Animal Contact breeds a wide range of animals, both domestic and wild. The studio possesses a female and a male wild boar. The Animal Contact team is composed of one specialized trainer per species and a veterinarian.
Animal Contact website: http://www.animal-contact.com/

Animal Contact possesses certificates of competence for the use and detention of non-domesticated animals.
Certificate number: 45-10-008, 45-12-008 and 45-12-009, by the French Government
Person in charge: Muriel Bec
E-mail: info@animal-contact.com
Address: Animal Contact, 47 Rue Jean-Martin Chambon, 45270 Ladon, France.

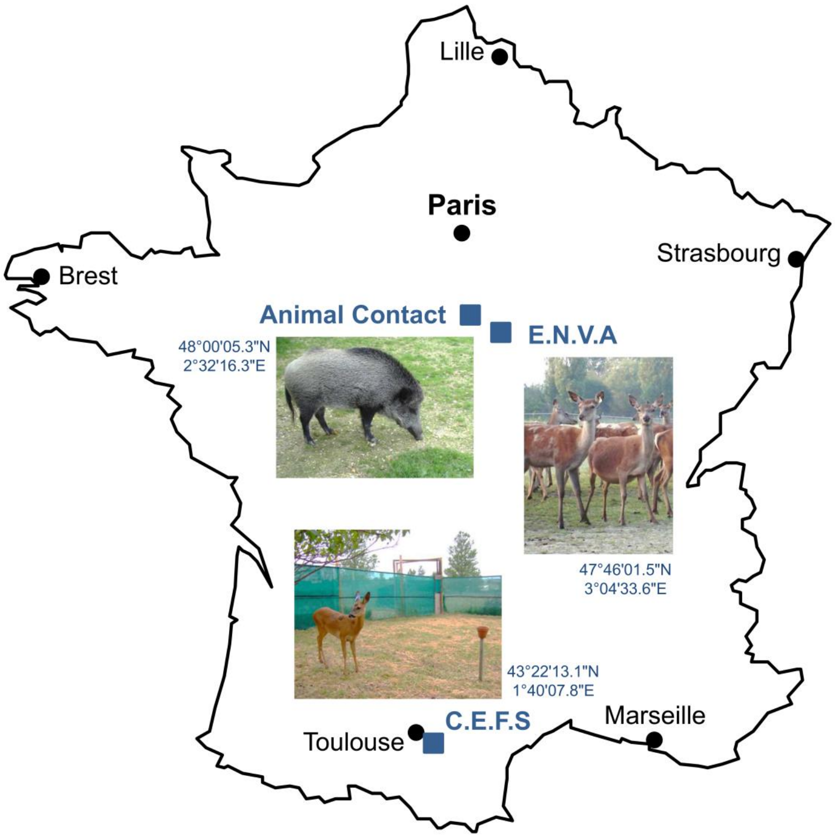
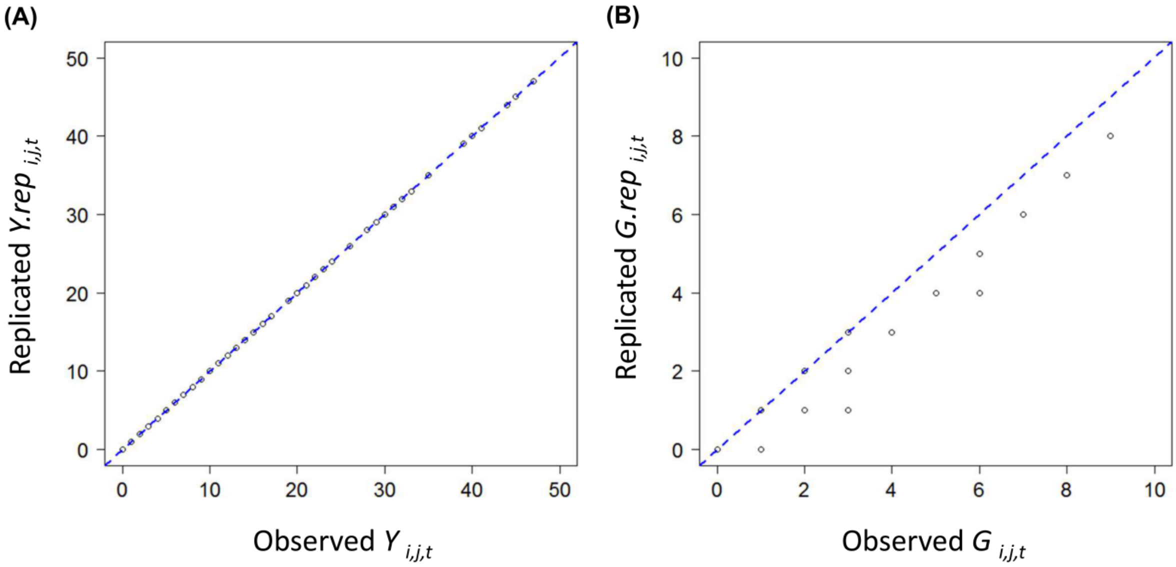


Figure: Map of France showing main French cities (black circles), the three study sites (blue squares): Ladon (Animal Contact, for wild boar), Champignelles (E.N.V.A, for red deer) and Gardouch (C.E.F.S, for roe deer), and their GPS coordinates (in Degrees, Minutes and Seconds).

Appendix 2 - Posterior predictive checking.

(A) Correlation between $Y.rep_{i,j,t}$ (replicated seed counts) and $Y_{i,j,t}$ (observed seed counts in the dissected sample). **(B)** Correlation between $G.rep_{i,j,t}$ (replicated seedling counts) and $G_{i,j,t}$ (observed seedling counts in the germination sample). A perfect fit corresponds to the 1-1 line (in blue).



Remarques méthodologiques :

❖ Les résultats présentés dans cet article sont basés sur un faible nombre de réplicats et présentent des intervalles de confiance relativement larges. Ils sont cependant cohérents avec ce que l'on connait à la fois de la physiologie digestive des ongulés sauvages et des traits partagés par les espèces végétales habituellement retrouvées dans les fèces des animaux. Il serait toutefois souhaitable d'acquérir plus de données pour calibrer le modèle, et éventuellement le simplifier ; mais cela impliquerait des moyens humains importants.

A titre d'exemple, les expériences menées durant ma thèse ont nécessité :
- deux sangliers (une femme et un mâle), cinq chevreuils (quatre femelles et un mâle) et quatre biches,
- 20 jours d'expérience,
- au moins 8 personnes pour mener les expériences,
- 5 mois de dépouillement des fèces (N = 154), à temps plein, pour une personne.

❖ Les probabilités de germination sont estimées à partir de graines mises à germer en conditions contrôlées (armoire à germination). Je n'ai donc pas abordés les effets des conditions biotiques et abiotiques du microsite où la graine est excrétée, bien que celles-ci jouent un rôle déterminant dans le succès de germination des graines et donc l'efficacité de la dispersion.

II. Distances de dispersion endozoochores

Après avoir modélisé la dynamique d'excrétion des graines, et pour compléter la phase de transfert, nous avons déterminé les distances potentielles parcourues pendant le temps de rétention. Pour ce faire, nous avons analysé des trajets d'animaux équipés de collier GPS. Comme ces colliers comprenaient des capteurs d'activité, nous avons pu déterminer où et quand l'animal s'alimentait. Nous avons ensuite couplé les durées de rétention des graines (Article 1) avec les mouvements des trois ongulés sauvages étudiés, afin d'estimer les distances potentielles de dispersion des graines associées à l'endozoochorie.

Les trois ongulés peuvent disperser les graines consommées à des distances moyennes supérieures à 2 km, au cours de trajets intra-forestiers de 48h. Les distances maximales de dispersion sont plus élevées pour les grands ongulés, cerf et sanglier (respectivement environ 3.5 et 3.1 km) que pour le chevreuil (environ 2 km). Les distances parcourues et donc les distances de dispersion varient selon la période de l'année. Le sanglier apparaît comme le meilleur disperseur, tant en termes de nombre de graines excrétées que de distances de dispersion.

Les grands ongulés comme le cerf et le sanglier peuvent disperser des graines sur de longues distances, permettant des flux de graines entre populations éloignées et potentiellement séparées par une matrice d'habitat défavorable. Le chevreuil, quant à lui, disperse les graines sur de plus courtes distances, et contribue à la fois aux dynamiques locales des populations de plantes et à la dispersion dans des paysages fragmentés formés de nombreux petits patchs d'habitat.

Article 2

A cross-comparative approach of long distance seed dispersal by common wild ungulates

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Abstract

Herbivore ungulates are key species in ecosystems, and their recent demographic and geographic expansion will influence global dynamics of plant species. Our objective is to identify the role of forest-dwelling ungulates in plant dispersal processes. Contrary to open habitats where most seeds are dispersed by the wind, long-distance seed dispersal essentially relies on animal movements in forest habitats. Due to their ability to cover long distances, large herbivores are supposed to be important vectors for former, current and future long-distance seed dispersal (> 100 m). To quantify this, we analyzed paths of roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), and wild boar (*Sus scrofa*), equipped with GPS collars. To estimate seed gut retention time, we experimentally monitored the fate of seeds from the moment they have been eaten to their release on the ground. We then combined animal movement and seed gut passage time to estimate seed dispersal curves induced by ungulates. Our results revealed that mean gut passage time and mean proportion of seeds passed were higher for wild boar than for deer species. Forest ungulates might on average disperse consumed seeds at distances longer than 2,000 metres, during a 48 hr-path in forest, and maximal dispersal distance was longer for red deer (3,467 m) and wild boar (3,151 m) than for roe deer (2,024 m).

Keywords: forest ungulates, long-distance seed dispersal, endozoochory, gut passage time, dispersal curve, Global Positioning System, daily paths, roe deer, red deer, wild boar.

INTRODUCTION

Herbivore ungulates have been recognized as important drivers in ecosystems (Naiman 1988, Schmitz et al. 2008), for example by accelerating return of organic matter or by modifying vegetal successions due to preferential consumption of some ligneous species (Tremblay 2005). Hence, the recent demographic and geographic expansion of wild ungulates will influence global dynamics of plant species (Maillard et al. 2010). Negative impacts of ungulates on vegetation, often linked to high densities, have widely been studied (Rooney and Waller 2003, Côté et al. 2004) whereas positive effects remain less known. One of the potential positive effects is their role in seed dispersal. In fact, herbivore ungulates are able to minimize their consumption effect on vegetation by releasing viable seeds at distance (Vellend et al. 2006).

Seed dispersal is a key process in population dynamics of plant species and communities, and thus will affect vegetal successions and evolution of ecosystems. In plants, for which dispersal is passive, diaspores are transported away from the parent plant by vectors that may be abiotic (wind, water) or biotic (animals) (Ridley 1930). Most seeds are dispersed over short distances (a few tens of meters, Howe and Smallwood 1982, Willson 1993). However, long-distance dispersal has a critical importance in the long-term persistence of plant species, as it influences the temporal and spatial dynamics of populations and communities together with their genetic and epidemiologic structures (Cain et al. 2000, Eycott et al. 2007). Due to their ability to cover long distances, large herbivores are supposed to be important vectors in long distance seed dispersal (> 100 m, Cain et al. 2000), and consequently in gene flow between populations in fragmented landscapes (Hardesty et al. 2006).

Seeds may be transported by animals (i.e., by zoochory) through several processes: epizoochory via external transport on animals' body, endozoochory via internal transport through the digestive system after ingestion, and dyszoochory corresponding to accidental dispersal when animals store the seeds for an ulterior consumption (Vittoz and Engler 2007). Endozoochory is effective only if seeds are consumed, survive ingestion and germinate after excretion (Schuup 2003, Schuup et al. 2010). The probability of ingestion of a seed by an animal directly depends on its diet (Cosyns 2004). For this, seed and foliage edibility and attractiveness are a starting point for endozoochorous dispersal (Janzen 1984). Second, seeds transported through endozoochory have been shown to share particular characteristics, such as small and round shapes and hard seed coats (Malo and Suárez 1995, Pakeman et al. 2002), although smaller proportions of nearly any seeds have been found in animal faeces (Heinken et al. 2002, Myers et al. 2004). Hence, Janzen (1984) suggests that endozoochory may be a usual dispersal mode for a large number of plant species, even in the absence of any particular adaptation. Recent direct observations of such seeds in animals' faeces support this hypothesis (Cosyns 2004).

Seed survival and dispersal distance are influenced by the duration of the passage of seeds through animals' digestive system. The passage through the digestive system can permit release from dormancy and germination (by abrading hard seed coats), reduce the number of seeds that are able to germinate, or delay their germination (von Oheimb et al. 2005). Overall, the survival percentage of most ingested seeds is relatively low, demonstrating the high cost imposed by endozoochory (Cosyns et al. 2005, Mouissie et al. 2005).

A critical point in spatial patterns of seed dispersal is about the scale of dispersal events, i.e., distance and direction (Brathen et al. 2007). These parameters depend on individual behaviour of animal (pattern of habitat use, displacement speed and alternation of active and inactive phases) and on seed retention time in the digestive system after ingestion, and strongly depend on animal species.

In forest habitats, long-distance seed dispersal essentially relies on animal movements (Heinken et al. 2002). Seed dispersal has been studied in a wide range of large herbivores, and particularly in native and domestic ungulates (Malo an Suárez 1995: fallow deer, red deer and cow; Heinken et al. 2002: roe deer and wild boar; Pakeman et al. 2002: sheep; Myers et al. 2004: white-tailed deer; Yamashiro and Yamashiro 2006: Kerama deer; Brathen et al. 2007: reindeer; Eycott et al. 2007: fallow deer, red deer, roe deer and muntjac; Pakeman and Small 2009: sheep). These studies generally provided the plant species and the number/proportion of seeds germinating from the faeces, according to animal species and habitat type where faeces were collected. However, few studies incorporated animal movement into models of seed dispersal by herbivores (Campos-Arceiz et al. 2008: Asian elephant; Will and Tackenberg 2008: sheep, cattle and deer) or more generally in other species (Westcott and Graham 2000: ochre-bellied Flycatcher; Westcott et al. 2005: southern cassowary; Russo et al. 2006: spider monkey). Seed shadow results from the movement and foraging activity of the animals eating the seeds. Hence, these dispersal vectors determine the identity, the quantity and the distance seeds are dispersed at. Moreover, the non-random space use and distribution of disperser activity in time will influence the shape and scale of dispersal curves of seeds (Schupp 1993, Levin et al. 2003, Westcott et al. 2005).

In this study, we aimed at quantifying the potential dispersal distances of seeds ingested by a guild of native ungulates. We aimed at identifying the potential effect of the season on the dispersal pattern. We adopted a cross-species comparative approach with the three most common wild ungulate species occupying European forests: roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*).

Based on Westcott et al. (2005)'s methodology, we incorporated behaviour of the animal dispersers in terms of movement and activity patterns in model of seed dispersal. We combined the movement rates of animals, estimated from high frequency GPS locations, with the gut passage rate of seeds, from feeding experiments, to estimate seed dispersal curves. We tested the following hypotheses:

(H1) Retention time is expected to be influenced by the body size of ungulate species (Illius & Gordon 1992). We thus expected a shorter retention time in the small-bodied roe deer compared to the large-bodied red deer and wild boar.

(H2) Due to the differences in digestion strategy, we expected an effect of the animal species on the proportion of excreted seeds, with a higher proportion in non-ruminant (wild boar) than in ruminant species (roe deer and red deer) (Cosyns et al. 2005).

(H3) Space use is mainly restricted to animal home ranges, which vary according to body mass, and should then differ among animal species. We then expected shorter seed dispersal distances in roe deer (mean seasonal home range sizes = 25-60 ha, Mysterud 1998, Saïd et al. 2005) than in red deer (250-600 ha, Licoppe 2006, Richard et al. 2011) and wild boar (250-1,000 ha, Saïd et al. 2012).

(H4) Due to intra-annual variations of animal space use according to animal biology (birth and lactation in May-August for red and roe deer, Saïd et al. 2005) and to hunting season (mainly from September to December, Saïd et al. 2012), we expected differences in seed dispersal distance among periods of the year.

METHODS

Gut passage

Study areas

Feeding experiments were conducted on captive animals in three different sites: INRA-CEFS (Haute-Garonne, France) for roe deer, ENVA (Yonne, France) for red deer, and Animal Contact (Loiret, France) for wild boar.

Feeding experiments

We conducted feeding experiment with captive animals of the three species: four roe deer, five female red deer, and two wild boars. The average weights of these animals were 21.2 ± 4.6 kg, 53.3 ± 5.2 kg, and 100 kg, respectively for roe deer, red deer and wild boar. We selected three plant species common in temperate plant communities: *Plantago media*, *Prunella vulgaris* and *Rubus fruticosus*, and also known to be consumed by the three studied ungulates (Eycott et al. 2007, Schmidt et al. 2004, von Oheimb et al. 2005). Table 1 describes plant characteristics: seed length and width extracted from Cappers et al. (2006), averaged seed mass, flowering season and seed shedding period. We estimated average seed mass for each plant species by weighting different sets of known numbers of seeds. Predetermined known quantities of seeds for each plant species were mixed together to make up the "seed mixture" (Table 1, following Cosyns et al. 2005). Feeding experiments were conducted from June 2009 to November 2010. Each animal was individually isolated in a cleaned box (red deer) or enclosure (roe deer and wild boar) and fed with a "seed mixture" integrated in its usual food (granules, Triticale and hay, and pear, respectively for roe deer, red deer and wild boar). From seed ingestion (t = 0), we collected fresh faeces by individual direct monitoring, each 3 hr during the first 24 hr and each 6 hr thereafter. We planned the experiment to last 54 hr after seed ingestion, according to Illius & Gordon (1992)'s equation relating mean retention time to animal body weight, so as to encompass the entire digestive process. We made six replicates per animal species. We obtained a total of 154 faeces (i.e., 154 episodes of defecation). The set of seeds not consumed was collected to ascertain the quantity of ingested seeds, obtained by subtracting the number of unconsumed seeds to the number of seeds in the seed mixture.

Faeces analysis

We extracted a random sample of 4 g for roe deer, or 8 g for red deer and wild boar, from each individual faeces, because we could not dissected all the collected faeces due to the heavy laboratory logistic required. We adjusted sample weights to best represent the average faeces weight of each species, which was lower for roe deer (24.1 g ± 17.7) than for wild boar (42.6 g ± 23.2) and red deer (61.9 g ± 32.9). The sample of each individual faeces was dissected under stereo microscope for seed identification and counting. For each sample, we obtained the number of excreted seeds of each plant species per gram of faeces, allowing us to estimate gut passage times. The number of seeds in the total weight of each faeces was extrapolated from the seed number in the dissected sample. We then calculated the percentage of excreted seeds relative to the number of ingested seeds (i.e., the proportion of seeds passed).

Animal movement

Study areas

Animal monitoring with GPS collars was conducted in three sites located in France: the Chizé reserve (2,614 ha of fenced deciduous broadleaved forest in western France; 46°05’N, 0°25’W) for roe deer, *la Petite-Pierre* National Hunting and Wildlife Reserve (2,674 ha of unfenced broadleaved/coniferous forest in north-eastern France; 48°49’N, 7°20’E) for red deer, and the state forest of Arc-en-Barrois (11,000 ha of unfenced deciduous broadleaved forest in north-eastern France; 48°02’N, 4°56’E) for wild boar.

Division in time periods

We chose to divide the year into three 4-months periods: January-April, May-August and September-December. This corresponds to a trade-off taking into account animal biology (birth and lactation in May-August for red and roe deer), hunting season (mainly from September-December to end of February), seed shedding (production and flowering of studied plants from May to September) and constraints on animal paths availability for the three species under study.

GPS monitoring of ungulates

Roe deer: fifteen different does were equipped with Lotek’s GPS_3000/3300 S radio-collars (Lotek Wireless, Fish & Wildlife Monitoring), in January-February 2003, 2004, 2006, 2007 and 2008. The collars provided information on GPS locations in differential mode (i.e., latitude, longitude, date and time) at pre-programmed intervals, fix quality (PDOP = Position Dilution Of Precision) and animal activity on two axes. We scheduled collars to provide one location every 5 minutes during 24-hr periods (from 0000 hr to 2355 hr) in order to obtain daily paths (ranging from two to twelve daily paths per animal according to the year). We added locations of the day before or after, i.e. a total of 18 positions per animal per day (three locations recorded at 20-minute intervals in six-hour long sessions: 0000-0100 hr, 0400-0500 hr, 0800-0900 hr, 1200-1300 hr, 1600-1700 hr, 2000-2100 hr) to obtain paths of 48 hr length. After removing poor quality locations (PDOP > 5 and 10, respectively for 2D and 3D locations, Lewis et al. 2007), from a maximum between 288 and 576 locations per path per animal, we obtained a mean of 232 locations (SD = 61.9, N = 110 paths), i.e., an average fix rate of 73 %.

Red deer: four different does were monitored with Lotek's GPS_3000/3300 S or L radio-collars in 2007 and 2008. Using the same schedule programming than for roe deer, we obtained eight 48 hr-paths in 2007 and five in 2008. After removing poor quality locations, from a maximum between 288 and 309 locations per path per animal, we obtained a mean of 243 locations (SD = 31.3, N = 21 paths), i.e., an average fix rate of 80 %.

Wild boar: four females and two males were equipped with Lotek's GPS_1000/3000 L radio-collars in 1999, 2004 and 2006. Due to nocturnal activity of hunted wild boar populations (Mauget 1980, Douaud 1983), we scheduled collars to provide locations during periods of one night (from 1800 hr to 0400 hr in 1999, 1800 hr to 0550 hr in 2004 and 1900 hr to 0645 hr in 2006) with one location every 15 minutes in 1999 and 2006, and every 10 minutes in 2004. Additional locations were also recorded at 1700 hr, 0500 hr, 0600 hr, 0900 hr and 0930 hr in 1999, and at 1100 hr and 1130 hr in 2004 and 2006. We obtained paths of 48 hr-period starting at 0900 hr the first day and ending at 0930 hr two days after, including only one night monitoring. In 2004 and 2006, the same procedure was done during 48 hr, starting at 1100 hr and ending at 1130 hr. After removing poor quality locations, from a maximum between 46 and 101 locations per path per animal, we obtained a mean of 61 locations (SD = 16.0, N = 22 paths), i.e., an average fix rate of 87 %.

Animal activity

For roe and red deer, activity of animals was recorded by sensors placed in the GPS collars. The sensors provided three activity variables recorded every 5 min: a count of vertical collar movements (Y, ranging from 0 to 255), a count of horizontal movements (X, ranging from 0 to 255) and the proportion of time the Y sensor was in an extreme position (i.e., the proportion of time the head was down, HD). We classified activity of each 5-min period of the day into one of the four following categories: resting ($X+Y \leq 30$ and HD = 0-100 %), slow locomotion ($30 < X+Y \leq 338$ and HD ≤ 50 %), feeding ($30 < X+Y \leq 338$ and HD > 50 %) and fast locomotion ($X+Y > 338$ and HD = 0-100 %) (Löttker et al. 2009, and unpubl. data). Collars placed on wild boar were not equipped with these sensors, thus feeding periods were determined from literature (Mauget 1980, Douaud 1983, for wild boar hunted populations). GPS used to monitor wild boar locations generally focus on dense night censuses and restrict the number of locations during daytime when animals are at rest. Consequently, we delimited the periods of the day animals were probably feeding (Table 2).

Data Analysis

Gut passage curves

We first plotted the average gut passage rates (i.e., the proportions of seeds passed) of the three studied plants against the gut passage times to estimate an average gut passage curve per animal (Westcott and Graham 2005). We also estimated the gut passage curves for each animal and plant species (Appendix 1).

Animal movement

To characterize space use by the three studied ungulates, we estimated daily home range size from GPS locations using the fixed kernel method with reference smoothing ('ad hoc', Worton 1989). We also calculated mean length and duration of paths and estimated fractal dimension (i.e., path tortuosity, Nams 2005).

Displacement curves

Displacement models were estimated following the method of Westcott and Graham (2005). During a daily path, a location is chosen and for each subsequent location the straight-line distance from the chosen location and the time elapsed is recorded. In order to reflect the animal behaviour and the potential periods when seeds are consumed, we selected locations during each daily path from two distinct distributions (i.e., two displacement scenarii). First, all the locations were chosen along the daily path (Total). The second distribution reflected animal behaviour (Weighted) and was determined from animal feeding activity (Table 2). We used Weighted distributions based on locations during Morning and Midday for roe deer, during Morning and Evening for red deer and during Night for wild boar (Table 2). Starting and ending hours of the feeding sessions changed according to the predefined period of the year (Table 2). For each period of the year and each displacement scenario, we averaged estimated displacement curves to obtain a single average curve per animal species and we also built a curve based on the maximum distance covered within each time lag.

Dispersal curve estimation

We combined gut passage curves and displacement curves to estimate dispersal curves of the studied plant species, by substituting the time axis on the gut passage plot with the distance values from the displacement curve corresponding to those times (Westcott and Graham 2005). We used the maximum dispersal distance possible for each gut passage time. We obtained a plot of the proportion of seeds passed according to the distance from the moment of ingestion. To reflect animal activity, we used the Weighted scenario to estimate the dispersal curves. We first assessed the dispersal curves for the three ungulates using the average gut passage rates of the seeds of the three plant species. We also estimated the dispersal curves for each plant species (Appendix 2).

RESULTS

Gut passage rates

Ungulates consumed almost all the seeds offered (between 94.2 % and 99.6 %) but most of the seeds eaten were not recovered in faeces, especially considering deer species (from 4.1 % to 20.6 % of seeds passed, Table 1). For wild boar, between 36.5 % and 55.8 % of seeds eaten were recovered (Table 1). The average proportion of the seeds passed was the highest for *Prunella vulgaris* in roe deer and for *Rubus fruticosus* in red deer and wild boar (Table 1 and Figure 1). The mean gut passage time did not differ among the three plant species (Kruskal-Wallis test: Chi-2 = 0.70, df = 2, p = 0.705). It was relatively similar between roe deer (from 1,489 to 2,100 min) and red deer (from 1,691 to 2,006 min) whereas it was longer for wild boar (superior to 2,255 min, Kruskal-Wallis test: Chi-2 = 17.27, df = 2, p < 0.001) (Table 1 and Figure 1).

Animal space use and movement quality

Daily home range area differed among animal species (Kruskal-Wallis test: Chi-2 = 64.76, df = 2, p < 0.001): large home ranges for wild boar (mean = 283 ha ± 191 SD), intermediate for red deer (mean = 81 ha ± 126 SD) and small for roe deer (mean = 17 ha ± 34 SD). For the three ungulate species, size of daily home ranges seemed to vary according to the period of the year (Table 3), with larger home ranges in September-December for roe deer, in January-April for red deer and in May-August for wild boar, but the differences were not significant due to very high variability among individuals (see standard deviations in Table 3, Kruskal-Wallis tests: roe deer, Chi-2 = 5.64, df = 2, p = 0.06; red deer, Chi-2 = 0.01, df = 2, p = 0.995; wild boar, Chi-2 = 2.50, df = 2, p = 0.287).

Duration of paths was approximately 43 hours (2,600 min) for the three ungulate species (Table 3). Mean length of 48 hr-paths was relatively similar for roe deer (mean = 7,049 m ± 1,879 SD, range = 3,149 - 15,647 m) and wild boar (mean = 6,311 m ± 2,792 SD, range = 3,200 - 15,254 m), but was slightly higher for red deer (mean = 9,640 m ± 4,049 SD, range = 2,556 - 20,729 m) (Table 3, Kruskal-Wallis test: Chi-2 = 17.50, df = 2, p < 0.001). We observed a gradient considering paths tortuosity among animal paths from straight ones in wild boar (mean Fractal D = 1.13 ± 0.05 SD), moderately tortuous in red deer (mean Fractal D = 1.33 ± 0.08 SD) to very tortuous in roe deer (mean Fractal D = 1.43 ± 0.11 SD) (Table 3, Kruskal-Wallis test: Chi-2 = 68.87, df = 2, p < 0.001). Speed between two successive locations (recorded every 5 minutes for roe and red deer and every 10 or 15 minutes for wild boar) ranged between 0.02 and 102.7 m/min (mean = 5.3 m/min ± 4.8 SD) for roe deer, 0.04 and 99.0 m/min (mean = 6.1 m/min ± 6.9 SD) for red deer and 0.05 and 68.2 m/min (mean = 7.7 m/min ± 9.3 SD) for wild boar. Displacement curves estimated using the two sampling distributions (Total and Weighted) for each ungulate species appear in Figure 2. Maximal straight-line distance was higher for wild boar (3,832 m for Total and Weighted scenarii) and red deer (3,467 m for Total and Weighted scenarii) than for roe deer (2,262 m and 2,051 m respectively for Total and Weighted scenarii) (Figure 2 and Table 3). Moreover, maximal straight-line distance varied according to the period, with higher values in September-December for roe deer (Kruskal-Wallis test: Chi-2 = 1,421.86 / 1,245.14 for the Total / Weighted scenario, df = 2, p < 0.001), in May-August for red deer (Kruskal-Wallis test: Chi-2 = 730.79 / 307.09 for the Total / Weighted scenario, df = 2, p < 0.001) and in January-April for wild boar (Kruskal-Wallis test: Chi-2 = 83.18 / 67.18 for the Total / Weighted scenario, df = 2, p < 0.001) (Figure 2).

Dispersal curves

To estimate dispersal curves using the average gut passage times of the three plant species, we used the Weighted displacement model (Figure 3). Estimated minimum dispersal distances ranged from 425 m (January-April) to 1,004 m (September-December) for roe deer, 193 m (January-April) to 924 m (May-August) for red deer and from 661 m (January-April) to 1,205 m (September-December) for wild boar. Estimated maximum and mean dispersal distances were smaller for roe deer than for red deer and wild boar (Kruskal-Wallis test: Chi-2 = 61.81, df = 2, $p < 0.001$). For the deer species, dispersal distances differed among the periods of the year: higher distances were reached in September-December for roe deer (Kruskal-Wallis test: Chi-2 = 56.20, df = 2, $p < 0.001$) and in May-August for red deer (Kruskal-Wallis test: Chi-2 = 18.93, df = 2, $p < 0.001$). Concerning wild boar, dispersal distances were slightly higher in January-April but there was no significant difference (Kruskal-Wallis test: Chi-2 = 4.68, df = 2, $p = 0.096$). Maximal mean dispersal distances were 809 m, 1,239 m and 2,024 m for roe deer, respectively in January-April, May-August and September-December; 2,737 m, 3,467 m and 2,011 m for red deer; and 3,099 m, 2,390 m and 3,151 m for wild boar. Mean dispersal distances were 553 m (± 111 SD), 924 m (± 185 SD) and 1,707 m (± 244 SD) for roe deer, respectively in January-April, May-August and September-December; 1,863 m (± 839 SD), 2,569 m (± 845 SD) and 1,608 m (± 350 SD) for red deer; and 2,164 m (± 697 SD), 1,625 m (± 579 SD) and 2,097 m (± 563 SD) for wild boar.

Dispersal curves were also estimated separately for each plant species (Appendix 2). Mean dispersal distances were similar for the different plant species tested within each animal species (Kruskal-Wallis tests: roe deer, Chi-2 = 0.07, df = 2, $p = 0.964$; red deer, Chi-2 = 0.25, df = 2, $p = 0.880$; wild boar, Chi-2 = 0.06, df = 2, $p = 0.970$).

DISCUSSION

This study demonstrates that forest-dwelling ungulates are relevant long-distance seed dispersal vectors through endozoochory. Our results provide a first GPS-based approach on endozoochorous dispersal by three common wild ungulates in forested temperate landscapes.

Animal characteristics and gut passage rate

Gut retention times differ according to the animal species but not among morphologically similar seeds of the three plant species we studied. We found gut retention time to be longer in the non-ruminant wild boar than in the ruminant red and roe deer, in accordance with our hypothesis H1. This may probably due to the difference in body weight, wild boar being twice heavier than red deer hinds in our study (average weights in our study: wild boar = 100 kg, red deer = 53.3 ± 5.2 kg and roe deer = 21.2 ± 4.6 kg). However, and contrary to what we expected, the difference in body weight between red and roe deer did not translate into longer gut retention time in the red deer. In agreement with H2, the proportion of seeds excreted also differed among animal species, with higher rates for wild boar than for deer species (roe deer = red deer), and despite the longer retention time we finally described for wild boar. This result might be explained by the detrimental effect of rumination on seeds in the digestive tractus of cervids. Seeds adapted to endozoochory, like those from *Rubus* fruticosus, which have a hard seed coat, were excreted in larger numbers at least by red deer and wild boar.

Animal movement

According to H3 and in agreement with the literature, daily home ranges were smaller in roe deer, than red deer than wild boar (Mysterud 1998, Saïd et al. 2005, 2012, Licoppe 2006, Richard et al. 2011). However, high inter-individual variability impeded to reveal seasonal differences in any animal species. Mean length of 48-hr paths was similar for roe deer and wild boar, but smaller than for red deer. As we found higher tortuosity of daily paths for roe deer, than for red deer than for wild boar, this led to higher dispersal distances by wild boar than roe deer.

Seed dispersal curves

Seed shedding of most temperate plants, including our three focal plants, occurs from spring to autumn, with a peak at the end of summer and beginning of autumn. Relating seed availability to animal movements implies to mainly focus on May to August and September to December periods. Distances covered the rest of the year may be specifically used for plants whose seeds are available earlier. A common feature of dispersal distances over the three periods of the year we delimited concerns the lower dispersal distances of seeds consumed by roe deer. From January to August, red deer hinds offer both longer seed dispersal distances and a wider range of distances covered than wild boar than roe deer. From September to December, roe deer and red deer are similar whereas wild boar exhibits the wider range and the higher dispersal distances. Thinking at the scale of the guild of ungulates, complementary seed dispersal distances and services are achieved by the three sympatric species at the different periods of the year, leading to the conclusion that each vector species has a unique role in long distance seed dispersal and may not be functionally replaced.

From January to April, and despite the low availability of seeds, potential maximal seed dispersal distances ranged from 400 to 800 m for roe deer, from 700 to 2800 m in wild boar, and from 200 to 2700 m for red deer. Red deer, due to faster gut retention time, might disperse seeds over a wider range of distances than wild boar, even if maximal dispersal distances are rather similar. Roe deer remains on smaller areas. The period from May to August, when seeds really start to be available for dispersal, offers the more scaled gradient regarding the potential distances covered. They range from 450 to 1250 m for roe deer, from 750 to 2400 m for wild boar, and from 900 to 3500 m for red deer. Roe deer exhibit the narrower range, whereas red deer offers the largest one, wild boar stating as an intermediary.

During hunting season, from September to December, seed dispersal distances peak for wild boar, ranging from 1200 to 3200 m, whereas distances are similar for cervids, simultaneously growing for roe deer (from 1000 to 2000 m) and diminishing for red deer (from 600 to 2000m) if we compare with the rest of the year. Longer retention time in wild boar appears to have no influence on dispersal distance because long distances (> 2,000 m) may be travelled over relatively very short times, i.e, 100 minutes (September-December). But this long retention time has a positive impact on endozoochorous seeds, such as *Rubus fruticosus*, that need long passage in digestive tractus to germinate.

Generally, the distances covered by the different vectors are in agreement with home range sizes, home range habitat composition and habitat requirements, being larger as animals get heavier. Many factors may thus interact and shape animals movements, among which hunting pressure, particularly for game species. As an antipredator strategy, wild boar are mainly active during the night when hunting pressure is released, staying hidden at rest during the day, whereas red deer and roe deer are more often active at dawn and dusk, foraging in the vicinity of forest cover. Outdoor activities (biking, hiking, orienteering, mushroom picking; Jeppesen 1987a, 1987b, 1984) may also lead to animal disturbance and induce extraordinary movements. Energy conserving strategy during winter-time may also affect animal activity and limit movements. The biological rhythm of the animals under study may also lead to reduced movements, particularly during birth and lactation, but we did not observe such a pattern for our female cervids from May to August. Exceptional distances may be covered during juvenile dispersal, but it generally occurs before the peak of seed availabity and only concerns male cervids, for which we had no location data. Reproductive dispersal may be more accurate for longer seed dispersal distances for male red deer, as it occurs during the rut in autumn, when seeds are more prone to be dispersed (distances covered during the rut : 10.3 km ; Adrados 2002).

Prospects

The coupling of movement data to seed retention time could be extended to epizoochorous seed retention time so as to give a complete picture of seed dispersal processed by large ungulates (Bullock et al. 2011). The seed release, through external (epizoochory) or internal transfer (endozoochory), relies upon different criteria that may lead to different dispersal kernels even for a same plant species.

The location data were not balanced among animal species. We particularly need more data on wild boar (both on feeding experiments and GPS locations) to confirm our results. For cervids, data over all the year and from January to August, and for wild boar, access to male animal locations would complete the pattern we depicted. Data on juvenile and reproductive dispersal would then highlight maximal distances seeds may be moved at.

In this study, we used morphologically similar seeds leading to similar gut retention time. The size, the shape, the presence of appendages may greatly affect gut retention time among seeds. Picard et al. (submited) particularly show that nearly any type of seeds may be dispersed by wild ungulates, whatever their main dispersal mode (endozoochorous, epizoochorous, anemochorous, barochorous and hydrochorous seeds).

Acknowledgements

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FIGURES

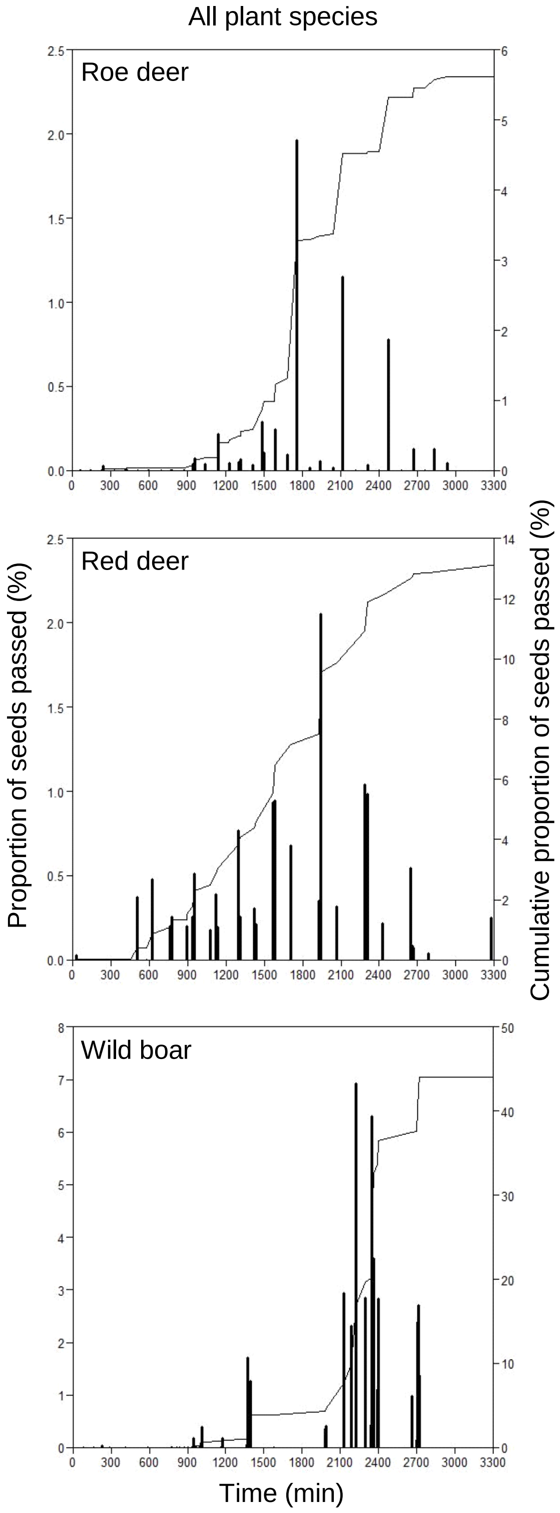


Figure 1: Combined gut passage rates of the seeds of the three plant species (*Plantago media*, *Prunella vulgaris* and *Rubus fruticosus*; Table 1) through each animal species (roe deer, red deer and wild boar).

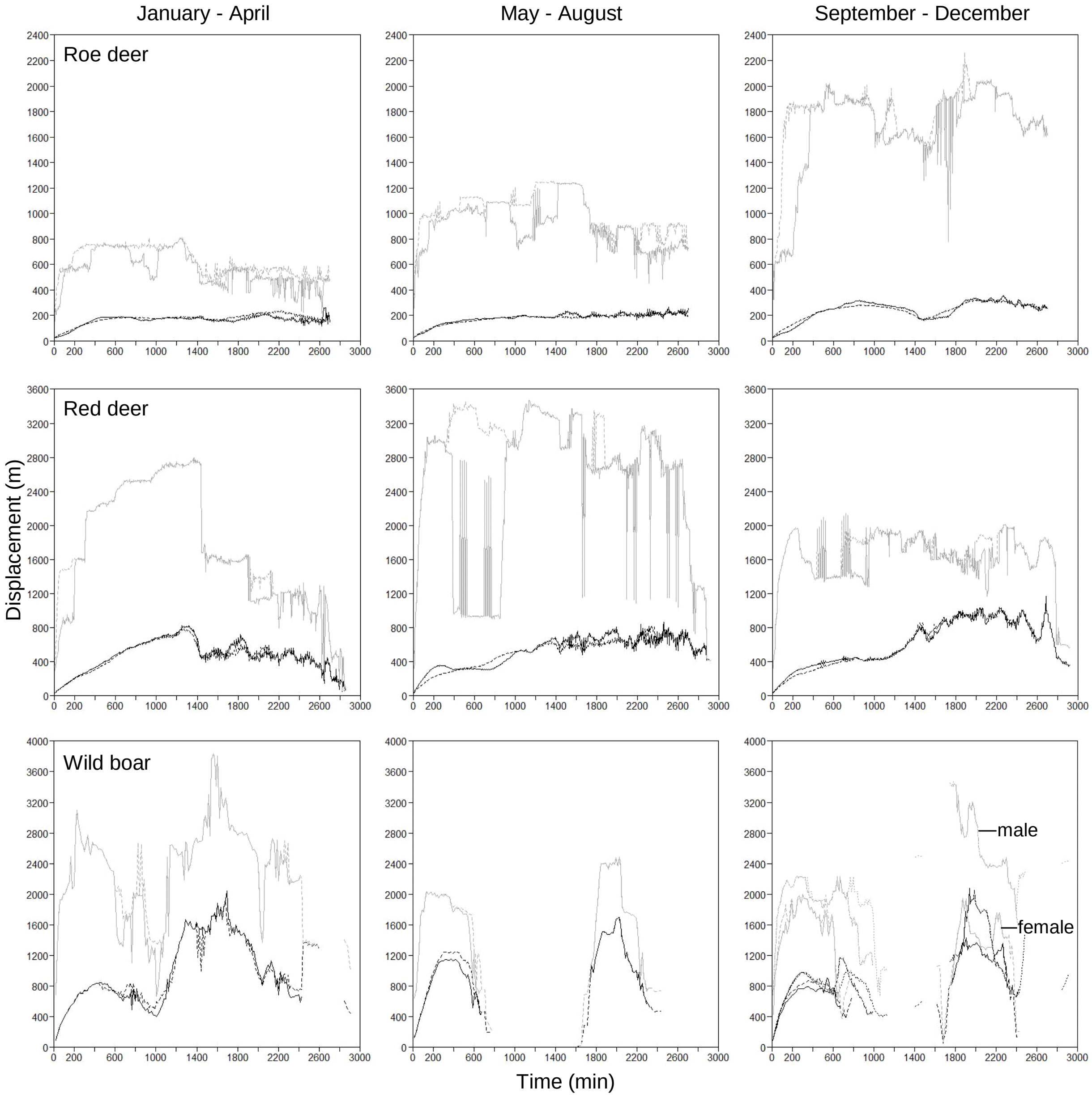


Figure 2: Mean and maximum displacement of each animal species per period using all the locations (Total) and using a sampling scenario based on animal activity (Weighted, Table 2): Mean Total = black dashed line; Mean Weighted = black solid line; Maximum Total = grey dashed line; Maximum Weighted = grey solid line. For male wild boar (September-December): Mean Total = black dotted line; Mean Weighted = black large dashed line; Maximum Total = grey dotted line; Maximum Weighted = grey large dashed line.

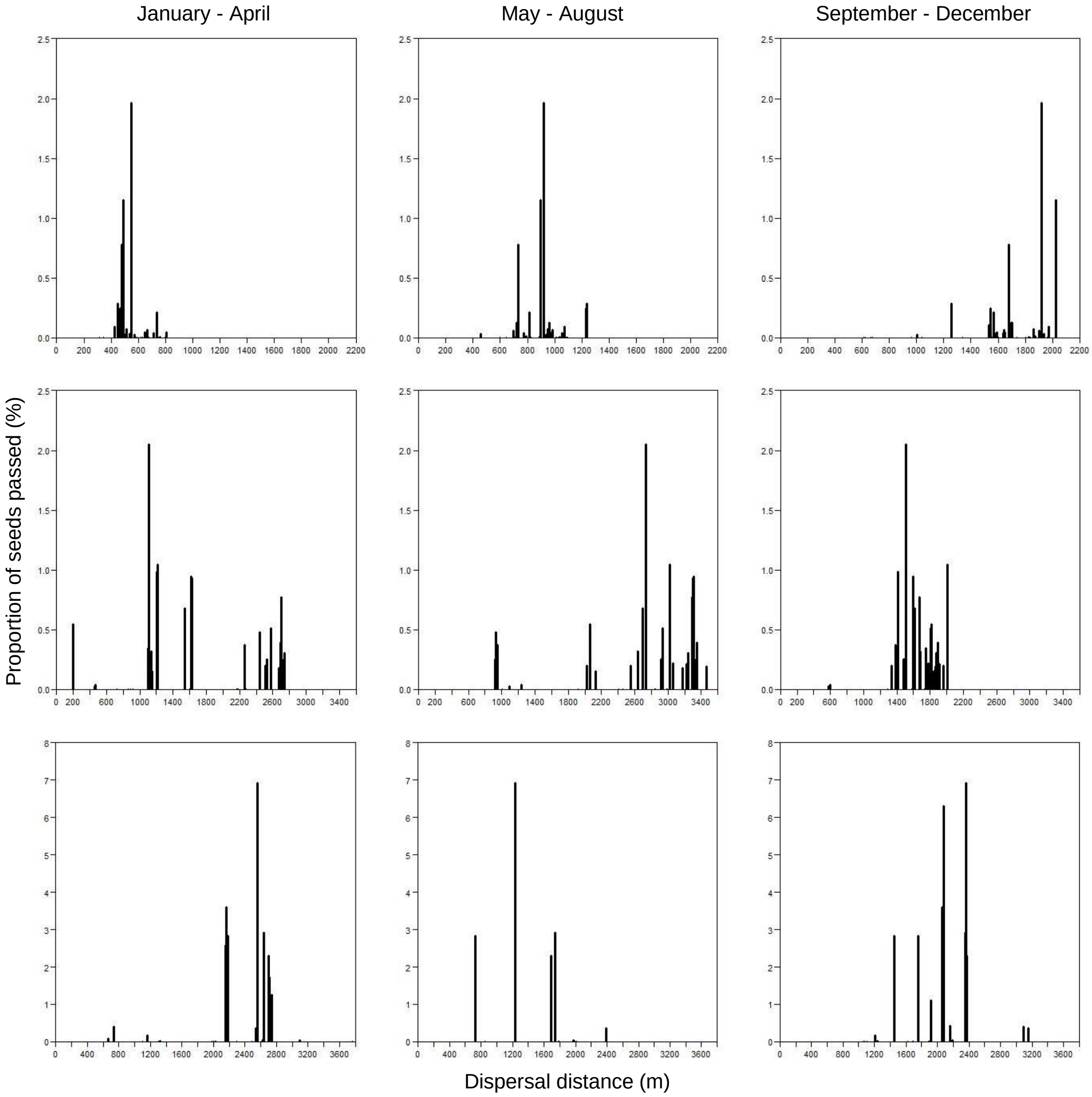


Figure 3: Dispersal curves estimated for seeds of the three plant species combined (*Plantago media*, *Prunella vulgaris* and *Rubus fruticosus*) using the maximum distances from the weighted displacement model of each animal species (roe deer, red deer and wild boar).

TABLES

Table 1: List of the three plant species used in the feeding experiments indicating the flowering season and the seed shedding period, the values of seed size (length x width) and mass, the number of seeds per plant species in the "seed mixture" provided to each animal, the mean proportion of seeds consumed and passed (i.e., excreted seeds) and the mean, the minimum and the maximum duration of gut passage time for each paired animal and plant species.

		Plantago media	***Prunella vulgaris***	***Rubus fruticosus***
Periods of flowering season (seed shedding)		May to August	July to September	June to July
Seed lenght x width (mm) from Cappers et al. 2006		2.61 x 1.19	2.04 x 1.15	3.08 x 2.02
Seed mass (mg) (our study)		0.44 ± 0.01	0.73 ± 0.06	3.53 ± 0.08
Number of seeds offered to each animal	Roe deer	1,500	1,500	1,500
	Red deer	2,000	2,000	2,000
	Wild boar	2,000	2,000	2,000
Mean proportion of seeds fed per animal (% ± SD)	Roe deer	94.2 ± 5.7	95.1 ± 5.4	98.5 ± 2.8
	Red deer	97.5 ± 2.2	98.4 ± 1.5	99.2 ± 0.7
	Wild boar	99.6 ± 0.9	99.5 ± 1.3	96.3 ± 8.0
Mean proportion of seeds passed per animal (% ± SD)	Roe deer	4.1 ± 7.9	7.6 ± 12.4	5.2 ± 7.6
	Red deer	12.9 ± 7.0	5.8 ± 4.7	20.6 ± 16.7
	Wild boar	36.5 ± 19.2	39.9 ± 20.2	55.8 ± 28.2
Mean gut passage time per animal (min ± SD)	Roe deer	1,489 ± 763	1,650 ± 246	2,100 ± 449
	Red deer	1,691 ± 512	2,006 ± 319	1,877 ± 370
	Wild boar	2,255 ± 146	2,288 ± 162	2,285 ± 144
Minimum - Maximum gut passage time (min)	Roe deer	240 - 2,835	945 - 2,835	1,320 - 2,940
	Red deer	25 - 3,278	25 - 3,278	505 - 3,278
	Wild boar	230 - 2,725	950 - 2,725	950 - 2,725

Table 2: Main feeding periods of each animal species (roe deer, red deer and wild boar) for the three periods of the year (January-April, May-August and September-December), determined from collar activity sensors for roe and red deer and from literature for wild boar (Mauget 1980, Douaud 1983).

Ungulate species	**Feeding periods**	**Periods of the year**		
		January-April	**May-August**	**September-December**
Roe deer	Morning	0000 hr-0400 hr	0000 hr-0400 hr	0000 hr-0430 hr
	Midday	1000 hr-1500 hr	1200 hr-1700 hr	1030 hr-1500 hr
Red deer	Morning	0000 hr-0900 hr	0000 hr-0700 hr	0000 hr-0830 hr
	Evening	1600 hr-2359 hr	1730 hr-2359 hr	1500 hr-2359 hr
Wild boar	Night	1900 hr-0700 hr	1900 hr-0600 hr	1900 hr-0600 hr

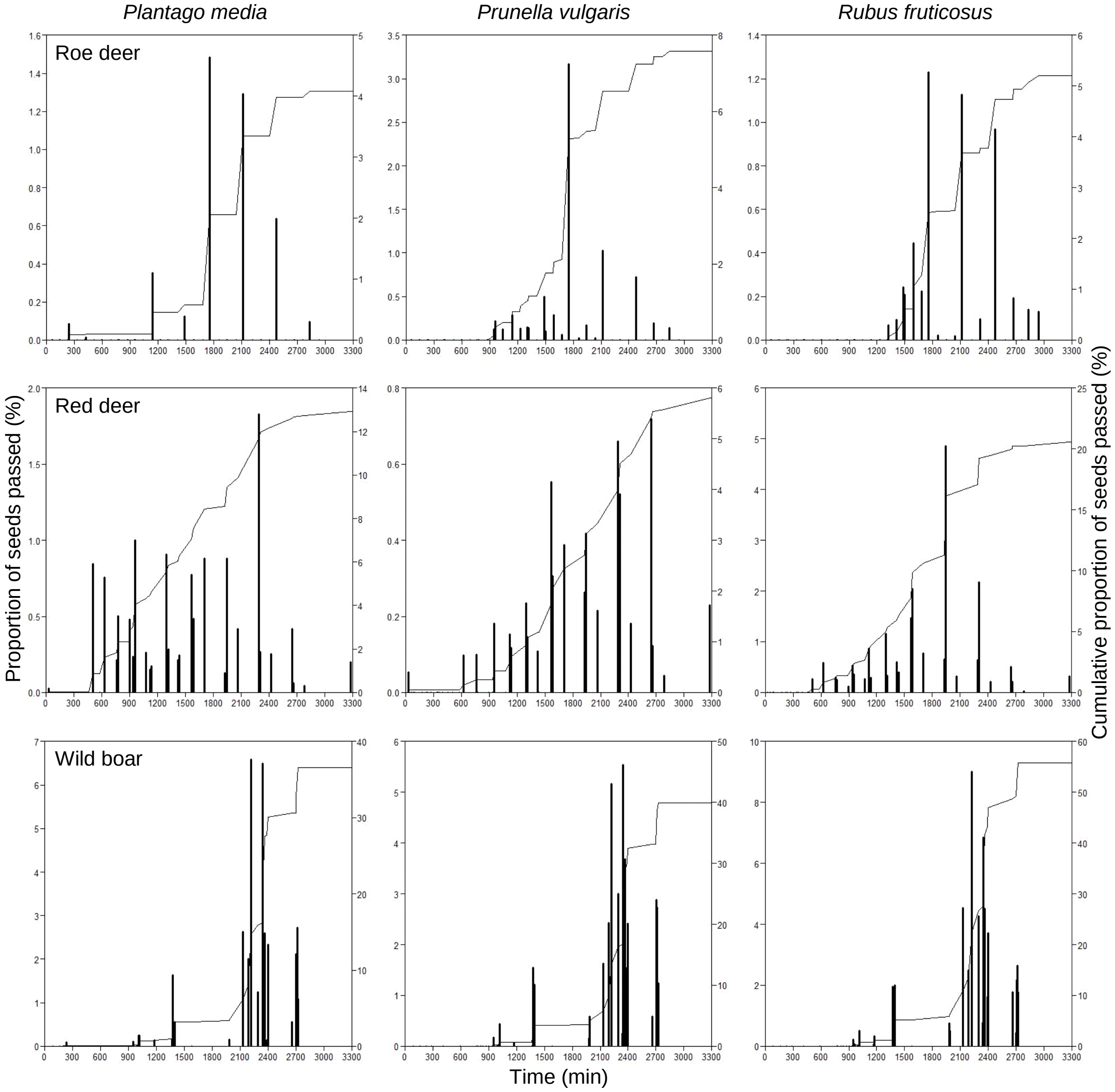
Table 3: Path characteristics for each animal species, estimated globally and for the three periods of the year (January-April, May-August and September-December). Home range areas were estimated using the fixed kernel method with reference smoothing. Speed was calculated between successive path locations (recorded every 5 minutes for roe and red deer and every 10 or 15 minutes for wild boar). Straight-line distances between path locations correspond to the distances calculated following the method of Westcott and Graham (2005). Fractal dimension D was estimated using the Fractal Mean estimator of Nams (2005).

	Ungulate species	**Global**	**Periods of the year**		
		(range of values)	**January-April**	**May-August**	**September-December**
Number of paths	Roe deer	110	30	43	37
	Red deer	21	6	10	5
	Wild boar	22	9	3	10
Mean daily home range area (ha ± SD)	Roe deer	17 ± 34 (0.5 - 257)	10 ± 9	12 ± 13	29 ± 52
	Red deer	81 ± 126 (0.7 - 492)	116 ± 189	71 ± 113	58 ± 52
	Wild boar	283 ± 191 (61 - 808)	246 ± 235	375 ± 90	293 ± 167
Mean length of animal paths (m ± SD)	Roe deer	7,049 ± 1,879 (3,149 - 15,647)	6,852 ± 1,473	6,619 ± 1,558	7,708 ± 2,327
	Red deer	9,640 ± 4,049 (2,556 - 20,729)	9,177 ± 3,906	9,753 ± 4,522	9,969 ± 4,051
	Wild boar	6,311 ± 2,792 (3,200 - 15,254)	5,777 ± 3,713	5,692 ± 874	6,976 ± 2,204
Mean duration of animal paths (min ± SD)	Roe deer	2,602 ± 639 (1,364 - 4,120)	2,539 ± 532	2,701 ± 786	2,537 ± 517
	Red deer	2,627 ± 527 (1,430 - 2,934)	2,465 ± 576	2,728 ± 455	2,619 ± 665
	Wild boar	2,579 ± 594 (711 - 2,910)	2,890 ± 21	2,405 ± 44	2,351 ± 811
Mean speed between two successive path locations (m/min ± SD)	Roe deer	5.3 ± 4.8 (0.02 - 102.7)	5.5 ± 4.5	5.3 ± 4.9	5.2 ± 4.9
	Red deer	6.1 ± 6.9 (0.04 - 99.0)	6.1 ± 6.7	6.2 ± 7.2	5.8 ± 6.6
	Wild boar	7.7 ± 9.3 (0.05 - 68.2)	5.9 ± 7.0	8.1 ± 9.1	8.6 ± 10.3

	Ungulate species	Global (range of values)	Periods of the year		
			January-April	**May-August**	**September-December**
Mean straight-line distance between path locations (m ± SD)	Roe deer	170 ± 213 (0.03 - 2,262)	141 ± 130	140 ± 145	207 ± 276
	Red deer	341 ± 464 (0.04 - 3,467)	372 ± 558	321 ± 439	339 ± 370
	Wild boar	726 ± 593 (0.39 - 3,832)	709 ± 626	862 ± 593	716 ± 575
Mean Fractal dimension D of animal paths (value ± SD)	Roe deer	1.43 ± 0.11 (1.22 - 1.73)	1.48 ± 0.11	1.41 ± 0.10	1.40 ± 0.11
	Red deer	1.33 ± 0.08 (1.21 - 1.53)	1.36 ± 0.09	1.32 ± 0.09	1.31 ± 0.06
	Wild boar	1.13 ± 0.05 (1.05 - 1.24)	1.13 ± 0.05	1.10 ± 0.02	1.12 ± 0.06

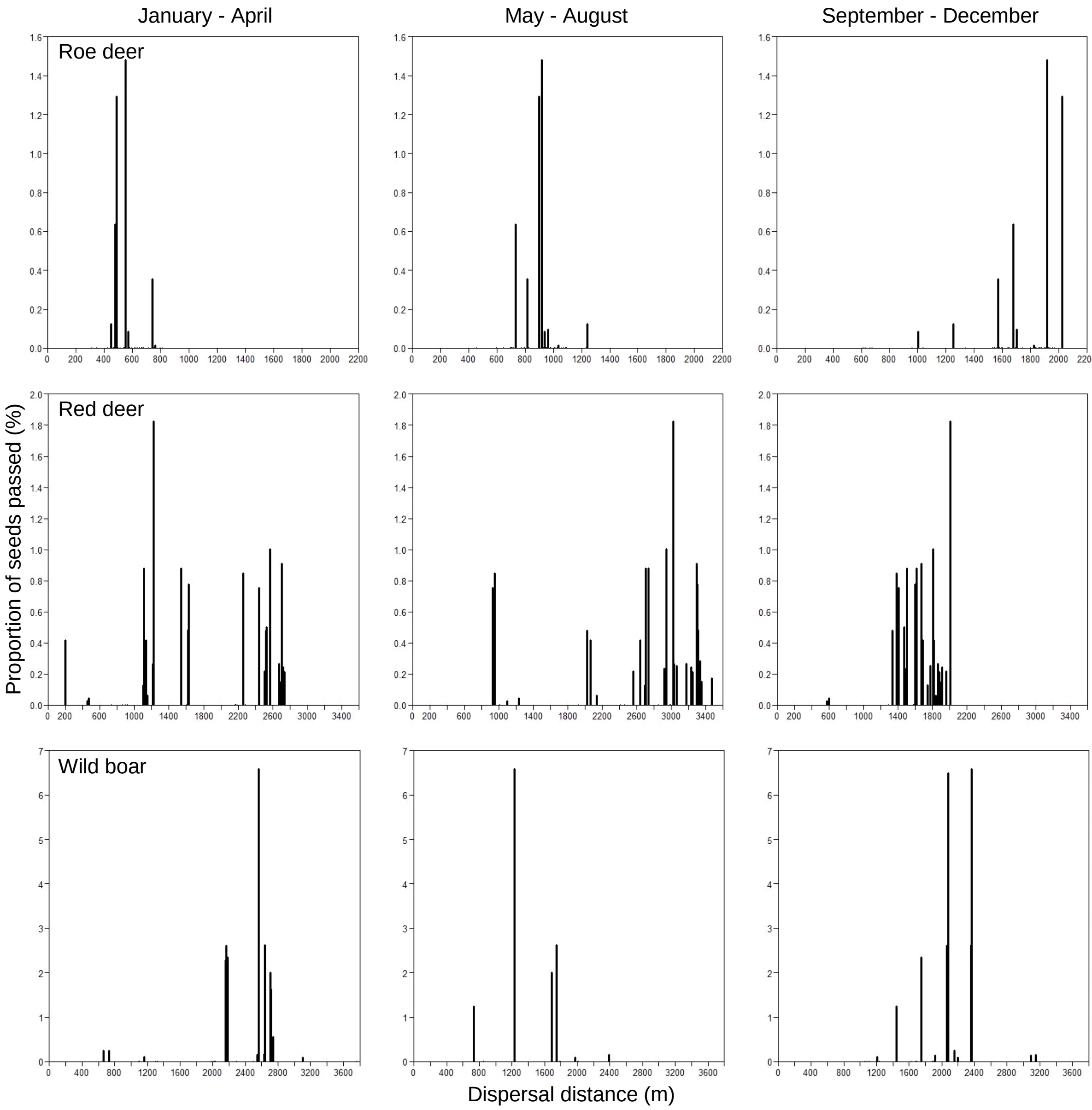
APPENDICES

Appendix 1: Gut passage rates of the seeds of each plant species (*Plantago media*, *Prunella vulgaris* and *Rubus fruticosus*; Table 2) through each animal species (roe deer, red deer and wild boar).

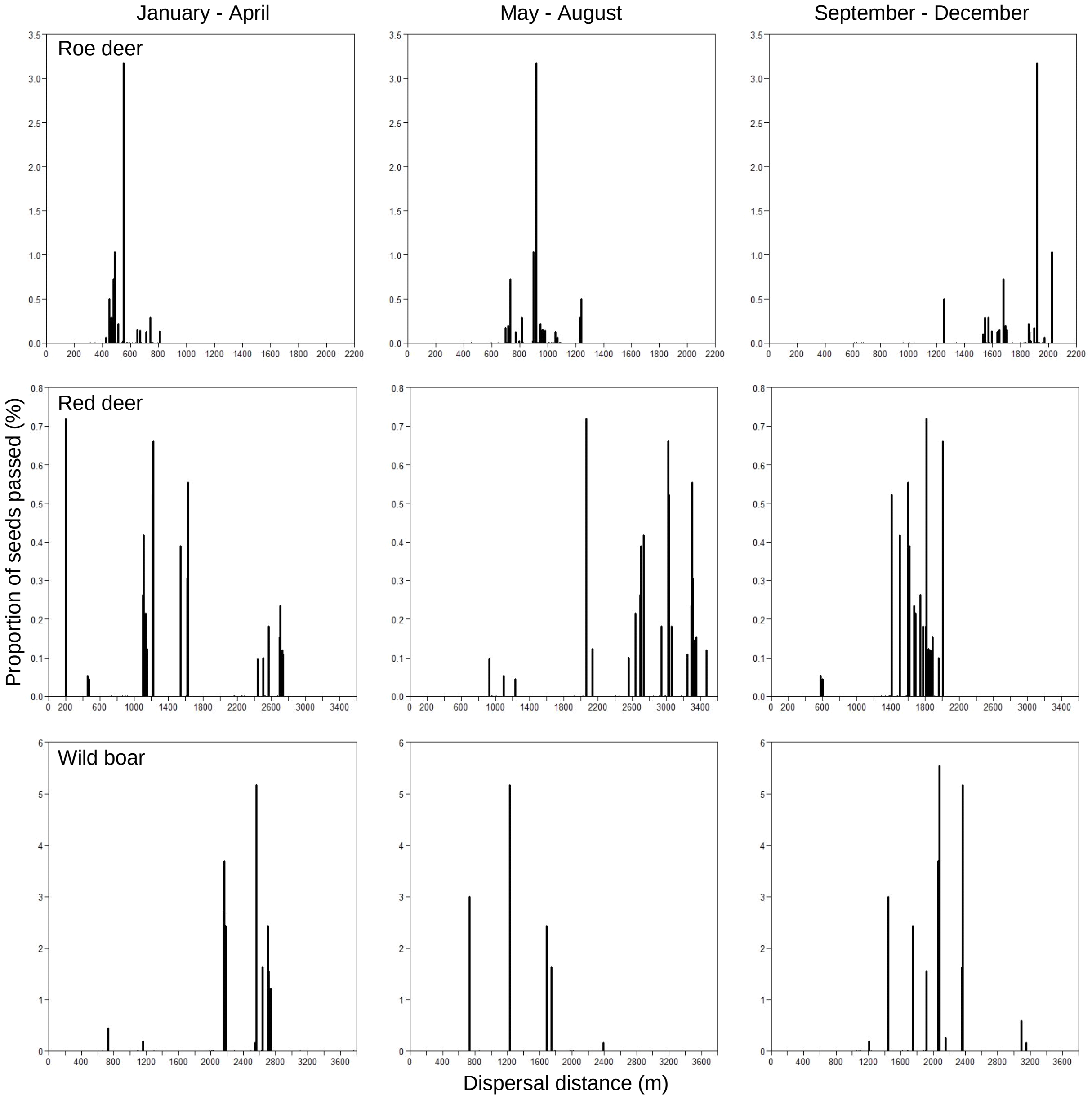


Appendix 2: Dispersal curves estimated for seeds of each plant species: **(a)** *Plantago media*, **(b)** *Prunella vulgaris* and **(c)** *Rubus fruticosus*; using the weighted displacement model of each animal species (roe deer, red deer and wild boar).

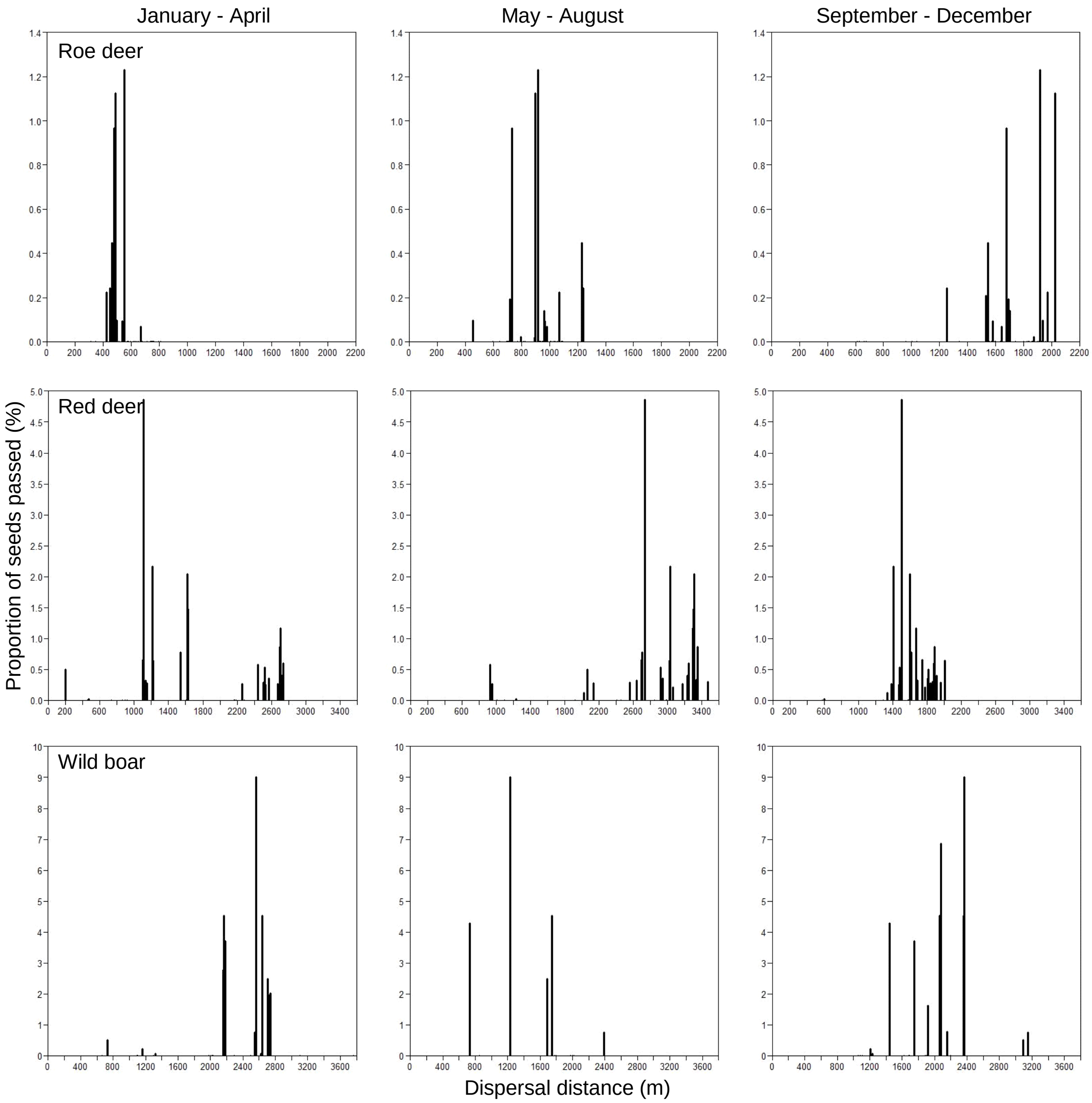
(a) *Plantago media*



(b) *Prunella vulgaris*



(c) *Rubus fruticosus*



CHAPITRE 2

La zoochorie : un filtre d’assemblage des communautés floristiques ?

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I. A l’échelle d’un département : endozoochorie

J’ai cherché ici à déterminer si les trois ongulés sauvages dispersent préférentiellement un assemblage d’espèces défini par des traits fonctionnels distincts de ceux de la flore régionale. Pour cela, j’ai placé des fèces des trois ongulés, récoltées dans deux forêts du Loiret, sous serre en conditions contrôlées, afin de forcer la germination de leur contenu. J’ai ensuite comparé la composition de l’assemblage d’espèces dispersées (en termes d’espèces et de leurs fréquences d’occurrence dans les fèces) à celle de la flore régionale, dans un espace fonctionnel multivarié constitué par les traits des graines et des plantes dont elles sont issues.

L’assemblage d’espèces dispersées n’est pas un échantillon aléatoire de la flore régionale, il est biaisé en faveur des espèces végétales non forestières. Les graines rondes, de petite taille et présentant une longévité élevée dans la banque de graines semblent sur-représentées, mais l’effet de l’habitat surpasse largement l’effet de ces traits. La présence d’adaptations morphologiques sur les graines (appendices, élaiosome ou mucilage) ne permet pas de différencier les espèces dispersées des espèces non dispersées. L’endozoochorie opère donc comme un filtre écologique indirect, qui agit non pas sur les traits des plantes, mais plutôt *via* les préférences d’habitat des vecteurs animaux. Elle pourrait influencer la composition des communautés végétales forestières, en permettant à des plantes de milieux ouverts de coloniser des habitats intra-forestiers.

Article 3

Influence of ungulate-mediated endozoochorous dispersal on the functional composition of seedling assemblages in an agro-forested landscape

Picard M., Chevalier R., Barrier R., Boscardin Y. and Baltzinger C.

Soumis à *Journal of Vegetation Science*

Abstract

Zoochory is a prominent dispersal process in a wide range of plant species, but its community-level effects have rarely been assessed. Morphological and physiological traits of both the vectors and the seeds are expected to influence dispersal probability, triggering signatures in the functional composition of local plant communities. In this study, we compared the taxonomic and functional composition of assemblages of seedlings dispersed by three wild ungulates to the characteristics of the regional flora in an agro-forested landscape of central France. We collected roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) faeces in two forests, and subjected the samples to germination under controlled conditions. We first examined how different vectors influence the composition of the dispersed plant assemblages by comparing the abundance and species richness of the seedlings that emerged from the faeces of the three ungulates. We then compared the functional characteristics of the dispersed pool with those of the regional flora in a multivariate functional space built from 20 relevant plant traits. A total of 754 seedlings and 46 plant species germinated from 300 faeces samples, with higher species richness and abundance in red deer. All three ungulates broadly use forest habitat, but the proportion of non-forest plants was higher in the faeces than in the regional species pool. Other traits such as seed shape, seed size or seedbank longevity affect dispersal probability, but their effects were overshadowed by the habitat effect. Seed morphology did not differentiate the dispersed species from the regional flora. Endozoochory acts as an indirect functional filter, filtering species according to the vectors' feeding habitat. It could affect the composition of forest plant communities by allowing plants from open habitats to colonize forested areas.

Keywords: seed dispersal, endozoochory, germination, traits, plant-animal interactions, assembly processes, filter, habitat use.

INTRODUCTION

Seed dispersal is a critical process in plant population spatial dynamics (Cain et al. 2000). Exchanging individuals between populations allows genetic flows and/or colonization of suitable areas, and lower intraspecific competition or pathogen prevalence (Howe & Smallwood 1982; García et al. 2007). By spreading individuals, dispersal influences the spatial patterns of plant diversity, but also has an impact on species assembly processes and through these processes, on community composition patterns (Cousens et al. 2008). Animals are frequent vectors of plant dispersal (Vittoz & Engler 2007). Many, but not all animal-dispersed plants bear morphological traits assumed to result from adaptations to epizoochory, including hooked or bristly seeds, or to endozoochory, for instance fleshy fruits or a resistant seed coat (Howe & Smallwood 1982; Pakeman et al. 2002; Cousens et al. 2008). Because many herbaceous seeds without such morphological adaptations, particularly the smaller ones, can be accidentally ingested in considerable quantities by large herbivores as they consume plant foliage ("foliage is the fruit", Janzen 1984), adaptations which improve seed resistance to digestion condition the effectiveness of endozoochorous dispersal (Pakeman et al. 2002). Seeds able to germinate after defecation by herbivores have accordingly been shown to share common characteristics including small size, round shape and low mass (Pakeman et al. 2002; Couvreur et al. 2005; Mouissie et al. 2005). Thompson et al. (1993) demonstrated that these seeds also have persistent seedbanks, which possibly explains their higher survival rates.

Studies on a variety of domestic and wild herbivores have demonstrated the large range of plant species dispersed through endozoochory (Pakeman et al. 2002; Mouissie et al. 2005; Eycott et al. 2007; Jaroszewicz et al. 2013). Furthermore, herbivores trigger "directed dispersal", as they vector plant species between similar habitats corresponding to their feeding grounds (Wenny 2001; D'hondt et al. 2012; Rico et al. 2014). Since their home ranges are larger than those of smaller mammals and domesticated species limited by human confinement, wild ungulates potentially disperse seeds over long distances and across various habitats in mosaic landscapes. Thus, large wild ungulates may not only link distant plant populations, but also promote colonisation of new areas, making them suitable models to address the effects of zoochory on plant distribution. Furthermore, as dispersal probability differs according to seed traits, wild ungulates could filter plant communities according to their dietary preferences and patterns of habitat use within their home ranges.

Most existing studies on the community-level consequences of endozoochory did not compare the dispersed assemblage to the composition of the regional flora (Mouissie et al. 2005; Cosyns et al. 2005; Jaroszewicz et al. 2013). Wild ungulates usually disperse small and round seeds, which have no particular morphological adaptations (i.e. pulp or appendages) (Pakeman et al. 2002; Heinken et al. 2002). Yet, the extent to which the prominence of seed morphological traits reflects their commonness in the regional assemblage remains untested, as does whether or not herbivores disperse traits randomly. Furthermore, while recent studies have suggested that combinations of traits explain seed survival after defecation (Couvreur et al. 2005; D'hondt & Hoffmann 2011), the studies that compared dispersed and non-dispersed species considered each plant attribute separately. In a lowland coniferous forest mosaic, Eycott et al. (2007) observed a lower proportion of seeds without physical dispersal adaptations (awns, burrs, fleshy fruit, nuts, wings or plumes) in faecal material than in their study area (25 vs. 39%). In contrast, Heinken et al. (2002), who studied zoochory by roe deer, wild boar, hare and marten in a deciduous forest, found that the proportion of light seeds without morphological adaptations to zoochory was higher in wild mammals' faeces than in the regional flora. Non-forest plant species were also significantly more dispersed.

In this study, we assessed whether forest ungulates act as a biotic filter for plants dispersed by endozoochory. In two forests of Centre France embedded in an agro-forested mosaic landscape, we sampled faeces from three wild ungulates: roe deer (*Capreolus capreolus*), a herbivorous ruminant browser; red deer (*Cervus elaphus*), an intermediate herbivorous ruminant mixed feeder; and wild boar (*Sus scrofa*), an omnivorous-frugivorous hindgut fermenter (Hofmann 1989; Clauss et al. 2008). We first compared the abundance and species richness of the seedlings dispersed by the three ungulates, to assess their relative contribution to the composition of the dispersed plant assemblages. We then compared the assemblages of species dispersed by each of the three animal species to the regional pool of species in a multivariate functional space built from ecological traits known to affect dispersal propensity. We specifically tested the following predictions: 1/ Due to their differing feeding strategies, the three wild ungulates would disperse different seed quantities and plant species richness. We predicted that red deer, as a mixed feeder with a wider feeding regime, would disperse more seeds and species than the more selective roe deer (Eycott et al. 2007; Jaroszewicz et al. 2013). We also predicted that wild boar would disperse fewer seeds and plant species than the two ruminant species (Heinken et al. 2002; Schmidt et al. 2004; Jaroszewicz et al. 2013). 2/ Species abundance in the faeces would reflect the animals' dietary preferences rather than the species abundance in the study area. 3/ Ecological traits relevant to dispersal should distinguish dispersed species from the species in the regional assemblages. We predicted that the dispersed pool of species would be biased towards small and round seeds, and that these species would also have a persistent seedbank. We also expected that the two herbivores would preferentially disperse herbaceous species, with shrubs in addition for roe deer, while the frugivorous wild boar would preferentially disperse seeds with pulp.

MATERIALS AND METHODS

Study area

We conducted our study in two forests in central France, the "Lorris" (14500 ha) and "Montargis" (4100 ha) forests, separated from each other by approximately 25 kilometres of agricultural mosaic composed of crops, pastures, villages and small woods (Figure 1.A). These two forests are managed through rotational clear-felling and are dominated by *Quercus petraea* (45 and 50 % cover in Lorris and Montargis respectively) and *Pinus sylvestris* (39 and 20 % cover respectively); they include approximately 5 % of open areas. They differ in soil and vegetation composition. Lorris is dominated by coniferous trees (*Pinus sylvestris, Pinus nigra*), while Montargis is mainly deciduous (*Quercus petraea, Fagus sylvatica*, *Carpinus betulus*). Lorris includes a number of ponds and bogs of various sizes, and the soils there are more acidic ($pH < 4.5$) than in Montargis. Roe deer and wild boar are present in both forests (approximately five and ten animals killed in 2009-2010 per km^2 in Lorris, five and two in Montargis; unpublished data from the French hunting federation), while red deer is present only in Lorris (about two animals killed per km^2 the same year).

Faeces collection and treatment

We collected faeces from the three animal species in the two forests, from May 2010 to December 2012. Each faeces sample corresponded to one defecation event. We collected faeces approximately every fortnight in 84 plots (44 in Lorris, 40 in Montargis); we stratified the search effort so as to reflect the diversity of stand age, structure and composition found in the two forests (Figure 1.B). We only collected fresh faeces and removed the lowermost layer in order to avoid contamination by seeds from the soil seed bank. We obtained a total of 300 faeces: 180 in Lorris and 120 in Montargis; 60 for each animal species. We dried the faeces samples at 20-25°C for two days, then weighed and stored them at 5°C until the end of field collection. To sort out the seeds contained in the faeces, we washed each sample through 2-mm and 200-µm sieves to remove large components (fibre fragments) and to retain the smallest seeds expected (*Juncus* species, according to local vegetation surveys). We then spread the concentrated content of the 200-µm sieve onto trays in a 3-to-5-mm-thick layer on sterilized potting compost, as recommended for seedbank analyses (Ter Heerdt et al. 1996). We kept the sample trays in a greenhouse, under moist conditions with controlled temperatures, set to 15°C in winter and 35°C in summer. In order to control for seed rain contamination in the greenhouse, we also placed ten control trays containing pure sterilized potting compost with no concentrated faecal content among the samples.

Estimation of viable seed content

During the course of one year, we regularly recorded and removed all seedlings from the trays as soon as they were large enough to be identified to prevent competition within the samples. After each identification session, we stirred the tray compost. We identified seedlings at the species level whenever possible, but 4 % died before identification was possible, and 36 % could only be identified to the genus level, with *Juncus* spp. representing 32 % of the latter. We excluded six species that also emerged in the controls and were considered to be contaminations: *Conyza canadensis*, *Epilobium tetragonum*, *Populus alba*, *Salix* spp., *Senecio vulgaris* and *Oxalis* spp.

Regional flora

We defined the regional flora as the flora hosted by all the surrounding municipalities embedding at least part of the study forest and its adjacent non-forest habitats, up to two kilometres from the nearest forest edge (Figure 1.A). We compiled separate regional species pools for the two forests from municipality-level plant species inventories (data available online, from the botanical conservatory of Centre France: http://cbnbp.mnhn.fr/cbnbp/, accession date: June 2014). Local plant diversity was higher in Lorris (818 species, for a surface area of 39941 ha) than in Montargis (672 species, for 22929 ha). We computed species occurrence frequency, separately for each forest, as the relative number of municipalities in which a species was present. We only considered spermatophytes, herbaceous and woody species. All plant species recorded in faeces samples were listed in the regional flora.

Trait matrix

We compiled 20 plant attributes known to be associated with endozoochorous dispersal (Table 1) from the LEDA Traitbase (Kleyer et al. 2008), the Ecoflora database (Fitter & Peat 1994) and the Baseflor (Julve 1998). We also retrieved the seedbank longevity index (SLI) from Thompson et al. (1997). We calculated seed shape (variance in dimensions: Vs) following Bekker et al. (1998): $Vs = \sum(x_i - \bar{x})^2 /3$, with x_1 = length/length, x_2 = width/length and x_3 = height/length. Seed coat hardness and leaf nutrient content, usually associated to seed resistance to digestion and to plant foliage attractiveness (Janzen 1984, D'hondt and Hoffman 2011), were available for less than 11 % of the species present in the regional flora; we therefore did not include these traits in our study. We completed the 19 % missing data (when considering each species-trait pair) as far as possible by carrying out supplementary searches in various sources of grey literature. Since multivariate analyses (see below) do not tolerate missing data, we filled the remaining 7% missing data with the mean value (for continuous traits) or the modal value (for categorical traits).

Data analyses

We tested for differences in seedling abundance and species richness among animal species, while accounting for possible phenological and forest-related variations in the seed pools. Due to the high level of zero inflation in our response variables (seedling abundance and species richness), we built hurdle models (Potts & Elith 2006) with animal species, sampling month and forest as covariates on the truncated-Poisson component and no covariate on the binomial component. We included the log-transformed weight of each faeces as an offset to ensure that sample size-related variations in the response variables were accounted for. We used similar hurdle models to check whether faeces collection date influenced species richness. We also built species accumulation curves based on the Chao2 estimator to check whether the composition of our seed samples reflected the actual species richness found in the two forests (Chao 1987).

We then compared the taxonomic and functional composition of the dispersed species pool to that of the regional flora. In a first step, we used Spearman's rank correlations to test whether species frequency of occurrence in our faeces samples was correlated to species frequency of occurrence in the regional flora. As a second step, we used a Hill and Smith multivariate analysis, an equivalent to principal component analysis which allows categorical and continuous data to be used simultaneous (Hill & Smith 1976), to test for differences between the functional composition of the dispersed species pool and that of the regional flora. The multivariate functional space was built from 20 plant traits, relevant for endozoochorous seed dispersal (see Table 1). We computed separate multivariate spaces for the two forests since we could not assume that regional plant assemblages were similar. We used species frequency of occurrence in the regional flora as the row weight, and retained the first two components of the analyses, which accounted for 19.6 % and 19.4 % of the total variance, for Lorris and Montargis respectively. We compared the functional characteristics of the species pool transported by each animal species to the regional flora using ellipses centered on the centroids of each pool, with points weighted by the species frequency of occurrence in faeces (for each forest-animal species pair), and with axes representing 1.5× the standard deviation of species' coordinates on each principal component. All statistical analyses were performed using R 3.1 software (R Development Core Team 2012) and the pscl, fossil and ade4 libraries (Dray & Dufour 2007; Zeileis et al. 2008; Vavrek 2011).

RESULTS

Qualitative results

A total of 754 seedlings of 46 plant species germinated from the 300 collected faeces, once contaminations and unidentified seedlings were excluded (Appendix S1). Two taxa dominated the dispersed pool in terms of seedling number: *Juncus* spp. (260 seedlings) and *Portulaca oleracea* (160 seedlings). We observed *Juncus* spp. in 12.7 % of all the faeces, while *Portulaca oleracea* was recorded in only 1 %. At least 48 % of the species only occurred in a single faeces, and 32 % of the species produced only one seedling, while no seed germinated in 63 % of the faeces.

Red deer dispersed more plant species and more seedlings than either wild boar or roe deer (Table 2). Red deer, wild boar and roe deer respectively exclusively dispersed 17, 10 and one plant species, while five species were shared by the three ungulates: *Agrostis capillaris, Calluna vulgaris, Juncus* spp., *Luzula* spp. and *Portulaca oleracea* (Appendix S1). These species had a frequency of occurrence > 50 % in the two forests, except *Portulaca oleracea* (36 %).

Seedling abundance and species richness

Red deer dispersed more seeds than either roe deer (difference between roe and red deer = -0.49 ± 0.17 (±s.d), $z = -2.89$, $p < 0.01$) or wild boar (difference between red deer and wild boar = -0.53 ± 0.10, $z = -5.56$, $p < 0.01$). The explained deviance was 27.8 %. Wild boar faeces also exhibited lower species richness than red deer faeces (difference between red deer and wild boar = -0.82 ± 0.24, $z = -3.42$, $p < 0.001$). Richness did not differ significantly between roe and red deer (-0.66 ± 0.52, $z = -1.26$, $p = 0.21$); however, this might be due to the low number of non-null data combined with the high variability in species richness dispersed by roe deer. Our model explained 17.8 % of the deviance in species richness. Both seedling abundance and species richness were higher between July and October, as a consequence of plant phenology; they were also higher in Lorris than in Montargis (see Appendix S2). Species richness was not correlated with the date of faeces collection (0.02 ± 0.01, $z = 1.52$, $p = 0.13$; Appendix S3). There was no correlation between species frequency of occurrence in faeces and in the regional flora ($\rho = 0.02$ and 0.001 for Lorris and Montargis respectively). Cumulative species richness curves (Figure 2) showed that a number of infrequently dispersed species may not have been recorded in our study, but did not suggest that this incomplete sampling could affect the results of our analyses (see also Table 2). The estimated species richness showed that wild boar dispersed a higher number of species than did roe deer.

Functional traits

Functional patterns were consistent among the two forests. The first axis of the Hill and Smith multivariate analysis segregated species according to their habitat preference, from forest species (phanerophytes, with fruits, high seed releasing height, and large and heavy seeds) to non-forest species (heliophilous species with persistent seedbanks) (Figures 3 and 4). The second axis differentiated species according to their seed morphology, with perennial monocots and species bearing few seeds with morphological adaptations (elongated or flat appendages, hooks, balloon structures) towards negative values; and shrubs and annual species with round seeds, without appendages towards positive values (Figures 3 and 4, and see coordinates of all traits in Appendix S4). The functional characteristics of the dispersed plant assemblages were similar for the three animal vectors (Figure 4). While the regional flora was spread along the two components of the Hill and Smith, the dispersed assemblage was dominated by non-forest species and covered a wide range of morphological characteristics along the second component (Figure 4).

DISCUSSION

Our results show that the species richness and abundance of plant seeds dispersed through endozoochory vary among three common ungulate vectors and differs in both taxonomic and functional composition from the regional flora. Ungulate-mediated dispersal could therefore act as a filter of plant assemblages and thus affect regional and local floristic patterns. In particular, our results suggest that ungulates could favor the intrusion of non-forest plants into forested areas.

Seedling abundance and species richness

The differences among the three ungulates in terms of dispersed seeds and species are consistent with their feeding preferences. Red deer dispersed higher seedling numbers, since this large-bodied mixed feeder has a rather generalist diet and large home ranges covering many habitats, and therefore encounters and consumes a wider range of plant species, than the smaller bodied and more selective feeder roe deer (Hoffman 1989). Roe deer is known to feed preferentially on leaves and buds rather than seeds and fruits (Schmidt et al. 2004): this may explain why it dispersed so few species in our study. We found that wild boar dispersed high larger quantities of seeds with higher species richness than did roe deer, suggesting that wild boar's diet in our study area may involve high seed intake, and probably only small amounts of rhizomes, roots or insects (Heinken et al. 2002). Depending on the relative abundance of the three vector species, plants which correspond to the feeding preferences of the most abundant vector may be dispersed in higher numbers.

Taking mean faeces weight and daily defecation rates into account (unpublished data), wild boar dispersed more species per day than did roe deer (3 species vs. 2 species), while red deer dispersed the most (8 species per day). Our results therefore suggest that wild boar could have a greater role in seed dispersal than was previously thought (Jaroszewicz et al. 2013, Schmidt et al. 2004), and that red deer provides the highest contribution in terms of dispersed seeds and species.

Wild boar also dispersed only one fruit species (*Rubus fruticosus*), suggesting that the typically large seeds from fruits were damaged during transit through digestive tract. Apple tree (*Malus sylvestris*) seeds and those from cultivated plants including maize and wheat (*Zea mays, Triticum aestivum*) were observed in wild boar faeces during sieving, but never germinated. In all the faeces samples from the three ungulates, we recorded only two species with fleshy berries (*Rubus fruticosus* and *Solanum nigrum*). Fruit plants may have developed adaptations to exclusive endozoochorous dispersal by frugivore birds or mustelids (Couvreur et al. 2005, Heinken et al. 2002). Moreover, the absence of germination in 63 % of the faeces suggested that the costs associated with endozoochory are rather high for plants bearing fleshy fruits.

Species occurrence frequency in faeces and in the regional flora

The plant species most frequently dispersed by the three animal species were present in the regional assemblage with a frequency of occurrence higher than 50% (except for two species dispersed only by roe deer: *Digitaria sanguinalis* and *Kickxia elatine*). Plant species that are abundant in feeding habitats have a higher probability of being consumed and, through a sampling effect, to be effectively dispersed. Nevertheless, species occurrence frequencies in faeces and in the study areas were uncorrelated, showing that many regionally abundant species are not dispersed by wild ungulates, consistent with their feeding preferences. All the plant species dispersed in our study had previously been found to be dispersed by roe deer, red deer, wild boar, fallow deer or white-tailed deer (except *Kickxia elatine*) in a primeval forest (Jaroszewicz et al. 2013), a coniferous forest mosaic (Eycott et al. 2007), a Mediterranean dehesa (Malo & Suárez 1995), and in European or North-American agro-forested landscapes (Heinken et al. 2002; Myers et al. 2004; Schmidt et al. 2004; von Oheimb et al. 2005). The fact that dispersed plants are similar in our two study areas and in these earlier studies irrespective of the species pool confirms that the composition of assemblages dispersed through endozoochory is driven by vector feeding preferences more than by plant occurrence, in spite of the relatively generalist diet of the three ungulates studied. Furthermore, a large proportion of the dispersed species, including regionally common ones, emerged in only one faeces, which seems to suggest that vector diet and opportunistic feeding behaviour, not plant occurrence, determines dispersal probability. Hence, wild ungulates could have a filtering effect on the composition of dispersed plant assemblages through their feeding preferences irrespective of the composition of the regional species pool.

Habitat and traits of the dispersed species

The pool of dispersed species corresponded to a non-random sample of the regional flora dominated by non-forest species, which reflects wild ungulate preference for open areas for feeding (Hemami et al. 2005). Heinken et al. (2002) also suggested that tree seeds are too large to survive gut passage and are produced in too low numbers to be ingested with a high probability or to survive their passage into the gut. In our functional trait space, the dispersed assemblages also corresponded secondarily to small and light seeds with a high seedbank longevity index. As suggested by Thompson et al. (1993), survival in the seedbank probably requires similar adaptations to those needed to survive passage through the digestive tract. However, seed morphology (appendages, elaiosome or mucilage) was similar in the regional and dispersed species pools, suggesting that seed morphological traits only slightly affect the probability of being dispersed by ungulates. Couvreur et al. (2005) also found that endozoochory was associated with a broad range of plant functional characteristics in donkeys, suggesting that low functional distinctiveness as compared to regional species pools may be a general characteristic of dispersed seed assemblages. Among traits that might distinguish dispersed from non-dispersed plants, plant edibility and attractiveness or nutrient content could have a significant influence (Janzen 1984), but will need to be more exhaustively quantified in trait data bases to assess their contribution to the composition of endozoochory-dispersed species assemblages.

Implications for endozoochory

Although it is thought that zoochory is the main mode of dispersal in forested areas (Heinken et al. 2002), forest species are rarely dispersed by ungulates (von Oheimb et al. 2005, Schmidt et al. 2004), probably because other vectors predominate, including birds or mustelids (Couvreur et al. 2005, Heinken et al. 2002). The rarity of forest species in dispersed seed assemblages could also contribute to the limited colonization capacities of most ancient woodland species (Hermy et al. 1999; Panter & Dolman 2012). As herbaceous non-forest species dominated the pool of dispersed species, and most wild ungulates forage in open habitat and sleep or shelter in the forest (Kuijper et al. 2009), seeds could be dispersed from open to forested areas, and thus enter the forest soil seed bank (van Calster et al. 2008). As the dispersed plants in our study also had a high seedbank longevity index, they may be able to lay dormant until suitable conditions for germination arise, and thus potentially colonize intra-forest gaps, like forest road edges or tree fall gaps (Naaf & Wulf 2007).

Conclusion

We showed that the composition of assemblages dispersed through endozoochory is driven by vector feeding preferences more than by seed traits. We therefore suspect that the composition of the dispersed species pool is mainly affected by the most abundant vectors. Endozoochorous dispersal may act as an indirect ecological filter, not associated with plant niche as in a classic ecological filter (Keddy 1992), but with a plant-animal interaction. Our results stress the need to better estimate the effect of plant-animal relationships on patterns of plant community assemblage in heterogeneous landscapes.

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FIGURES

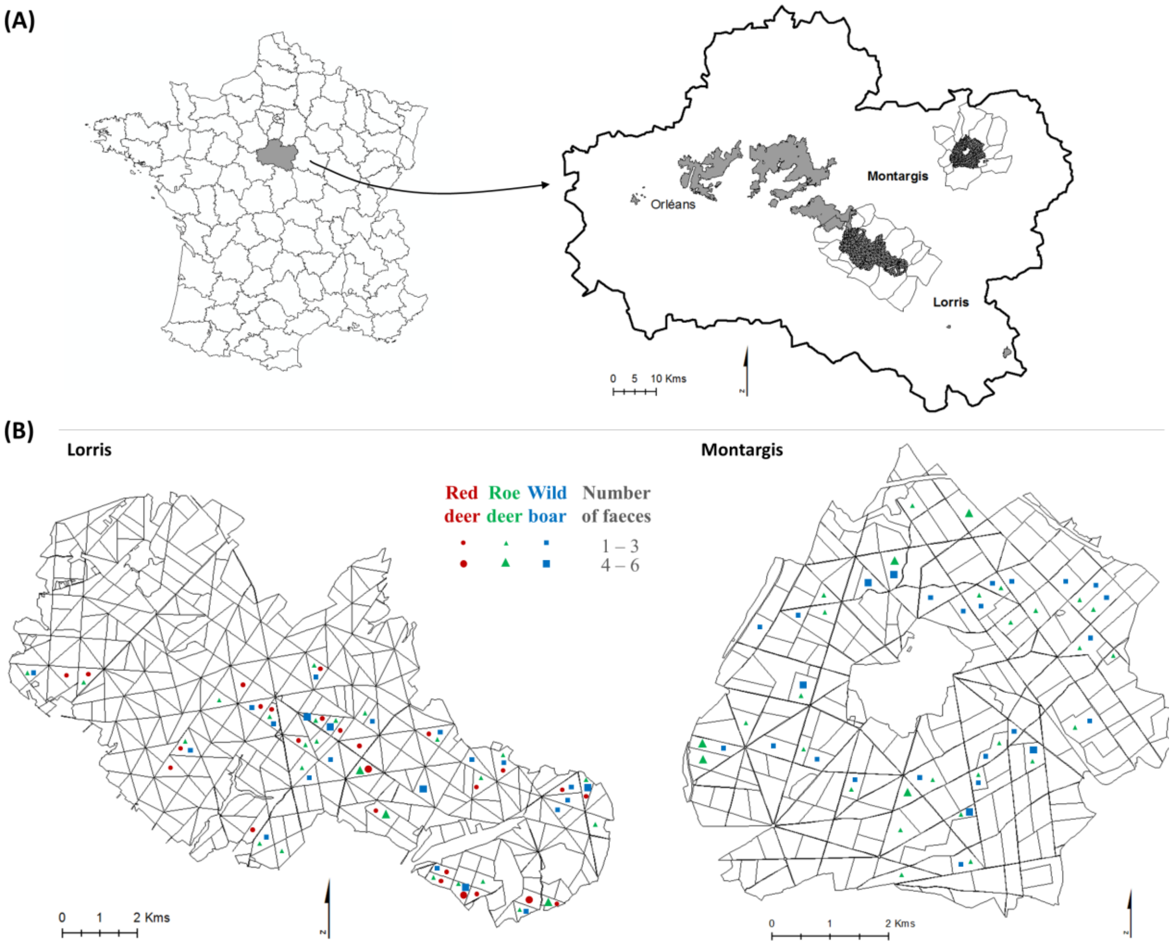


Figure 1: (A) Map of the regional district where the two study areas are located, showing the “Lorris” and “Montargis” forests and the surrounding municipalities considered to constitute the regional plant species pool (14 for Lorris, 13 for Montargis), and (B) location and number of faeces samples collected per forest and animal species.

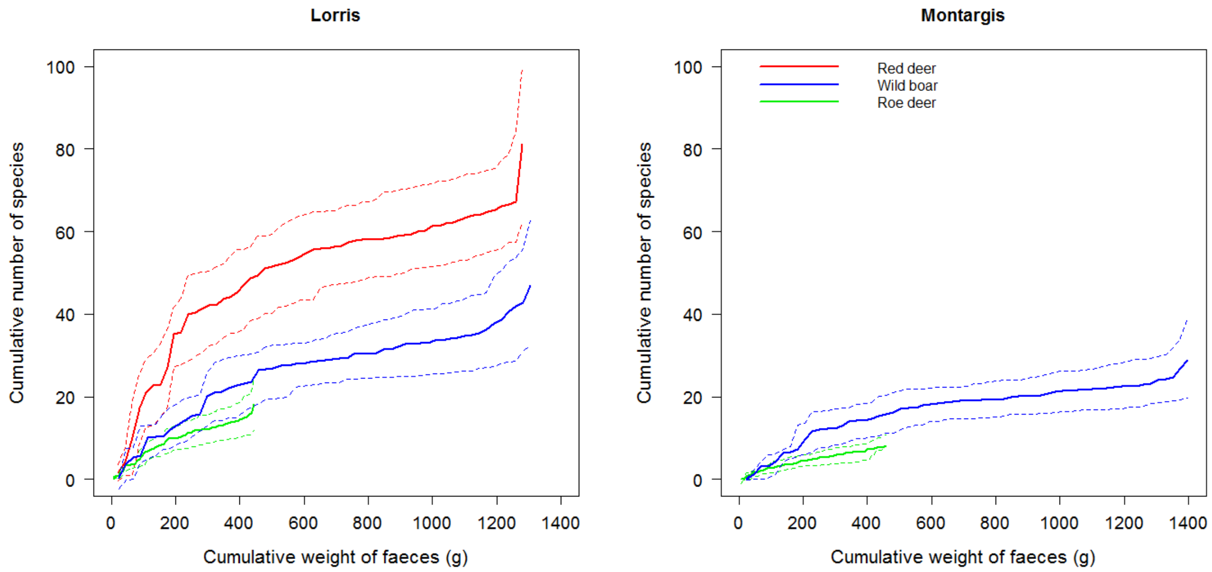


Figure 2: Cumulative number of plant species dispersed by each animal species, with increasing cumulative faeces weight (red deer: 1302 g, roe deer: 444 g, wild boar: 1374 g) in Lorris (left) and Montargis (right). Solid lines correspond to Chao2 estimations of species richness, and dotted lines are the 95% confidence intervals.

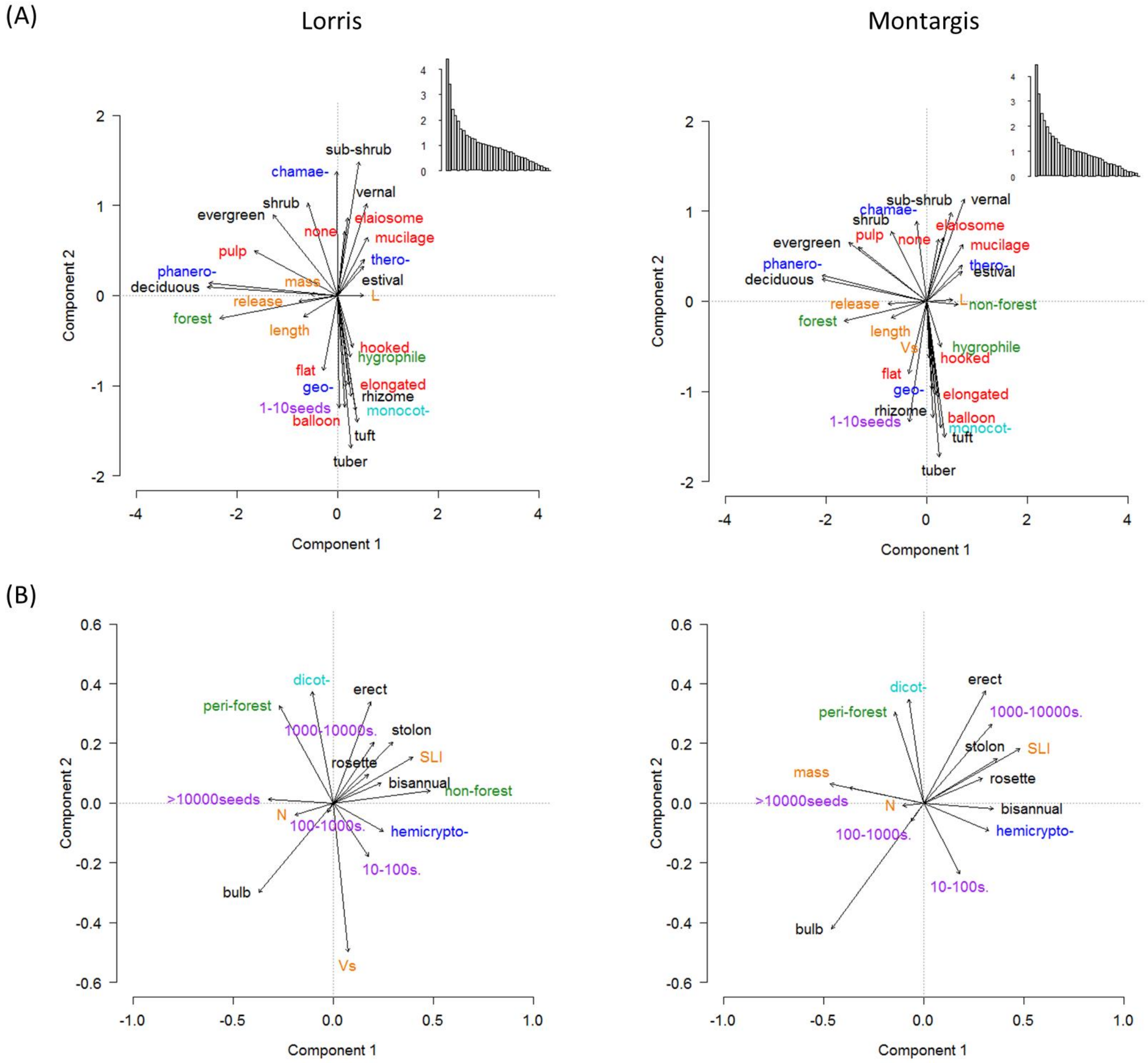


Figure 3: Correlations between 20 plant attributes (see Table 1 for description) along the two first components of the Hill and Smith analyses, in Lorris (left) and Montargis (right). The insets show the variance explained by each component. For better readability, plant attributes with coordinates > 0.5 (A), and < 0.5 (B) are shown separately.

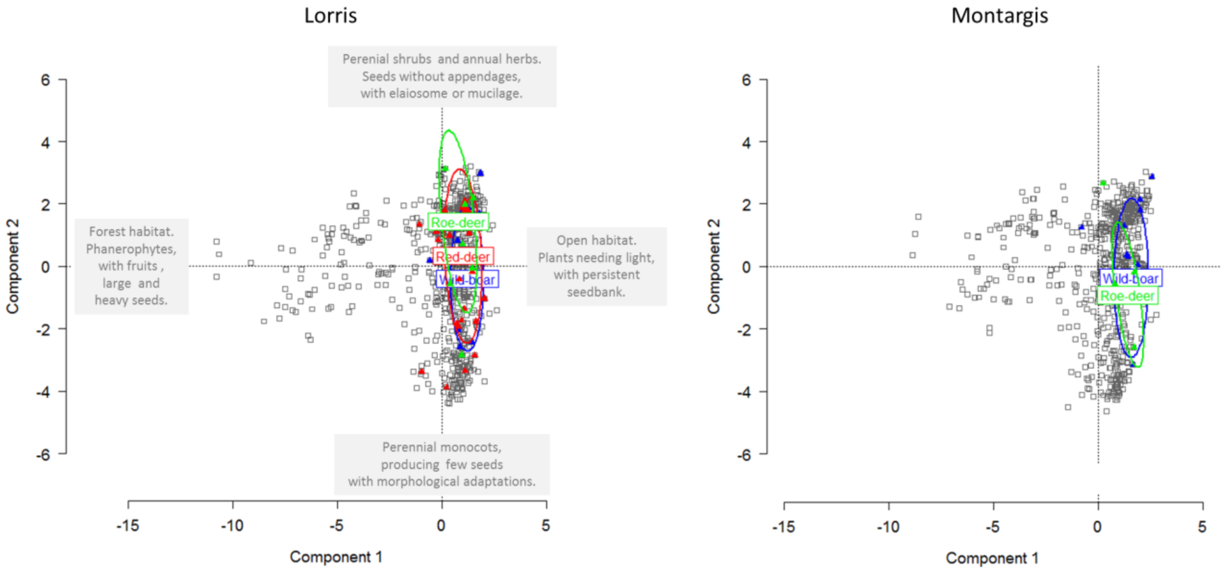


Figure 4: Distribution of the plant species in the regional vegetation along the two first components of the Hill and Smith analyses built on 20 plants attributes (see Figure 3). Ellipses are centered on the centroids of the plant species dispersed by each of the animal species: red deer, roe deer and wild boar in Lorris (left), and roe deer and wild boar in Montargis (right). The axes of the ellipses represent 1.5× the standard deviation of the species' coordinates on each component. Grey boxes recall the functional complexes of plant attributes, applicable both for Lorris and Montargis.

TABLES

Table 1. Attributes and ecological traits used in our analyses.

Attribute or trait	Expected effect on endozoochory	Categories or span (unit)	Source
Plant traits:			
Plant class	Browser ruminants preferentially feed on dicots, grazers on monocots (Hoffman 1989)	monocot, dicot	Baseflor
Plant habitat preference	Plants and their vectors must be in contact	forest, peri-forest, non-forest, hygrophile*	Baseflor
Life form	A proxy of plant phenology and of seed accessibility for animals	chamaephyte, geophyte, helophyte, hemicryptophyte, hydrophyte, phanerophyte, therophytes	Ecoflora, Baseflor
Life span		bisannual, vernal, estival, deciduous, evergreen, shrub, sub-shrub, bulb, rhizome, tuber, stolon, erect, rosette, tuft	Baseflor
L Ellenberg indicator value	Light requirement; a proxy of habitat openness	2 (shade) - 9 (light)	Ecoflora, Baseflor, Tela Botanica[1]
N Ellenberg indicator value	High-nutrient plants are more attractive for herbivores (Janzen 1984)	1 (oligotrophy) - 9 (eutrophy)	Ecoflora, Baseflor, Tela Botanica
Seed production	If higher, enhances contact probability with an animal	1-10, 10-100, 100-1000, 1000-10.000, > 10.000 (seed number / plant)	LEDA, Ecoflora
Seed releasing height	Gives an idea of seed accessibility for animals	0.003 – 55 (meters)	LEDA

Attribute or trait	Expected effect on endozoochory	Categories or span (unit)	Source
Seed traits:			
No appendages	Well dispersed by endozoochory (Janzen 1984)	Yes / No	LEDA, Ecoflora, Digital Seed Atlas of the Netherlands[2] (Cappers et al. 2006)
Elongated appendages	Favours epizoochory		
Hooks			
Flat appendages	Favours anemochory		
Balloon structure	Favours hydrochory		
Pulp	Favours endozoochory by frugivores		
Elaiosome	Favours myrmecochory		
Mucilage	Sticky substance which favours epizoochory		
Length	Small seeds germinate better (Pakeman et al. 2002)	0.29 – 58.75 (millimetres)	LEDA
Mass	Light seeds germinate better (Couvreur et al. 2005)	0.01 – 4753 (milligrams)	LEDA
Shape (Vs)	Round seeds germinate better (Janzen 1984)	0.0 (spherical) - 0.2 (disc- or needle-shaped)	Bekker et al. (1998)
Seedbank longevity index (SLI)	Seeds from persistent seedbank germinate better (Pakeman et al. 2002)	0 to 1	Thompson et al. (1997)

Categorical traits: Plant class, plant habitat preference (*with a separate category for hygrophile species which mostly depend upon highly specific microclimatic and local edaphic conditions), plant life form, life span, and seed production. Continuous traits: L and N indicator values, seed length, mass, shape, releasing height, and seedbank longevity index. Binary traits: Seed morphology (presence of appendages, elongated or flat appendages, hooks, balloon structure, pulp, elaiosome and mucilage).

[1] http://www.tela-botanica.org/site:accueil; accession date: June 2014.

[2] http://seeds.eldoc.ub.rug.nl/?pLanguage=en; accession date: June 2014.

Table 2. Summary of the dispersed species assemblage.

Plant species	**Red deer**	**Wild boar**	**Roe deer**	**Total**
Sample size	60	120 (60 + 60)	120 (60 + 60)	300
Total number of seedlings dispersed	416	276	62	754
Total number of species dispersed	34	24	10	46
Chao2 estimator of total number of species dispersed (± sd, standard error)	63 ± 14	40 ± 11	13 ± 25	72 ± 22
Total number of genus dispersed	25	20	9	34
Total number of families dispersed	16	14	7	19
Top five plant species, in terms of frequency in faeces:	*Juncus* spp. *Calluna vulgaris* *Plantago major* *Poa annua* *Agrostis capillaris*	*Juncus* spp. / *Juncus effusus* *Digitaria sanguinalis* *Chenopodium album* *Urtica dioica*	*Calluna vulgaris* *Juncus* spp. *Digitaria sanguinalis* *Urtica dioica / Kickxia elatine / Agrostis capillaris*	
Seedling abundance / faeces (± sd)	7.05 ± 20.12	2.34 ± 11.82	0.51 ± 1.92	
Specific richness / faeces (± sd)	1.56 ± 1.78	0.66 ± 1.04	0.25 ± 0.50	
Mean weight of faeces (± sd)	21.7 ± 10.6 g	22.9 ± 18.2 g	7.4 ± 4.4 g	
Mean seedling density / g (± sd)	0.30 ± 0.60	0.13 ± 0.62	0.09 ± 0.24	
Mean species density / g (± sd)	0.08 ± 0.09	0.05 ± 0.09	0.06 ± 0.15	

APPENDICES

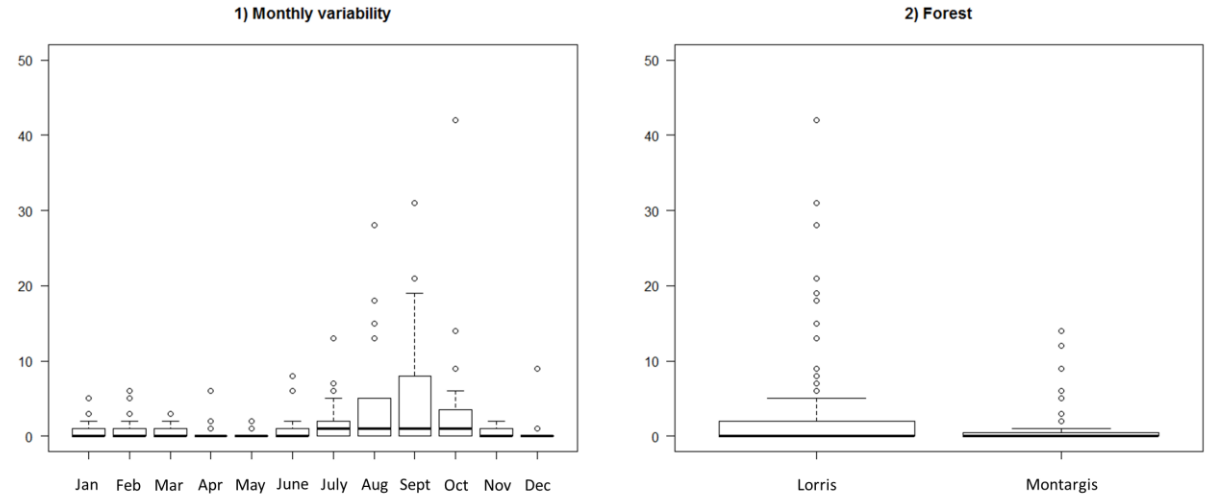
Appendix S1: List of plant species that germinated in the faeces samples, for each animal species, in the Lorris and Montargis forests. Plant species identified to the genius level only but that were assumed to have already been identified to the species level are marked by * and were not counted in the total number of dispersed plant species. Plant habitat is also indicated: hygro = hygrophile, periF= peri-forest, F= forest, nonF = non-forest.

Plant species	**Lorris**			**Montargis**		**Plant habitat**
	Red deer	**Wild boar**	**Roe deer**	**Wild boar**	**Roe deer**	
Agrostis canina	2	1				hygro
Agrostis capillaris	27	18	2			nonF
Agrostis stolonifera		3				nonF
Callitriche stagnalis		1				hygro
Calluna vulgaris	16	2	9		5	periF
Capsella bursa-pastoris	1			5		nonF
Carex pilulifera	1	2		1		nonF
Carex sylvatica	1					F
Cerastium fontanum	1					nonF
Cerastium glomeratum	1					nonF
Cerastium ssp. *	5					nonF
Chenopodium album	5			17		nonF
Deschampsia flexuosa	1					periF
Digitaria sanguinalis		1		11	4	nonF
Echinochloa crus-galli		1				nonF
Euphorbia peplus		1		1		nonF
Galium mollugo	1					periF
Juncus spp. *	212	30	6	2	10	nonF
Juncus bufonius	4		1			nonF
Juncus effusus	2	14		6		nonF
Juncus tenuis				2		nonF
Kickxia elatine	2		3			nonF
Lathyrus hirsutus	2					nonF
Medicago ssp.	5					nonF
Luzula forsteri		2				F
Luzula multiflora		1				nonF
Luzula spp. *	4		1	2		periF
Lycopus europaeus	1					hygro
Persicaria maculosa	7					nonF
Plantago coronopus	1					nonF
Plantago major	28	3				nonF

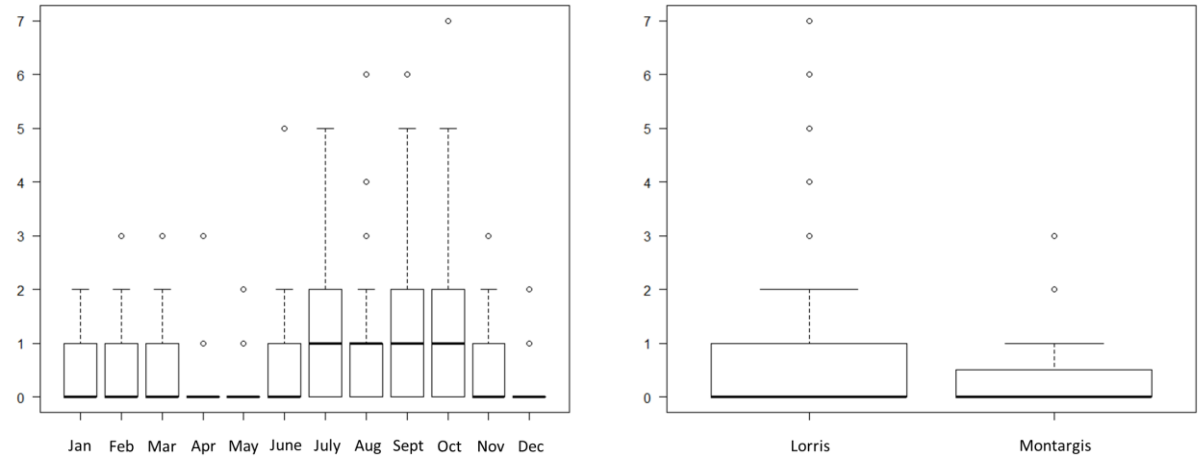
Plant species	**Lorris**			**Montargis**		**Plant habitat**
	Red deer	**Wild boar**	**Roe deer**	**Wild boar**	**Roe deer**	
Poa annua	10	4				nonF
Polygonum aviculare	2					nonF
Portulaca oleracea	30	113	17			nonF
Rubus fruticosus	2			2		periF
Rumex conglomeratus					1	nonF
Potentilla reptans				1		nonF
Solanum nigrum	2					nonF
Sonchus asper	1					nonF
Stellaria media	11	2				nonF
Trifolium arvense	5					nonF
Trifolium dubium	5					nonF
Trifolium spp. *	12					nonF
Trifolium pratense	1					nonF
Trifolium repens	1					nonF
Matricaria perforata				3		nonF
Tuberaria guttata		1				nonF
Urtica dioica		3	2	20	1	periF
Veronica persica	2					nonF
Veronica serpyllifolia	2					nonF
Number of seedlings dispersed	**416**	**203**	**41**	**73**	**21**	
Number of species dispersed	**37**	**19**	**8**	**13**	**5**	
Sample size (i.e. number of faeces)	**60**	**60**	**60**	**60**	**60**	

Appendix S2: Monthly variability (1) and difference between the two forests (2), in seedling abundance (A) and species richness (B).

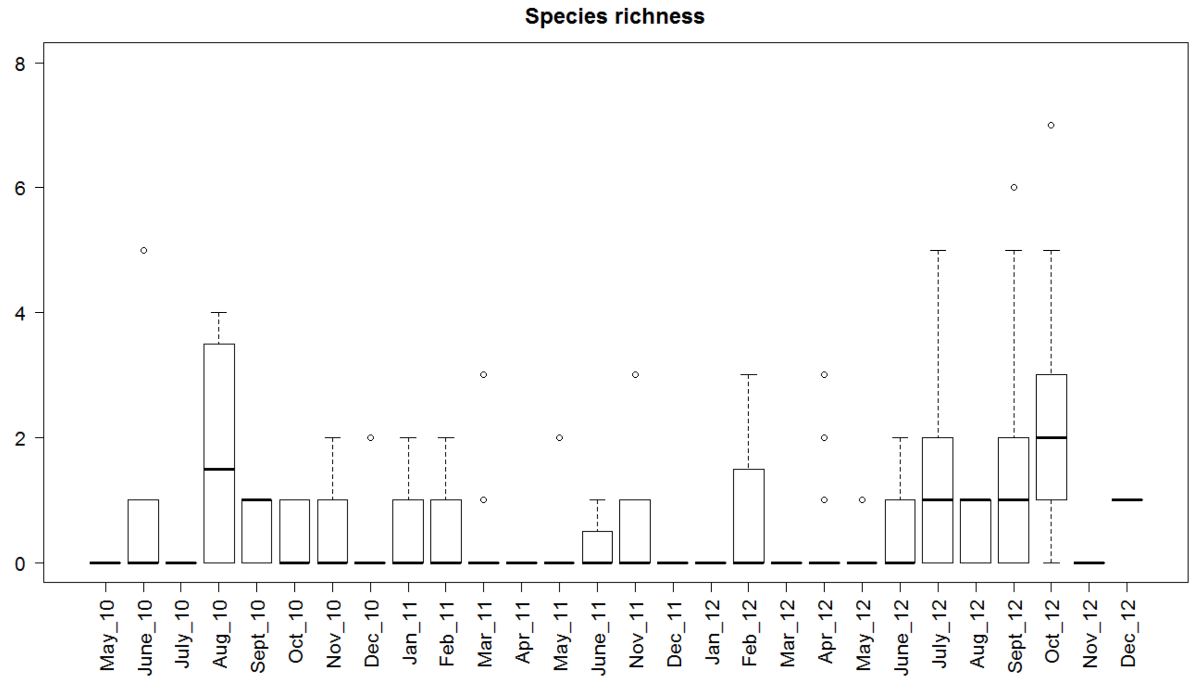
(A) Number of seedlings



(B) Species richness



Appendix S3: Species richness according to date of collection, from May 2010 to December 2012. There was an interruption in faeces collection from July to October 2011.



Appendix S4: Coordinates of plant attributes on the first two components of the Hill and Smith analyses, for Lorris (A) and Montargis (B). In black: attributes with coordinates >0.5; in gray: attributes with coordinates <0.5.

(A) Lorris

Plant attribute	Component 1	Component 2
group: dicot	-0.105259714	0.373330362
group: monocot	0.359922008	-1.276554992
habitat: forest	-2.339010642	-0.249463049
habitat: hygrophile	0.259959664	-0.68358767
habitat: non-forest	0.484162415	0.042078236
habitat: peri-forest	-0.268370216	0.3261294
life form: chamaephyte	-0.016918835	1.378468625
life form: geophyte	0.155633447	-1.01547094
life form: hemicryptophyte	0.25156593	-0.094894512
life form: phanerophyte	-2.553901452	0.13514665
life form: therophyte	0.531274358	0.400133496
life span: bisannual	0.241114814	0.06741897
life span: bulb	-0.371592687	-0.299478905
life span: deciduous	-2.582107352	0.097460576
life span: erect	0.186993902	0.3400727

Plant attribute	Component 1	Component 2
life span: sub-shrub	0.43362992	1.485324458
life span: tuber	0.273148744	-1.692845515
life span: tuft	0.396227282	-1.400937907
life span: vernal	0.582689243	1.017071338
L Ellenberg indicator value	0.520342904	0.003029929
N Ellenberg indicatore value	-0.191625612	-0.040291095
no appendages: no	-0.159619455	-0.741371249
no appendages: yes	0.152876711	0.710053786
elongated appendages: no	-0.116078391	0.511635288
elongated appendages: yes	0.224190148	-0.988156274
hooks: no	-0.020555086	0.038818879
hooks: yes	0.303782917	-0.573702892
flat appendages: no	0.052347686	0.156339189
flat appendages: yes	-0.278816666	-0.832701011
balloon structure: no	-0.050844132	0.423491633

Plant attribute	**Component 1**	**Component 2**
life span: estival	0.524974842	0.324544298
life span: evergreen	-1.280756404	0.899356666
life span: rhizome	0.266959941	-1.120722375
life span: rosette	0.176903057	0.096172041
life span: shrub	-0.595288209	1.024398209
life span: stolon	0.298016324	0.204918842
mucilage: no	-0.056023296	-0.05975299
mucilage: yes	0.603881186	0.644083959
seed production: 1-10	0.030886297	-1.244514314
seed production: 10-100	0.176402479	-0.178074046
seed production: 100-1000	-0.026343365	-0.031096583
seed production: 1000-10000	0.202836167	0.20303798
seed production: >10000	-0.323745768	0.013263834

Plant attribute	**Component 1**	**Component 2**
balloon structure: yes	0.149032522	-1.241323705
pulp: no	0.127150094	-0.038351238
pulp: yes	-1.644644678	0.496060655
elaiosome: no	-0.014746965	-0.062610925
elaiosome: yes	0.20300138	0.861879331
releasing height	-0.767986362	-0.065330317
seed length	-0.669601407	-0.236148358
seed shape (Vs)	0.075212502	-0.498585158
seed mass	-0.527246318	0.017813513
seedbank longevity index (SLI)	0.399076556	0.154524676

(B) Montargis

Plant attribute	Component 1	Component 2
group: dicot	-0.072670775	0.348314458
group: monocot	0.292668808	-1.402775427
habitat: forest	-1.629725306	-0.222967791
habitat: hygrophile	0.284959207	-0.504124875
habitat: non-forest	0.625376327	-0.034453162
habitat: peri-forest	-0.143935929	0.305154009
life form: chamaephyte	-0.201685398	0.885024467
life form: geophyte	0.111353092	-0.980878356
life form: hemicryptophyte	0.327122552	-0.092182427
life form: phanerophyte	-2.078988924	0.283823154
life form: therophyte	0.711986905	0.398027449
life span: bisannual	0.348779651	-0.019135348
life span: bulb	-0.459649276	-0.421344302

Plant attribute	Component 1	Component 2
life span: deciduous	-2.079458781	0.243150284
life span: erect	0.310395341	0.376172607
life span: estival	0.708467769	0.329398578
life span: evergreen	-1.54428607	0.649252285
life span: rhizome	0.232634269	-1.060197334
life span: rosette	0.293915328	0.084264821
life span: shrub	-0.703116332	0.772321646
life span: stolon	0.369155156	0.150072218
life span: sub-shrub	0.49482337	0.984615175
life span: tuber	0.247603559	-1.726045411
life span: tuft	0.364494658	-1.506146427
life span: vernal	0.749591639	1.131380842

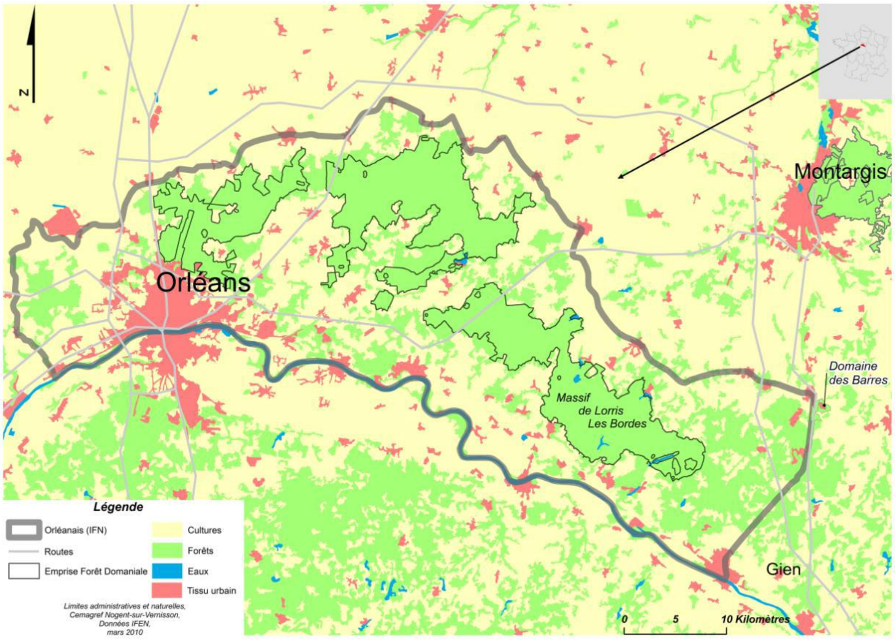
Plant attribute	**Component 1**	**Component 2**
L Ellenberg indicator value	0.516829123	0.01490327
N Ellenberg indicatore value	-0.102692716	-0.008665989
no appendages: no	-0.233046666	-0.661040678
no appendages: yes	0.243651565	0.691121646
elongated appendages: no	-0.086922701	0.500819205
elongated appendages: yes	0.178999365	-1.031333799
hooks: no	-0.004609915	0.0503783
hooks: yes	0.057379729	-0.627059991
flat appendages: no	0.066028474	0.150656302
flat appendages: yes	-0.35042643	-0.799563383
balloon structure: no	-0.038055168	0.401446526
balloon structure: yes	0.122086916	-1.287903092
pulp: no	0.166889781	-0.074089201
pulp: yes	-1.355971449	0.601971194

Plant attribute	**Component 1**	**Component 2**
elaiosome: no	-0.030701781	-0.065584069
elaiosome: yes	0.331643356	0.708444922
mucilage: no	-0.065936934	-0.056965585
mucilage: yes	0.7252396	0.626563835
seed production: 1-10	-0.346073709	-1.338608112
seed production: 10-100	0.180752654	-0.236590098
seed production: 100-1000	-0.061247133	-0.061267505
seed production: 1000-10000	0.341984226	0.264738779
seed production: >10000	-0.370295045	0.051786231
releasing height	-0.765053739	-0.028461827
seed length	-0.695826419	-0.185985155
seed shape (Vs)	0.073296158	-0.519323644
seed mass	-0.466893442	0.064162994
seedbank longevity index (SLI)	0.482632258	0.182415904

Résultats supplémentaires, non présentés dans l'article :

- Le nombre de graines qui ont germé est relativement faible. Nous avons cependant constaté que la flore dispersée est plus rudérale[1] sur le massif de Montargis que sur celui de Lorris. De plus, à Montargis, cette flore rudérale est majoritairement composée d'espèces commensales des cultures, aux dépends d'espèces de milieux sub-naturels. Dans la mesure où nous avons récolté les fèces à des dates similaires pour les deux massifs, et où nous les avons traitées de la même façon, il est peu probable que cette différence entre massifs soit due aux aléas de l'expérimentation. Les massifs de Lorris et de Montargis diffèrent par leur taille et par les habitats qui les entourent. Notamment, le massif de Montargis est accolé à un habitat urbain (voir carte ci-après). On peut ainsi supposer que la composition des espèces dispersées varie selon la position de l'habitat forestier dans le paysage.

- De plus, le sanglier, qui contribue fortement à la dispersion d'espèces commensales des cultures (espèces généralistes), peut enrichir les communautés végétales forestières. En revanche, si cet apport de plantes généralistes conduit à la suppression des plantes spécialistes forestières, le sanglier pourrait accentuer l'effet de la fragmentation et de l'anthropisation forestière sur l'homogénéisation taxonomique ou fonctionnelle des communautés végétales forestières.



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[1] *Les plantes rudérales poussent spontanément dans les friches, dans les décombres, le long des chemins et souvent à proximité des zones urbaines.*

II. A l’échelle de l’Europe : épizoochorie et endozoochorie

Après avoir testé l’effet filtre de l’endozoochorie à l’échelle d’un département, nous proposons de généraliser nos résultats et de tester l’effet de filtre écologique du processus de dispersion zoochore à l’échelle de l’Europe, en réalisant une méta-analyse. Nous avons considéré à la fois l’endozoochorie et l’épizoochorie, en distinguant l’épizoochorie *via* le pelage de celle *via* les sabots des animaux, et à la fois les ongulés sauvages et domestiques. Nous avons retenu 52 études européennes, pour lesquelles nous avons estimé les pourcentages de variations de 10 traits, moyennés à l’échelle des communautés, afin de comparer la flore dispersée à la flore non dispersée.

Les plantes nitrophiles, de milieux ouverts, à banque de graines persistante et de forme allongée sont plus fréquemment dispersées, quel que soit le mode de dispersion considéré. A l’inverse, les fruits à pulpe ne semblent pas dispersés par les ongulés. L’endozoochorie tend à légèrement sélectionner les graines possédant de longs appendices ; alors que l’épizoochorie filtre positivement les espèces pour lesquelles les graines sont disposées à des hauteurs relativement élevées, ainsi que les graines à appendices allongés ou à crochets pour la dispersion *via* le pelage, et les graines légères et sans crochets pour la dispersion *via* les sabots. Nous mettons en évidence une différence de sélectivité du filtre entre les modes de dispersion : l’épizoochorie, qu’elle ait lieu *via* le pelage ou les sabots, explique plus de 75 % de la variation entre les traits des communautés dispersées et non dispersées, alors que l’endozoochorie en explique moins de 25 %.

Ces résultats démontrent que l’effet filtre de la zoochorie varie selon le mode de dispersion considéré, et confirment que l’endozoochorie est un processus qui exerce un filtre peu sélectif sur les traits des espèces.

Article 4

Seed dispersal by ungulates as an ecological filter: a trait-based meta-analysis

Albert A., Auffret A., Cosyns E., Cousins S., D'hondt B., Eichberg C., Eycott A., Heinken T., Hoffmann M., Jaroszewicz B., Malo J. E., Mårell A., Mouissie M., Pakeman R., **Picard M.**, Plue J., Poschlod P., Provoost S., Schulze K. and Baltzinger C.

Soumis à *Oikos*

Abstract

Plant communities are often dispersal-limited and zoochory can be an efficient mechanism for plants to colonize new patches of potentially suitable habitat. We predicted that seed dispersal by ungulates acts as an ecological filter— which differentially affects individuals according to their characteristics and shapes species assemblages—and that the filter varies according to the dispersal mechanism (endozoochory, fur-epizoochory and hoof-epizoochory). We conducted two-step individual participant data meta-analyses of 52 studies on plant dispersal by ungulates in fragmented landscapes, comparing eight plant traits and two habitat indicators between dispersed and non-dispersed plants. We found that ungulates dispersed at least 44% of the available plant species. Moreover, some plant traits and habitat indicators increased the likelihood for plant of being dispersed. Persistent or nitrophilous plant species from open habitats or bearing dry or elongated diaspores were more likely to be dispersed by ungulates, whatever the dispersal mechanism. In addition, endozoochory was more likely for diaspores bearing elongated appendages whereas epizoochory was more likely for diaspores released relatively high in vegetation. Hoof-epizoochory was more likely for light diaspores without hooked appendages. Fur-epizoochory was more likely for diaspores with appendages, particularly elongated or hooked ones. We thus observed a gradient of filtering effect among the three dispersal mechanisms. Endozoochory had an effect of rather weak intensity (impacting six plant characteristics with variations between ungulate-dispersed and non-dispersed plant species mostly below 25%), whereas hoof-epizoochory had a stronger effect (eight characteristics included five ones with above 75% variation), and fur-epizoochory an even stronger one (nine characteristics included six ones with above 75% variation). Our results demonstrate that seed dispersal by ungulates is an ecological filter whose intensity varies according to the dispersal mechanism considered. Ungulates can thus play a key role in plant community dynamics and have implications for plant spatial distribution patterns at multiple scales.

INTRODUCTION

The limitations of diaspore supply strongly influence local patterns of species composition, diversity and species' local and regional population persistence (Cornell and Lawton 1992, Eriksson 1993, MacArthur and Wilson 1967). Seed dispersal can therefore be seen as a potential ecological filter, along with abiotic limitations and *in situ* species interactions (Brooker et al. 2008, Díaz et al. 1998, Marteinsdóttir and Eriksson 2013, Myers and Harms 2011). Indeed, dispersal limitation often outweighs abiotic limitations to establishment (Butaye et al. 2001, Tofts and Silvertown 2002, Zobel et al. 2000). According to George & Bazzaz (1999), 'an ecological filter "sifts" through the initial seed populations of a whole community and determines emergent community characteristics such as species composition, productivity, and spatial distribution patterns'. Thus, if a particular dispersal mechanism is 'available' for only certain groups of species then we can consider that dispersal mechanism an ecological filter. The presence or absence of specific dispersal vectors could therefore influence the characteristics of a range-limited pool of species (i.e. species able to reach the community in ecological time, regardless of their habitat preferences; Gramling 2006).

Ungulates interfere at different stages of the plant life cycle (Olff & Ritchie 1998) and more specifically if we focus on the successive phases of the dispersal process: emigration, transfer and settlement. First, habitat choice restrains the plant species that ungulates come across, and the selective foraging behaviour of ungulates further determines the seeds ingested (the emigration phase). Secondly, ungulates may transport plants over variable distances depending on the dispersal mechanism concerned (the transfer phase). For endozoochory, seed retention time may depend on the diet (Clauss, Lechner-Doll & Streich 2002; Cosyns & Hoffmann 2005) and ungulate body mass (Clauss et al. 2003; Weyenberg, Sales & Janssens 2006) while fur quality may determine seed retention time for epizoochory (Couvreur, Verheyen & Hermy 2005). Whatever the mechanism, ungulates are considered long-distance dispersal agents (i.e. > 100 m; Cain, Milligan & Strand 2000), transporting plant species, usually across supra-kilometric distances (Fischer, Poschlod & Beinlich 1996; Mouissie et al. 2005b). Finally, ungulates are also viewed as powerful ecological engineers that modify the environment the diaspores are released in, thereby affecting plant establishment (the settlement phase). They promote nitrogen cycling through localized urine and feces deposition (Hobbs 1996, Steinauer and Collins 1995) and they create small-scale disturbances through trampling, wallowing and grubbing activities (Faust et al. 2011, Rosenthal et al. 2012). These effects may create regeneration niches (Bakker and Olff 2003), help incorporate diaspores into the soil (Eichberg et al. 2005, Heinken et al. 2006), and stimulate seed bank germination (Beyschlag et al. 2008).

Here, using data from meta-analyses of 52 studies, we ask whether dispersal by ungulates affects plants randomly or if their dispersal role is limited to particular plant species or functional groups. The regional distribution patterns of such plants could hence vary according to ungulate mobility (Boulanger et al. 2011).

Although many researchers have investigated the potential role of ungulates in dispersing seeds, surprisingly few of them have quantitatively compared dispersed plant species with the species available in the disperser's home range (e.g. Couvreur et al. 2005a, Heinken et al. 2002, Picard and Baltzinger 2012), despite often regarding seed dispersal as a selective process. This type of comparison is necessary to distinguish actual plant selection from consumption and subsequent dispersal according simply to plant availability on the study site (Pakeman and Eastwood 2013). Even fewer of these comparisons incorporated plant traits (Bakker et al. 2008, Heinken and Raudnitschka 2002, Picard and Baltzinger 2012), though trait-based approaches could enable generalizations and thus provide insights into ecosystem functioning (Garnier et al. 2004, Kotze and O'Hara 2003).

Several studies, most of them carried out in Europe, have underlined that seed dispersal was specific to the ungulate species considered, i.e. different ungulate species dispersed plants bearing different traits (Albert et al. submitted, Couvreur et al. 2005b, Mouissie et al. 2005c). We can thus hypothesize that plant species dispersed by ungulates are not a random sample drawn from the plant species available at the study site. In other words, seed dispersal by ungulates probably acts as an ecological filter based on specific plant characteristics. It should also vary among the three dispersal mechanisms ungulates mediate: endozoochory, fur-epizoochory and hoof-epizoochory (Albert et al. submitted, Couvreur et al. 2005a, Picard and Baltzinger 2012). In particular, seed survival after endozoochory should be favored by a low diaspore mass, a rounded diaspore shape, and was found to relate also with the ability to form persistent seed banks (Cosyns and Hoffmann 2005, Mouissie et al. 2005b, Pakeman et al. 2002). With respect to fur-epizoochory, the probability of dispersal would be increased by a diaspore releasing height from 60 to 200 cm, a low diaspore mass, an elongated shape, and the presence of hooked or elongated appendages (Couvreur et al. 2004b, Fischer et al. 1996, Römermann et al. 2005, Tackenberg et al. 2006). Finally, few authors have studied hoof-epizoochory and associated trait-based hypotheses are rather scarce. However, we can logically predict that the probability of hoof-epizoochory would be increased for relatively light, round and persistent diaspores (see Table 1 for specific predictions for each trait and each dispersal mechanism based on the literature). In the present study, we first looked for the main differences between ungulate-dispersed and non-dispersed plant species, all animals and dispersal mechanisms combined. Further, we performed two-step individual participant data meta-analyses (Riley et al. 2009) to determine, through a trait-based approach, how ecological filtering varies according to each of the three zoochorous dispersal mechanisms analyzed.

MATERIALS AND METHODS

Data selection

We based our selection of studies on a recent systematic literature review that aimed to predict ungulate disperser traits within Europe from basic traits of dispersed plants, either through epi- or endozoochory; see Albert et al. (submitted) for the detailed protocol. Among the 74 papers that matched the search criteria, only three papers compared the traits between dispersed and non-dispersed species. We scanned the 74 papers to find authors in possession of sample-level data on both seed dispersal by ungulates and vegetation composition in their study area. In total, we contacted 22 European researchers of which 15 provided published (from 18 papers) and unpublished data sets. In most cases, single papers or unpublished data sets comprised several comparisons with respect to either ungulate species, type of zoochory or site. As we considered an individual study to be a comparison between dispersed and non-dispersed plant species for a given ungulate species and type of zoochory at a particular site, we identified 52 studies (comparisons) among the data sets. We only focused on the emigration phase of the dispersal process, taking into account neither the transfer nor the establishment phases.

We included studies of domestic and wild ungulates carried out in semi-natural terrestrial ecosystems. We considered the dung, fur or mud on the hooves sample—as defined by the article authors—as the dispersal sampling unit. As analyses were based on standardized relative abundances (see below and box 1), differences such as dung sample unit (liter, gram, single dropping) were not expected to influence the outcome. For vegetation surveys, we considered the plot where plant species abundance was measured as the sampling unit, and both estimates of the percentage cover or species frequency counts were accepted. Although the number and size of samples was highly variable across studies, we considered the data to be representative of dispersed and non-dispersed species of the local flora in each study site, as all studies had rigorous sampling protocols at an equivalent spatial scale for both data sources (cf. Material and Methods of each study; see Supplementary material Appendix 1 Table A1 in Supporting Information).

We gathered data from the 52 individual studies (Supplementary material Appendix 1 Table A1), comprising 34 studies on endozoochory, 11 on fur-epizoochory, and seven on hoof-epizoochory. About half of the studies were performed in open habitat types ($N = 27$), mainly grasslands, while the remaining half were performed in forest-dominated habitats ($N = 18$) or in study sites with a mixture of habitat types ($N = 7$) (Supplementary material Appendix 1 Table A1). Seed dispersal data were obtained for three domestic and six wild ungulate species. They encompassed animals with various digestion systems, diets and morphological characteristics (Table 2), with short to long and straight to curly hair. *Ovis aries* (sheep) was the most commonly studied ungulate species.

Having access to raw data, we were able to perform two-step individual participant data meta-analyses (IDP-MA ; Riley et al. 2009). Compared to the more commonly used aggregate data approach, based on summary results, IDP-MA offers numerous advantages. These include the standardization of statistical analyses in each study, the direct derivation of the desired summary results—independent of study reporting and significance—and the meta-analysis for specific subgroups of participants across studies (Riley et al. 2009).

Plant traits and habitat indicators

We used the Taxonomic Name Resolution Service (Boyle et al. 2012, The Taxonomic Name Resolution Service 2012) and the Plant List (2010)—complying with the Angiosperm Phylogeny Group taxonomy—to standardize plant names across studies. We gathered data on easily-measurable plant and diaspore traits as well as habitat indicators related to seed dispersal, hereafter called plant characteristics, using several trait databases (see Appendix B in Albert et al. (submitted) for the detailed protocol). We standardized the traits according to LEDA trait standards (Knevel et al. 2005). We selected ten plant characteristics: two habitat indicators : [1] plant habitat openness (open, forest) as well as [2] Ellenberg indicator value for nitrogen (Ellenberg et al. 2001); and eight traits: [3] diaspore releasing height, [4] diaspore mass, [5] diaspore shape (variance in dimensions; Bekker et al. 1998), [6] seed bank longevity (seed bank longevity index; Thompson et al. 1998), and diaspore morphology traits such as [7] presence of [8] elongated and/or [9] hooked appendage(s), and [10] presence of pulp (Supplementary material Appendix 1 Table A2). 'Open' habitats included grasslands, scrublands, open wetlands and cropland, while 'forest' habitats included forest and forested wetlands. We were aware that plant species' optima for abiotic resources vary across large biogeographical gradients and therefore that Ellenberg indicator values for nitrogen may not be relevant to all study sites. However, 49 out of 52 studies were carried out in countries with a temperate, seasonal climate. Thus, we assumed that the original values proposed by Ellenberg et al. (2001) were reasonable proxies for the entire data set. We considered the diaspore as the dispersal unit (either as an infructescence, a fruit (entire or part) or a seed).

Data preparation

We defined species independently at the study level as being dispersed or non-dispersed (i.e. a species could be dispersed in one study and not dispersed in another). We considered dispersed plant species as those species for which at least one seed had been observed among dispersal samples at a study site. Non-dispersed plant species were identified by subtracting dispersed plant species from the species list of vegetation composition data in the study area. We also corrected for the differences related to the type of raw data used for dispersed and non-dispersed data (Box 1). The abundance measure was the number of seeds for the former, while percentage cover or frequency counts of plant species for the latter. As a consequence of the seed mass:seed number trade-off, small-seeded species would be expected to be over-represented compared to large ones in the dispersal data set compared to the non-dispersal data set. However, higher numbers of small seeds in dung samples do not necessarily appear to be related to a morphological advantage, but rather to their higher number in the vegetation (Bruun and Poschlod 2006). To take varying seed production into account, we weighted abundance in dispersal samples by seed mass. Thus, we converted seed abundance to seed biomass. Moreover, we used relative data so that values for dispersed and non-dispersed data ranged from zero to one. We also weighted these relative abundances in samples by the relative abundance of the plant species within vegetation (Lavorel et al. 2008, Pakeman et al. 2008). Next, we multiplied these relative weighted abundances to the plant characteristics' values of each species in each sample (see Box 1 for detailed formulae). Finally, we computed the mean plant characteristic value for each sample, which is thus the community-weighted mean. We standardized the data and calculated the mean and standard deviation of dispersed and non-dispersed data sets for each study.

Box 1. Steps followed for the standardized weighting of plant characteristic values

1) Relative weighted abundance of the species *i* in a sample in a study:

for dispersed species: or non-dispersed species:

$$RAS_i = \frac{AS_i \text{ x } mass_i}{\sum_{i=1}^{n}(AS_i \text{ x } mass_i)} \qquad RAS_i = \frac{AS_i}{\sum_{i=1}^{n}(AS_i)}$$

where *n* represents the number of species and AS_i the abundance of *i* in the sample measured in number of seeds for dispersed species, and percentage cover or frequency counts for non-dispersed species.

2) Relative abundance of the species *i* in the vegetation of the study:

$$RAV_i = \frac{AV_i}{\sum_{i=1}^{n}(AV_i)}$$

where AV_i represents the abundance of the species *i* in the vegetation of the study.

3) Relative abundance of the species *i*: $RA_i = \frac{RAS_i}{RAV_i}$

4) Weighted trait value = RA_i x characteristic value

Statistical analysis

We tested whether zoochory through ungulates acts as an ecological filter by comparing the characteristic signature for dispersed and non-dispersed plants. Analyses were carried out using R v 3.0.1 (R Development Core Team 2013).

Main characteristic differences between dispersed and non-dispersed plant species

First, we compared the characteristics of dispersed and non-dispersed plant species for all dispersal mechanisms and individual studies combined, using a Mann Whitney-*U* test for continuous data and *G*-test for frequencies. We also performed a Hill and Smith principal component analysis (PCA_{hs}; Hill and Smith 1976) of the plant species-characteristics matrix, for all dispersal mechanisms and studies combined. We could thus test, at the scale of the guild of ungulates, for all zoochorous mechanisms considered, and without weighting, whether characteristics for dispersed plant species differed from those of non-dispersed ones. We thereby tested the overall potential of ungulates to disperse seeds within studied vegetation communities and whether ungulate zoochory involves a small or large proportion of plant species in the given plant species-characteristics space. We used the functions *dudi.hillsmith* and *s.class* in the package *ade4* (Dray and Dufour 2007).

Ecological filtering variation according to dispersal mechanisms

Based on the weighted characteristic values, we calculated the log response ratio (LRR) effect size which gives an estimate of the percentage of variation in species traits between dispersed and non-dispersed plant species (Gurevitch and Hedges 2001). Thus, a positive effect size means that a specific characteristic has a higher value for dispersed than for non-dispersed species. We used the function *escalc* in the package *metaphor* (Viechtbauer 2010). The ‘ROM’ measure option computes the log transformed Ratio Of Means (i.e. LRR). We added a constant to every mean to make them all positive and enable the computation.

After that, we performed meta-analyses, one per plant characteristic, on the calculated LRR values to test whether particular characteristics increased or decreased the probability for seeds being dispersed by ungulates. We built meta-analysis models with random effects (REMA) using the effect sizes as response variables and taking the restricted maximum-likelihood estimator (REML) as the heterogeneity estimator since it is approximately unbiased and quite efficient (Viechtbauer 2005). We rejected the null hypothesis (i.e. dispersed and non-dispersed species have similar characteristics) if the 95% confidence interval (CI) did not overlap zero. We used the function *rma* in the package *metaphor* (Viechtbauer 2010).

Next, to highlight differences among the three dispersal mechanisms considered (endozoochory, fur-epizoochory and hoof-epizoochory), we added the dispersal mechanism as a categorical moderator (REMAM). As ecological data are often subject to uncontrolled variations (Pullin and Stewart 2006), we assumed that the study effect sizes had been sampled from a distribution of effect sizes. The between group heterogeneity ($Q_{between}$) and residual heterogeneity (Q_{within}) were tested against a chi-square distribution to respectively highlight a difference among moderator categories (i.e. dispersal mechanisms) and the potential presence of variables not considered in the model. Finally, to improve our understanding of some results, we also checked for correlations between some plant traits. We used the function *rcorr* in the package *Hmisc* (Harrell Jr 2013).

RESULTS

Descriptive results of the data set

In total, the study material encompassed 635 plant species (76 plant families) where Asteraceae (80 species) and Poaceae (78 species) were the most commonly represented plant families (Supplementary material Appendix 1 Table A2). Among these species, 278 species (44%) were observed to be dispersed at least once by endozoochory (*N* = 248), fur-epizoochory (*N* = 62) or hoof-epizoochory (*N* = 41), and 42 species were always dispersed whereas 357 were never observed to be dispersed. The average number of plant species per study was 92 ± 51 species (mean ± SD; range = 16-218) of which on average 29 ± 19% (range = 3-75%) were found to be dispersed by ungulates (Table 3).

Main characteristic differences between dispersed and non-dispersed plant species

Dispersed plant species had a lower releasing height, lower diaspore mass and were able to build more persistent seed banks than non-dispersed species (Fig. 1). However, they were similar according to every other studied characteristic. Indeed, they showed similar nitrophily and diaspore shape (Fig. 1), and comparing dispersed to non-dispersed plant species, 93% *vs* 85 % were from open habitats (*G*-test, *P* = 0.396), 50% *vs* 53% had an appendage (*P* = 0.675)—of which 84% *vs* 79% had an elongated one (*P* = 0.579) and 12% vs 9% a hooked one (*P* = 0.352)—and 4% *vs* 9% produced fleshy fruits (*P* = 0.041).

The PCA$_{hs}$ of plant species—pooling all dispersal mechanisms and individual studies together— revealed a similar pattern to that suggested by the comparison of dispersed and non-dispersed species. It showed no clear difference in characteristics between dispersed and non-dispersed species, both co-occurring in all regions of the PCA$_{hs}$ scatter-plot (Fig. 2).

However, we observed a similar clustering for both dispersed and non-dispersed species, according to the first principal axis. The first two principal components explained 42% of the total inertia. The first axis was positively correlated with diaspore shape (loading: 0.61), the absence of appendage (0.71) and the presence of an elongated appendage (0.67). The second axis was positively correlated with the diaspore releasing height (0.44) and plants from open habitats (0.42).

Ecological filtering variation according to dispersal mechanisms

The REMA showed that, once weighted by abundance, dispersed and non-dispersed plant species differed according to their characteristics, as indicated by the log response ratio effect sizes calculated for the entire study set (Table 4). Plants dispersed by ungulates were mainly species from open habitats, nitrophilous, with high diaspore releasing heights, low diaspore mass, persistent and elongated diaspores with elongated appendages, but no pulp. Seven of these characteristics showed a variation above 25% between ungulate-dispersed and non-dispersed species.

However, the REMAM also highlighted variations among dispersal mechanisms (Fig. 3). Six characteristics predicted endozoochory, whereas nine and eight characteristics were predictors for fur- and hoof-epizoochory, respectively. Moreover, the variations between traits of dispersed and non-dispersed plant species were mostly below 25% (ranging from 16 to 40%) for endozoochory whereas they were mostly above 75% for fur-epizoochory (44-102%) and hoof-epizoochory (27-130%). Thus, the filtering effect of the various dispersal mechanisms on a given trait could be highly variable, e.g. endozoochory induced 16% variation in diaspore shape between dispersed and non-dispersed plant species, whereas fur-epizoochory and hoof-epizoochory induced 92% and 129% variation respectively (Fig.3). The test for residual heterogeneity (Q_{within}) was significant for every characteristic ($P < 0.001$).

Longevity was highly positively correlated with diaspore shape ($r = 0.65$, $P < 0.001$) and mass ($r = 0.07$, $P < 0.001$). Moreover, the presence of pulp was highly positively correlated with diaspore mass ($r = 0.38$, $P < 0.001$).

DISCUSSION

Our 52-study analysis comparing ungulate-dispersed with non-dispersed plant species does support the prediction that ungulate seed dispersal acts as an ecological filter. However, we also stress that the magnitude of the filtering effect varies according to the dispersal mechanism considered (i.e. among endozoochory, fur-epizoochory, and hoof-epizoochory). Some plant characteristics clearly increased the likelihood of being dispersed through endozoochory and epizoochory (via fur and hoof).

When all dispersal mechanisms and studies were pooled together (PCA_{hs}, Figs 1 and 2), there was no clear difference between ungulate-dispersed species and non-dispersed species. Therefore, it seems as though almost any plant species has the opportunity of being picked up and carried out by an ungulate. This result highlights a complementarity among dispersal mechanisms (according to the meta-analyses results) and probably among ungulate species (Albert et al. submitted). Thus a guild of various ungulate species could help to restore a plant community, whereas a single ungulate species could filter some plant species. However, this does not tell us how far a species is carried out through endozoochory compared to fur-epizoochory or hoof-epizoochory. Indeed, dispersal distances depend on specific retention time inside or outside the animal, which would probably induce highly different spatial distribution patterns between endozoochory and epizoochory.

Through our meta-analyses, we showed that ungulates were seemingly able to endozoochorously transport many kinds of diaspore away from parent plants. This represents an important pre-requisite for successful seed dispersal, limiting density-dependent responses of predators and pathogens, and allowing colonization of new habitats (Howe and Smallwood 1982). The individual-participant data meta-analysis was therefore useful in distinguishing enhanced dispersal from simply opportunistic dispersal. Indeed, our meta-analyses showed that some characteristics may either increase or decrease the probability for seeds to be dispersed according to the dispersal mechanisms considered (Fig. 3). One striking result was the difference in magnitude effect between endozoochory and epizoochory according to the studied characteristics. We may thus observe a gradient of filtering effect among the three dispersal mechanisms: an effect of weak intensity for endozoochory (impacting six plant characteristics with variations between ungulate-dispersed and non-dispersed plant species being mostly below 25%), a stronger effect for hoof-epizoochory (eight characteristics included five ones with above 75% variation), and an even stronger effect for fur-epizoochory (nine characteristics included six ones with above 75% variation). Thus epizoochory (via fur or hoof) appears more specialized (i.e. this is a stronger ecological filter) than endozoochory. This may have consequences on seedling establishment given variations related to each dispersal mechanism (e.g. retention time, spatial distribution pattern, secondary dispersal). Thus, more than distinguishing among ungulate species, it is necessary to distinguish among dispersal mechanisms. Moreover, given that we did not take into account the seedling establishment phase in our analysis, we can hypothesize that ecological filtering through ungulate seed dispersal might be stronger due to a multi-step process (trampling, secondary dispersal, germination etc.), and that the community species pool might be additionally modified by environmental filtering processes (e.g. drought stress).

Our meta-analyses secondarily allowed us to test predictions about the plant species characteristics related to seed dispersal by ungulates (Table 1). For endozoochory, our results were in line with seven predictions out of ten, although three results were not significant. We also validated nine predictions (one result being not significant) for fur-epizoochory, and six predictions (one being not significant) for hoof-epizoochory.

We observed several similarities among dispersal mechanisms in agreement with our predictions (Table 1). First, plant species from open habitats were more likely to be dispersed by ungulates. This is in accordance with results from previous studies (Eycott et al. 2007, Heinken and Raudnitschka 2002, Jaroszewicz et al. 2013, Panter and Dolman 2012).

Another similarity was that nitrophilous plants were more often dispersed by ungulates. The reason for this may be that herbivores are attracted by foliage with high nutrient value and consequently they are more likely to consume the seeds of such plants. This hypothesis can then be extended to epizoochory, whereby the presence of high quality foliage would increase the encounter rate between ungulates and diaspores, as was previously suggested by Couvreur et al. (2005a).

Plant species bearing elongated diaspores were more often dispersed by ungulates whatever the dispersal mechanism. This result was expected for fur-epizoochory. Ungulates were more likely to disperse via fur those diaspores with a shape increasing their adhesivity. Thus, elongated diaspores were frequently dispersed, because they may burrow deeply inside the ungulate's fur, thus improving their adhesion (Mouissie et al. 2005b, Pakeman et al. 2002). However, contrary to our predictions, elongated diaspores were also likely to be dispersed via endozoochory and hoof-epizoochory. This may be due to the over-representation of Asteraceae and Poaceae in the data set and also possibly due to the positive correlation observed between seed longevity and diaspore shape. This correlation was unexpected since rounded diaspores appear more likely to persist into the soil (Thompson et al. 1993). However, since we took into account the seed mass:seed number trade-off, we could expect differences between our result and those usually observed, as stated by Pakeman & Eastwood (2013).

Persistent species were more likely to be dispersed by ungulates via every dispersal mechanism. This result was expected for endozoochory and hoof-epizoochory, but not for fur-epizoochory. For endozoochory, Pakeman et al. (2002) hypothesized that seed adaptations to improve gut passage survival are similar to those required for persistence in the seed bank. Thus, the evolutionary forces which shaped seed bank persistence may have simultaneously pre-adapted species for gut survival. Ungulates were also likely to disperse via hooves plant species with a persistent seed bank; this was expected since the mud they transport likely contains diaspores from the seed bank (Table 1). This result highlights the important ecological role ungulates may have through trampling (Rosenthal et al. 2012). Indeed, by mixing the soil they may bring persistent species toward the soil surface and stimulate germination from the soil seed bank (Beyschlag et al. 2008). Contrary to what we expected, our results showed that species with a transient seed bank were unlikely to be dispersed via fur-epizoochory. By contrast, Couvreur et al. (2004a) showed that epizoochory was positively associated with species with a transient seed bank. They hypothesized that transient species are more susceptible to have developed traits allowing a spatial dispersal to offset their short temporal survival. Our contradictory result could be due to the highly positive correlation we observed between seed longevity and diaspore shape in our analysis.

A last similarity was that plants bearing fleshy fruits were the only ones unlikely to be dispersed by ungulates, whatever the considered mechanism. For endozoochory, this highlights the difference between the seed dispersal syndromes of herbivores and frugivores, such as many birds (Herrera 2002), although some fleshy-fruited species (e.g. *Rubus idaeus*) were reported to be dispersed by all members of an ungulate guild in a forest ecosystem

(Jaroszewicz et al. 2013). For epizoochory, this result was expected since fleshy fruits are usually too large and heavy to adhere to fur and under hooves (Heinken and Raudnitschka 2002). However, we also further observed differential filtering effects according to the dispersal mechanism considered.

Endozoochory

Despite the apparently weak filtering effect of endozoochory by ungulates (impacting six plant characteristics which varied from 16 to 40% between ungulate-dispersed and non-dispersed plant species, Fig. 3), 357 out of a total 635 species were never found to be dispersed. Non-morphological traits such as the level of chemical substances in plants can influence herbivory by changing the palatability and nutritional value of plants (Bonn 2004) and consequently reduce the probability of endozoochory. Moreover, dispersal sampling generally requires high sampling efforts to accurately detect infrequent species (Jaroszewicz et al. 2013), and intensifying efforts would probably reveal higher shares of dispersed species. This remark might be relevant for all dispersal mechanisms. Further, some plant species may have been present in dung samples, but by remaining dormant were not detected by the seedling emergence method used in most studies (Pakeman and Small 2009).

Fur-epizoochory

Highlighting the strong filtering effect of fur-epizoochory (impacting nine plant characteristics varying from 44 to 102% between ungulate-dispersed and non-dispersed plant species), we found, as expected (Table 1), that ungulates predominantly dispersed species through fur-epizoochory when they appear in open habitats, where plant species are probably more adapted to epizoochory than temperate forest plant species (Heinken and Raudnitschka 2002). However, we have to point out that, in our data set, ungulates known to disperse many seeds in their fur (such as sheep) were mainly studied in grasslands, which may have oriented the results towards plants from open habitats.

We could also confirm that ungulates were also very likely to externally disperse diaspores with a high releasing height. European ungulates are rather large herbivores with a shoulder height ranging from 50 to 180 cm that fits well with high diaspore releasing heights. This is also in accordance with the results of Fischer *et al*. (1996) showing that most diaspores dispersed by sheep had a releasing height above 60 cm. Indeed, diaspores are probably less likely to be retained in the lower-down, comparatively short and straight hair covering the shank of many ungulates' legs.

Furthermore, ungulates were more likely to disperse via fur those diaspores with a morphology increasing their adhesivity. Thus, diaspores with an appendage, particularly elongated and/or hooked one were more likely to be dispersed in the fur (Couvreur et al. 2004b, Heinken et al. 2006, Mouissie et al. 2005a).

Hoof-epizoochory

We showed that several plant characteristics influenced the likelihood of diaspores to be transported in hooves leading to a specific characteristic signature related to hoof-epizoochory, highlighting its strong filtering effect (eight characteristics varying from 27 to 130% between ungulate-dispersed and non-dispersed plant species). First, light diaspores were more likely to be dispersed via the ungulates' hooves. This result was expected according to the usual thinking that persistent diaspores are also relatively light (Thompson et al. 1993). However, in our study, we observed that persistent species had higher diaspore mass when corrected by seed mass, which is in accordance with some other studies (Pakeman and Eastwood 2013, Yu et al. 2007). In fact, small diaspores are probably more simply incorporated into the soil under the hooves and stay attached better.

We expected the presence and shape of appendages to have no impact on seed dispersal via hooves. Because it is mainly the mud substrate that allows the diaspores to adhere to the hooves, the presence of appendages on diaspores embedded into the mud should not confer any advantage in sticking onto the smooth hoof surface. Diaspores may also lose their appendages due to trampling or weathering.

Finally, diaspores released higher above the ground were more likely to be dispersed. Intuitively, one could think either that releasing height does not have any impact on seed dispersal via hooves, or that low-growing species from trampled areas are favored by hoof-epizoochory. However, this result may highlight some complementarity between dispersal mechanisms. Indeed, seeds releasing too high to be dispersed endozoochorously or epizoochorously via fur may fall and be secondarily dispersed via hooves.

Research gaps and implications for analyses of plant community dynamics

This meta-analysis was an opportunity to point out the lack of relevant information and several problems in seed dispersal studies on ungulates. First we highlighted the lack of studies on epizoochory, particularly hoof-epizoochory. However, we observed that epizoochory by ungulates was more likely to act as an ecological filter for plants bearing particular characteristics. Boulanger et al. (2011) already showed that this mechanism, more than endozoochory, could have important implications for plant colonization.

We hypothesized that ecological filtering through ungulate seed dispersal might be much stronger than what we observed through our data set, since effective seed dispersal also includes seedling establishment, a topic that we could not address with our data set. Indeed, in order to quantify the entire ecological filtering effect of ungulates, one also needs to take into account the fate of seeds, including phenomena such as diplochory (Vander Wall and Longland 2004), improvement of soil-seed contact (Faust et al. 2011), and post-dispersal predation (Janzen 1986, Manzano et al. 2010).

We observed that less than half of the available species were found to be dispersed by ungulates. However, the $\mathrm{PCA}_{\mathrm{hs}}$ showed that ungulates were able to disperse plant species bearing almost any traits. On the one hand, the reason of this apparent contradiction may be due to relatively low sampling efforts and relatively low diaspore presence of many species. We expect that many more dispersed species would have appeared with more extensive sampling and particularly with the study of several dispersal mechanisms on a given site. Performing seed feeding experiments (Cosyns et al. 2005b, D'hondt and Hoffmann 2011) and seed attachment experiments (Couvreur et al. 2004b) might reveal more insight in the potential of the rarer species to be dispersed by ungulates. On the other hand, the contradiction may be due to traits not taken into account in this analysis. For example, as endozoochory is associated with foraging, chemical content of plants—changing their taste, odor or palatability—may influence their chances to be consumed by animals and dispersed. However, chemical traits of plants were not considered in this study because such data were not available. Additionally, seed anatomical traits (e.g. thickness and/or impermeability of the seed coat) might also affect potential endozoochorous dispersal success (e.g. D’hondt et al. 2010).

The test for residual heterogeneity was significant for every characteristic, possibly indicating that other moderators not considered in the model were influencing dispersal. For example, it would have been interesting to use the ungulate species or even some ungulate traits (e.g. diet, body mass, hair curliness) as moderators since we know that seed dispersal differs among ungulates (Albert et al. submitted, Couvreur et al. 2005b, Mouissie et al. 2005c). However, sample size for most ungulate species would have been too small and strongly reduced the statistical power of our models.

When comparing species dispersed to species present in the vegetation, we realized that many species were dispersed without being detected in the vegetation samples. It may highlight either a bias—the vegetation data being not representative of the ungulates' home range—or long-distance seed dispersal events or it may highlight the multistep aspect of colonization—many seeds and their seedlings perish during post-dispersal processes, failing to establish. This shows the necessity to sample vegetation on a wide area around the dispersers' home range, and particularly to include a representative sample of the regional species pool.

Further, we observed a clustering in the $\mathrm{PCA}_{\mathrm{hs}}$, possibly due to differences among plant species characteristics according to studies performed in different habitats (open, forest and mosaic habitats) or grouped in different European regions. This pattern may highlight the need for research in a wider range of sites.

We also realized the high variation among the protocols used to study seed dispersal. We urge researchers to define a standardized protocol (with an exhaustive list of the important data to collect and make available) and guidelines that could be commonly used. We particularly recommend data on vegetation to be always collected in addition to dispersal data and encourage the use of common sampling units.

Finally, to better understand the magnitude of ungulate seed dispersal as an ecological filter, future research should have a stronger integrative approach. All three dispersal mechanisms should be investigated for several ungulate species at the same sites to allow comparisons among dispersal mechanisms and dispersal vectors. Thus, one could i) quantify the complementarity among dispersal mechanisms, ii) analyze the similarity between emerging plant assemblages, iii) measure the net effect of each ungulate species on the local plant community, and iv) point out the individual role of ungulate species.

Conclusions

Our results demonstrated that different ungulate seed dispersal mechanisms can be considered as different ecological filters. Ungulates were found to disperse 44% of all the species available in the vegetation, indicating that seeds from a significant proportion of the regional species pool can be transported by ungulates. While several characteristics were related to ungulate epizoochory, the weak filtering effect of endozoochory on plant species underlines the potential contribution that ungulates can deliver to seed dispersal and vegetation dynamics. Our results should thus be seen in a wider perspective whereby plants do not rely on a single type of dispersal or a single vector (as illustrated in some very strong mutualistic interactions), but rather they can be dispersed in ways in which they are not apparently adapted, increasing the chances of successful dispersal for both long- and short-distances. Ungulate seed dispersal may therefore be an important component in understanding plant community dynamics at multiple spatial scales.

We further showed that particular characteristics affect the chances of seeds to be transported by ungulates, and that the association between characteristics and dispersal depends on the type of zoochory. Thus, we confirmed known relationships between morphological adaptations to fur-epizoochory and enhanced chances for seed dispersal by ungulates, as well as between seed bank persistence and seed survival just after dispersal.

Finally, we showed that a high proportion of available plant species had at least a minimal likelihood of being dispersed by ungulates, probably over long distances. Along with the diversity that ungulate species show with regard to their habitat and diet preferences, and natural and managed range sizes, this indicates that ungulates probably play a key role in plant community dynamics in various ecosystems and may act as dynamic ecological corridors for plants in changing landscapes. Particularly in human-dominated landscapes, often with highly fragmented habitat patches, ungulates could be useful tools for restoring plant diversity through seed dispersal (Cosyns et al. 2005a, Couvreur et al. 2004a, Wessels-de Wit and Schwabe 2010). As climate and land-use changes threaten a large number of plant populations (Thuiller et al. 2005, Walther et al. 2002), seed dispersal is a key process in assuring the colonization and genetic exchange abilities of plant species (Higgins and Richardson 1999, McConkey et al. 2012) because species with low adaptability will only survive if they are able to disperse into new and sometimes distant suitable habitat patches.

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TABLES

Table 1. Predictions based on the literature for each dispersal mechanism (endozoochory, fur-epizoochory and hoof-epizoochory), comparing the plant characteristics used in the meta-analysis for dispersed and non-dispersed plant species. + / - means a positive / negative selection is expected for dispersed compared to non-dispersed plant species. 0 means there is no selection expected.

Plant characteristics	Endozoochory		Fur-epizoochory		Hoof-epizoochory	
Open habitat	+	ungulates disperse mainly grassland species [1,2]	+	grassland species more adapted to epizoochory [3]	0	function of habitat use
Nitrophily	+	ungulates look for highly nutritional fodder [4]	+/0	encounter rate higher with high nutritional fodder [4,5]	+/0	encounter rate higher with high nutritional fodder [4,5]
Diaspore releasing height	-/0	most ungulates feed on the lowest vegetation layer (table 2)	+	encounter rate higher with diaspores at flank height [6,7,8]	0	every diaspore falls on the ground [9]
Diaspore mass	-/0	light diaspores more prone to be defecated undamaged [10,11,12]	-/0	better attachment of light diaspores [13,14]	-	light diaspores more prone to remain attached to the hooves
Diaspore shape	-	rounded diaspores more prone to be defecated undamaged [11]	+	elongated diaspores incorporate deeply inside ungulates' fur	-	rounded diaspores more likely to persist into the soil [15]
Seed bank longevity	+	convergence to survive digestion and persist in seed bank [16]	-	epizoochory associated with transient species [17]	+	any diaspore able to persist in the seed bank [9]
Absence of appendage	+	no adaptation [1, 18, 19]	-	lower attachment [13]	+	no adaptation
Hooked and/or elongated appendage	-	lengthens and hampers digestive transit [1, 18, 19]	+	better attachment and retention in ungulates' fur [13]	-	limit diaspore incorporating into the mud
Presence of pulp	-	herbivores disperse few fleshy fruits [5, 19]	-	lower attachment of heavy fleshy fruits lacking appendages [3]	-	lower attachment of heavy fleshy fruits

[1]Heinken et al. (2002), [2]Auffret and Plue (2014), [3]Heinken and Raudnitschka (2002), [4]Janzen (1984), [5]Couvreur et al. (2005a), [6]Fischer et al. (1996), [7]Dutoit et al. (2003), [8]De Pablos and Peco (2007), [9]Schulze et al. (in press), [10]Cosyns and Hoffmann (2005), [11]Mouissie et al. (2005b), [12]Bruun and Poschlod (2006), [13]Couvreur et al. (2004b), [14]Römermann et al. (2005), [15]Thompson et al. (1993), [16]Pakeman et al. (2002), [17]Couvreur et al. (2004a), [18]Couvreur et al. (2005b), [19]Eycott et al. (2007).

Table 2. Characteristics of ungulates investigated in studies taken into account in the analysis

Ungulate species	Wild/Domestic	Number of studies	Mean shoulder height (cm)*	Diet†	Digestion system‡
Bison bonasus	Wild	1	180	Grass and roughage eater	Foregut fermenter
Bos taurus	Domestic	8	130	Grass and roughage eater	Foregut fermenter
Capreolus capreolus	Wild	6	70	Concentrate selector	Foregut fermenter
Cervus elaphus	Wild	4	120	Intermediate mixed feeder	Foregut fermenter
Dama dama	Wild	2	85	Intermediate mixed feeder	Foregut fermenter
Equus caballus	Domestic	5	125	Grass and roughage eater	Hindgut fermenter
Muntiacus reevesi	Wild	1	50	Concentrate selector	Foregut fermenter
Ovis aries	Domestic	17	70	Grass and roughage eater	Foregut fermenter
Sus scrofa	Wild	8	60	Omnivore	Hindgut fermenter

*Montulet (1984), †Hofmann (1989), ‡Feldhamer et al. (2007)

Table 3. Summary data of the dispersal data set for endozoochory, fur-epizoochory and hoof-epizoochory. *N*: number of samples

	N	Mean ± SD number seeds/sample (range)	Mean ± SD number species/sample (range)
Endozoochory	1214	116 ± 386 (1-5705)	6 ± 7 (1-38)
Fur-epizoochory	112	93 ± 201 (1-1300)	4 ± 4 (1-16)
Hoof-epizoochory	49	29 ± 84 (1-418)	3 ± 4 (1-21)

Table 4. Effect of the studied plant characteristics on dispersal by ungulates in Europe (meta-analysis models with random effects, REMA). We took into account in the analyses 52 studies for all characteristics. We rejected the null hypothesis (i.e. dispersed and non-dispersed species have similar characteristics) if the 95% confidence interval (CI) did not overlap zero (in bold). Variation: difference in species traits between ungulate-dispersed and non-dispersed plant species, expressed as a percentage calculated with the log response ratio. $Q_{between}$: between group heterogeneity tested against a chi-square distribution (in the meta-analysis models with random effects using a moderator). * p-value < 0.001

Plant characteristics	Effect size [95% CI]	Variation (%)	$Q_{between}$	
Open habitat	**0.34[0.22,0.47]**	41.1	45.5	*
Nitrophily	**0.40 [0.30,0.51]**	49.8	92.5	*
Releasing height	**0.25 [0.14,0.36]**	28.7	93.6	*
Diaspore mass	**-0.14 [-0.25,-0.04]**	-13.3	12.5	*
Diaspore shape	**0.35 [0.23,0.47]**	41.9	74.8	*
Seed bank longevity	**0.48 [0.36,0.60]**	61.8	90.3	*
No appendage	-0.01 [-0.16,0.15]	-1.0	24.2	*
Elongated appendage	**0.27 [0.15,0.39]**	30.8	33.3	*
Hooked appendage	0.01 [-0.11,0.13]	1.1	31.9	*
Pulp	**-0.34 [-0.45,-0.24]**	-29.1	86.1	*

FIGURES

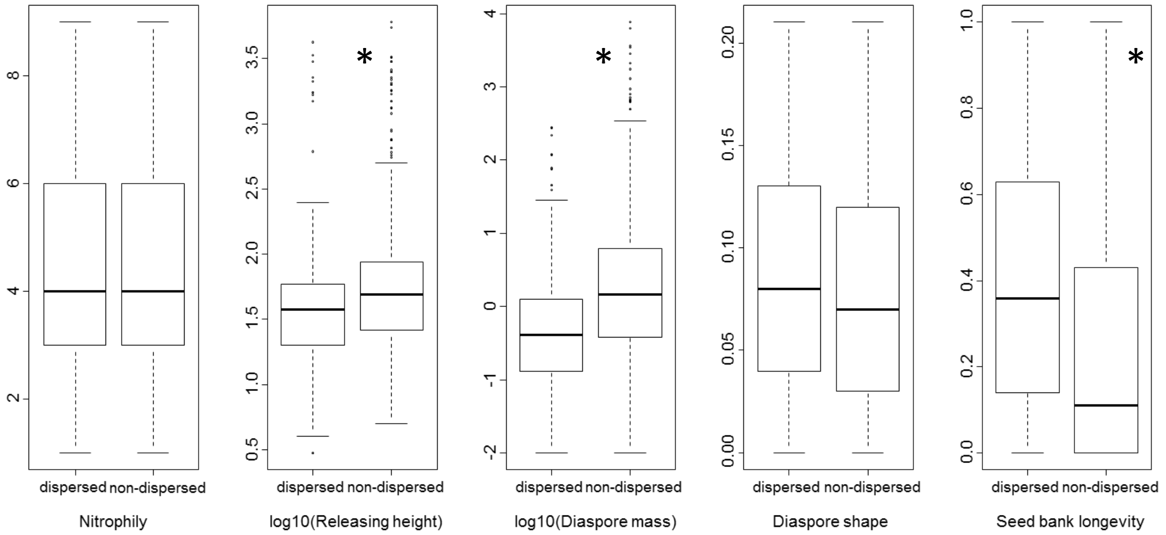

Fig. 1. Characteristics of plant species observed to be dispersed at least once (*N* = 278) and never dispersed (*N* = 357) by ungulates. The diaspore releasing height and diaspore mass were $\log_{10}$ transformed for better readability, although $\log_{10}$ transformation was not used in the analyses. Boxes indicate upper and lower quartiles, wide horizontal lines indicate the median, whiskers indicate the range, and circles indicate the outliers. * p-value < 0.001 (Mann-Whitney *U*-test).

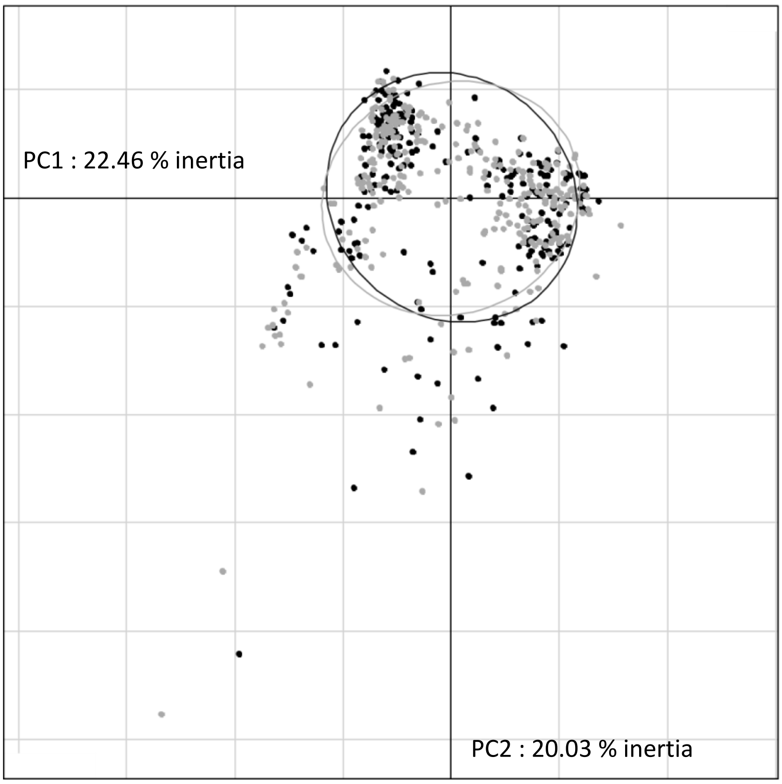

Fig. 2. Hill and Smith principal component analysis (PCA_{hs}) plot highlighting an apparent similarity between dispersed (black) and non-dispersed (grey) plant species according to their plant characteristics. We based the PCA on the plant species-characteristics matrix (N = 46,348 observations). Ellipses are graphical summaries of the data where a point has a 95% probability to be included.

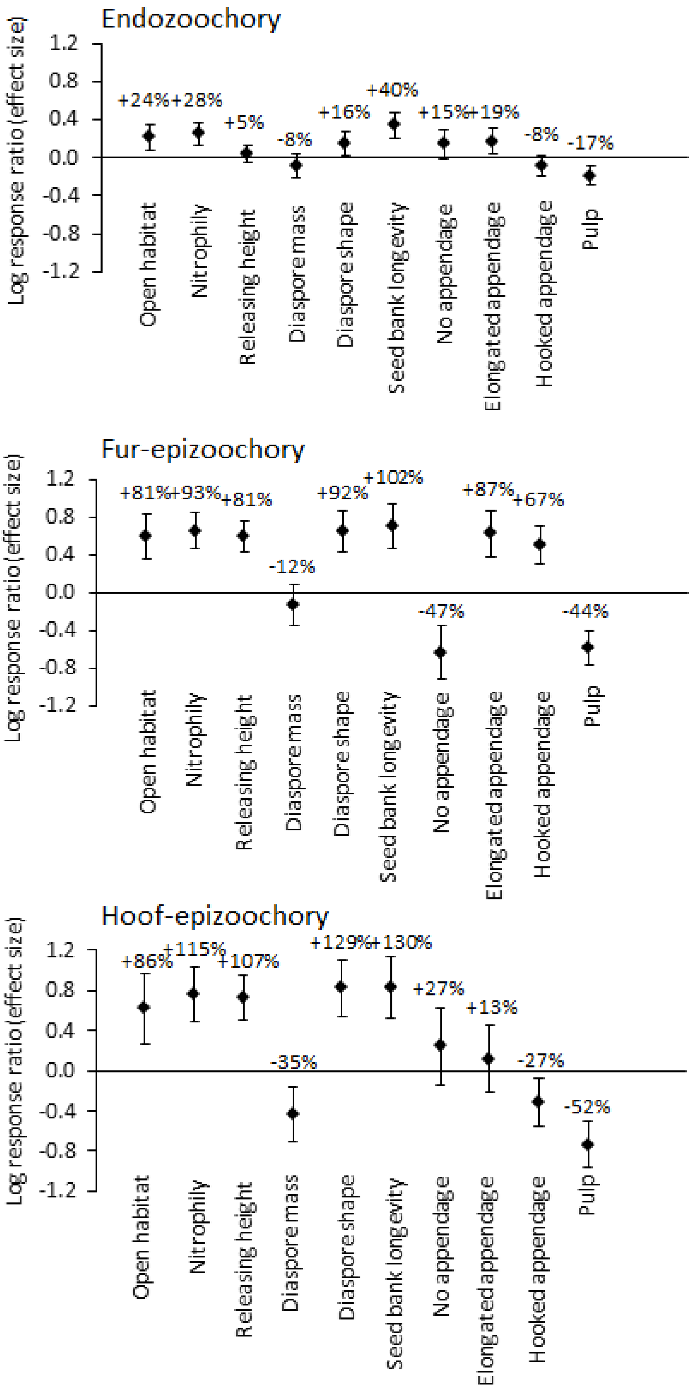

Fig. 3. Plant characteristics related to dispersal by ungulates in Europe. We plotted results of the meta-analysis models with random effects (estimate ± 95%CI of the log response ratio and % variation) when the dispersal mechanism was added as a moderator: endozoochory, fur-epizoochory and hoof-epizoochory. We took into account in the analyses 34, 11 and 7 studies respectively for endozoochory, fur-epizoochory, and hoof-epizoochory, for all characteristics. A positive variation means that a plant characteristic had a higher value for ungulate-dispersed than for non-dispersed species. We rejected the null hypothesis (i.e. dispersed and non-dispersed species have similar characteristics) if the 95% confidence interval did not overlap zero.

APPENDICES

Appendix 1 Table A1 Summary of the studies on endozoochory (endo), epizoochory via fur (epi-fur) and epizoochory via hooves (epi-hoof) included in the meta-analysis. *N* = Number of individual sampling units. Vegetation data were either published with the dispersal data or unpublished, except for studies 4-6: see Auffret and Cousins (2011).

Study ID	Disperser	Dispersal mechanism	Habitat type	Country	N dispersal samples	N vegetation plots	Size of vegetation plots (m²)	Source for dispersal data
1	*Bos taurus*	Endo	Grassland and Forest	Sweden	11	170	1	Auffret et al. (2012)
2	*Ovis aries*	Endo	Grassland and Forest	Sweden	7	170	1	Auffret et al. (2012)
3	*Capreolus capreolus*	Endo	Grassland, deciduous woodland, settlements	Sweden	219	8	4	Auffret and Plue. (2014)
4	*Bos taurus*	Endo	Grassland	Sweden	24	215	1	Auffret and Cousins (2013)
5	*Equus caballus*	Endo	Grassland	Sweden	3	215	1	Auffret and Cousins (2013)
6	*Ovis aries*	Endo	Grassland	Sweden	4	215	1	Auffret and Cousins (2013)
7	*Bos taurus*	Endo	Coastal (Forest, scurb, grassland, dune, wetland)	Belgium	33	225	4	D'hondt et al. (2012)
8	*Ovis aries*	Endo	Grassland	Germany	17	6	80	Eichberg (2005), Eichberg et al. (2007)
9	*Ovis aries*	Endo	Grassland	Germany	19	8	80	Eichberg (2005), Eichberg et al. (2007)
10	*Ovis aries*	Endo	Grassland	Germany	13	8	80	Eichberg (2005), Eichberg et al. (2007)
11	*Ovis aries*	Endo	Grassland	Germany	12	5	80	Eichberg (2005), Eichberg et al. (2007)
12	*Ovis aries*	Endo	Grassland	Germany	18	7	80	Eichberg (2005), Eichberg et al. (2007)
13	*Ovis aries*	Epi-fur	Grassland	Germany	3	6	80	6
14	*Ovis aries*	Epi-fur	Grassland	Germany	3	8	80	Eichberg (2005)
15	*Ovis aries*	Epi-fur	Grassland	Germany	3	8	80	Eichberg (2005)
16	*Ovis aries*	Epi-fur	Grassland	Germany	3	5	80	Eichberg (2005)
17	*Ovis aries*	Epi-fur	Grassland	Germany	3	7	80	Eichberg (2005)

Study ID	Disperser	Dispersal mechanism	Habitat type	Country	N dispersal samples	N vegetation plots	Size of vegetation plots (m²)	Source for dispersal data
18	*Muntiacus reevesi*	Endo	Forest (lowland conifer)	England, UK	296	535	9	Eycott et al. (2007)
19	*Capreolus capreolus*	Endo	Forest (lowland conifer)	England, UK	225	535	9	Eycott et al. (2007)
20	*Cervus elaphus -Dama dama*	Endo	Forest (lowland conifer)	England, UK	235	535	9	Eycott et al. (2007)
21	*Dama dama*	Endo	Forest (mainly mixed oak-hornbeam)	Germany	6	43	400	Heinken et al. (2002), Heinken et al. (2001)
22	*Sus scrofa*	Endo	Forest (mainly mixed oak-hornbeam)	Germany	6	76	225	Heinken et al. (2002), Heinken et al. (2001)
23	*Sus scrofa*	Endo	Forest (mainly mixed oak-hornbeam)	Germany	6	43	400	Heinken et al. (2002), Heinken et al. (2001)
24	*Capreolus capreolus*	Epi-fur	Forest (mainly acidic pine)	Germany	25	76	2000	Heinken et al. (2002), Heinken and Raudnitschka (2002)
25	*Capreolus capreolus*	Epi-hoof	Forest (mainly acidic pine)	Germany	25	76	2000	Heinken et al. (2002), Heinken and Raudnitschka (2002)
26	*Sus scrofa*	Epi-fur	Forest (mainly acidic pine)	Germany	9	76	2000	Heinken et al. (2002), Heinken and Raudnitschka (2002)
27	*Sus scrofa*	Epi-hoof	Forest (mainly acidic pine)	Germany	9	76	2000	Heinken et al. (2002), Heinken and Raudnitschka (2002)
28	*Equus caballus*	Endo	Coastal (scrub, grassland, dune)	Belgium	14	232	4	Cosyns and Hoffmann (2005)
29	*Bos taurus*	Endo	Coastal (scrub, grassland, dune)	Belgium	14	350	4	Cosyns et al. (2005)
30	*Equus caballus*	Endo	Coastal (scrub, grassland, dune)	Belgium	14	350	4	Cosyns et al. (2005)
31	*Bos taurus*	Endo	Coastal (forest, scurb, grassland, dune, wetland)	Belgium	14	225	4	Cosyns et al. (2005)
32	*Equus caballus*	Endo	Coastal (forest, scurb, grassland, dune, wetland)	Belgium	14	225	4	Cosyns et al. (2005)
33	*Bos taurus*	Endo	Open holm oak woodland (dehesa)	Spain	192	12	0.04	Malo and Suarez (1995)
34	*Dama dama*	Endo	Open holm oak woodland (dehesa)	Spain	192	12	0.04	Malo and Suarez (1995)
35	*Cervus elaphus*	Endo	Open holm oak woodland (dehesa)	Spain	192	12	0.04	Malo and Suarez (1995)
36	*Bos taurus*	Endo	heathland, grassland, and woodland	The Netherlands	55	12	1	Moussie (2004)
37	*Equus caballus*	Endo	heathland, grassland, and woodland	The Netherlands	10	12	1	Moussie (2004)

Study ID	Disperser	Dispersal mechanism	Habitat type	Country	N dispersal samples	N vegetation plots	Size of vegetation plots (m²)	Source for dispersal data
38	*Ovis aries*	Endo	heathland, grassland, and woodland	The Netherlands	10	12	1	Moussie (2004)
39	*Ovis aries*	Endo	Grassland	Scotland	30	5	4	Pakeman et al. (2002)
40	*Ovis aries*	Endo	Grassland	Scotland	30	5	4	Pakeman et al. (2002)
41	*Ovis aries*	Endo	Heathland	Scotland	30	5	4	Pakeman et al. (2002)
42	*Ovis aries*	Endo	Grassland	Scotland	648	30	0.09	Pakeman and Small (2005)
43	*Cervus elaphus*	Epi-fur	Forest (sessile oak and Scots pine)	France	49	34	2000	Picard and Baltzinger (2012)
44	*Cervus elaphus*	Epi-hoof	Forest (sessile oak and Scots pine)	France	49	34	2000	Picard and Baltzinger (2012)
45	*Capreolus capreolus*	Epi-fur	Forest (sessile oak and Scots pine)	France	58	34	2000	Picard and Baltzinger (2012)
46	*Capreolus capreolus*	Epi-hoof	Forest (sessile oak & Scots pine)	France	58	34	2000	Picard and Baltzinger (2012)
47	*Sus scrofa*	Epi-fur	Forest (sessile oak & Scots pine)	France	39	34	2000	Picard and Baltzinger (2012)
48	*Sus scrofa*	Epi-hoof	Forest (sessile oak & Scots pine)	France	39	34	2000	Picard and Baltzinger (2012)
49	*Sus scrofa*	Epi-fur	Forest (sessile oak & hornbeam)	France	26	15	2000	Picard and Baltzinger (2012)
50	*Sus scrofa*	Epi-hoof	Forest (sessile oak & hornbeam)	France	26	15	2000	Picard and Baltzinger (2012)
51	*Bos taurus*	Endo	Grassland	Germany	18	75	9	Poschlod et al. (Unpublished data)
52	*Bison bonasus*	Epi-hoof	Grassland and forest	Germany	4	3	150,000	Schulze et al. (2014)

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Appendix 2 Table A2. Raw data available from DRYAD: entry doi: xx.xxxx/dryad.xxxx

CHAPITRE 3

Conséquences de la dispersion zoochore sur la composition fonctionnelle des communautés végétales

Nous avons montré à travers une méta-analyse que l'épizoochorie filtre la flore locale en fonction des traits des espèces dispersées, mais que l'endozoochorie imprime un filtre moins stringent essentiellement dépendant du vecteur. J'ai cherché à détecter un signal de ces processus locaux dans les patrons de composition fonctionnelle des communautés végétales à large échelle spatiale. Pour ce faire, j'ai travaillé à l'échelle du quart nord-est français, couvrant ainsi 28 départements et 12694 relevés de végétation en milieu forestier. En utilisant une analyse multivariée RLQ, j'ai mis en relation les densités de populations d'ongulés, des variables locales décrivant le peuplement forestier, et des variables de configuration paysagère, avec les traits des espèces végétales présentes dans la flore forestière locale (morphologie, masse, mode de dispersion principal).

L'analyse RLQ montre que l'habitat et le paysage sont les principaux déterminants de la composition fonctionnelle des communautés, mais que les ongulés ont aussi une forte influence, suggérant un impact détectable à large échelle des interactions plantes-herbivores sur les patrons floristiques.

Aucun patron clair n'émerge des relations entre les traits des plantes et les densités d'ongulés. L'épizoochorie semble liée au milieu forestier, alors que l'endozoochorie n'est associée ni à un habitat, ni à un ensemble de traits distincts. Les fortes densités de cerf et de sanglier sont corrélées à une grande diversité de traits, avec des plantes possédant des adaptations pour la zoochorie (appendices allongés, graines rondes) ou l'anémochorie (appendices plats, aérenchymes). Ces résultats suggèrent que la zoochorie influe peu, ou de manière non sélective, sur les patrons de composition fonctionnelle des communautés végétales. L'effet des ongulés, dont les préférences alimentaires sont peu sélectives, est probablement dominé par l'herbivorie à cette échelle spatiale.

L'effet des interactions plantes-animaux s'ajoute donc à celui des filtres environnementaux sur la composition des communautés végétales forestières en milieu tempéré. L'absence de signal clair d'un effet de la zoochorie ne contredit pas nécessairement les résultats obtenus à échelle locale, mais suggère que la dispersion a un effet limité sur les processus d'assemblage, qui s'estompe lorsqu'on accroit le grain spatial.

Article 5

Influence of ungulate population densities on the trait composition of plant communities

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En préparation pour *Ecography*

Abstract

Plant-animal interactions have been widely studied under evolutionary and behavioral perspectives, but less is known on how they affect community-level patterns of species coexistence and diversity. Animal-mediated seed dispersal has particularly been overlooked among processes that shape spatial patterns of plant community composition, by contrast with other processes including herbivory and fertilization. In this article, we attempt to disentangle the influences of herbivory and zoochory from those of environmental filtering on plant community composition. We used a RLQ multivariate framework to investigate the relationships between species occurrence patterns, their life-history traits, major land-use gradients and vector abundance, focusing on herbaceous assemblages of North-Western France and wild ungulates. Ungulate abundance and landscape gradients had distinct effects on the trait composition of plant communities, implying that plant-animal interactions have a strong influence on assembly processes, distinct from that of environmental filtering. No distinct pattern emerged in the relationship between plant trait occurrences and ungulate abundance, suggesting that neither herbivory nor zoochory leave a clear signature in the functional composition of plant communities. We suggest that ungulate trophic generalism associated with the absence of adaptations to zoochory in our plant regional assemblage may explain these results. Refined studies at more local scales coupled with the calibration of metacommunity models with experimental data may help quantifying the relative influence of biotic processes on plant community assembly

Keywords: functional traits, seed dispersal, herbivory, wild ungulates, RLQ, community assembly.

INTRODUCTION

Niche filtering and competition are usually considered as the main counter acting processes limiting species diversity (Diamond, 1975; Gotelli and McCabe, 2002). However, in plant communities, species regularly coexist even on a few resources without excluding each other, suggesting that other biotic interactions are also influencing assembly processes (Loreau and Mouquet, 1999; Ovaskainen et al., 2010; Ricklefs, 2004; Tilman and Pacala, 1993). Accordingly, the influences of various positive or negative interactions have been suggested to impact community processes: predation (Coley and Barone, 1996; Pacala and Crawley, 1992), facilitation (Brooker et al., 2008; Callaway, 1995), pathogens (Ricklefs, 2012) or mutualism (Bascompte and Jordano, 2007). Biotic interactions may also influence community assembly indirectly through other processes, as is the case for animal-mediated seed dispersal (zoochory). While the complexity of such processes makes them hard to monitor directly, they may leave identifiable signals in community composition patterns.

Plant dispersal influences the spatial structure of populations and communities in conjunction with environmental filters and other biotic interactions (Boulangeat et al., 2012). At the individual level, seed dispersal determines where seedlings and future adult plants come to be located, and is therefore central to population spatial dynamics (Cousens et al., 2008). Because plant dispersal is passive, seeds may or not end up in suitable habitats, increasing the costs of mobility. In animal-mediated dispersal, this cost is reduced if the vectors have well-defined habitat requirements, as they tend to move primarily from one patch of suitable habitat to one other, increasing the probability that a seed collected in a given habitat will end up in similar environmental conditions (“directed dispersal”, Wenny, 2001). Animal vectors may therefore connect isolated populations and mediate colonization of new suitable areas, especially as they are assumed to disperse seeds on longer distances than other processes (Cain et al., 2000; Pakeman, 2001; Vellend et al., 2003). Zoochory is therefore known to influence plant species distribution, interaction networks and communities at various spatial scales (Allouche et al., 2008; Fagan et al., 1999; Kneitel and Chase, 2004). However, how zoochory influences patterns of plant communities has hardly been investigated over large spatial scales, except in the specific case of fruit dispersal by birds.

How wild ungulates impact plant community composition has emerged as a question of conservation concern as the abundances of red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus)* and wild boar (*Sus scrofa*) have increased in the last century in various European regions (ONCFS). As they are selective foragers, herbivores like deers may modify the composition of plant communities through herbivory as a result of their dietary preferences and through internal and external seed dispersal (Vellend et al., 2006). Depending on the environmental context, deer-mediated herbivory can restrict local distributions or decrease or enhances diversity. In particular, grazing alters the growth and survival of shrub and tree species, favouring the diversity of ground vegetation through increased light penetration and fertilization (Augustine and Mcnaughton, 2004; Jacobs and Naiman, 2008; Olff and Ritchie, 1998). On the other hand, in cases of overbrowsing, Côté et al. (2004) showed that plant cover and diversity are reduced. Although it has received less attention, ungulate-mediated dispersal following consumption (endozoochory) or on animals' body (epizoochory) can favour patch colonization, possibly at relatively large spatial scales (D'hondt et al., 2012; Westcott et al., 2005). Yet, Vellend et al. (2006) modelled the antagonistic effects of seed dispersal and herbivory by white-tailed deer and demonstrated that migration rates of *Trillium grandiflorum* are maximum at low rates of herbivory (< 15 %). Therefore, the relative outcomes of herbivory and zoochory are antagonistic and may leave distinct signatures in plant communities.

The impact of wild ungulate on plant assembly processes is most likely to be reflected by the ecological traits that prevail in local communities, i.e., their functional composition (McGill et al., 2006). If ungulate grazing is the main dominant biotic driver of plant communities, functional composition should be driven mainly by traits related to herbivory. Wild ungulates preferentially consume woody and high nutrient-containing species (Jacobs and Naiman, 2008; Janzen, 1984), and high deer densities tend to reduce the three cover (Augustine and Mcnaughton, 2004; Boulanger et al., 2009). Therefore, herbivory should deplete these trait abundances. Zoochory should leave a different imprint because wild ungulates probably do not disperse all the plant species they consume equally. In particular, seeds bearing particular adaptations to zoochory are expected to be preferentially transported. Seeds transported through endozoochory have characteristics which make them resistant to digestive enzymes:

generally small, round and with a hard seed coat (Malo and Suárez, 1995; Pakeman et al., 2002). Some species may even need to be abraded by digestive enzymes for the release of dormancy and germination (Cosyns et al., 2005; Mouissie et al., 2005; von Oheimb et al., 2005). Seeds exhibiting morphological adaptations such as hooked and/or elongated appendages are usually though to be dispersed through epizoochory, because of a high rate of hitching in the animals' fur (Heinken and Raudnitschka, 2002). Therefore, the functional composition of communities in which zoochory overcomes the effects of herbivory should be dominated by these traits.

In this study, we searched for signals of herbivory and zoochory into the functional composition of plant communities. We compared the influences of habitat gradients and of red deer, roe deer and wild boar population densities on the functional composition of forest plant communities within a multivariate space, at the scale of North-Eastern France. We predicted that [1] although habitat should explain a larger proportion of the compositional variability of plant communities (Ricklefs, 2004), wild ungulates should leave a marked signature, distinct from that of the environment. We further predicted that [2] this signature would be structured by the dominant plant-animal interaction, ranging from herbivory to zoochory along a gradient of ungulate densities.

MATERIAL AND METHODS

Study area

The study area covered the North-East of France and spread over a region of 169 369 km² (Figure 1). This area was separated into two parts defined by forest composition: the East is mainly composed of fir forests dominated by *Abies alba*, while western forests are dominated by *Quercus petraea* and *Quercus robur*.

Vegetation data

We used a database of vegetation surveys provided by the Institut Géographique National (IGN) including 12694 community-plots sampled in forest areas from 1988 to 2006 (see all plots in Figure 1). A plot was a circle of 15 m diameter; we used them to define local plant communities. Within each plot, species abundances were recorded using a cover frame with six classes (1: from 0 to 5 %; 2: from 5 to 25 %; 3: from 25 to 50 %; 4: from 50 to 75 %; 5: up to 75 %; according to Braun-Blanquet, 1946). These data represent a conservative assessment of plant occurrences and relative abundances in France, and although some false presences/absences may exist, they represent the best available existing data. A total of 628 species were recorded in the entire study area. Trees were not taken into account because the way vegetation data were recorded did not allow determining if tree species corresponded to young trees available for animals, or to adults. Moreover, we did not keep species for which we could not recover all functional traits (see below). We therefore based our analyses on a site*species matrix including 232 plant species, hereafter "L matrix" (see Appendix 1 for the list of these plant species).

Functional traits

We compiled seven plant attributes known to be associated with zoochorous dispersal from the LEDA Traitbase (Kleyer et al., 2008) (Table 1). We defined "dispersal vectors" as the vectors known from the literature to disperse the seeds of a given plant. "Dispersal type" clarifies the type of zoochory, either epizoochory or endozoochory. The morphology of the dispersal unit indicates if seeds bear appendages or not, the kind of appendages (flat or elongated), if seeds are hooked or not, if they possess an elaiosome or a balloon structure, or if they are embedded in a nutrient structure like pulp. Plant growth form is a proxy of plant height and seed accessibility for the animals (defined according to Raunkiær, 1907). The seed number corresponds to the seed production per individual plant and reflects plant productivity within a reproduction event. We calculated seed shape (variance in dimensions: Vs) following Bekker et al. (1998): $Vs = \sum(x_i - \bar{x})^2 /3$, with x_1 = length/length, x_2 = width/length and x_3 = height/length, which indicates if seeds are rather round or flat. Seed mass was also included in our analyses. We log-transformed the two continuous variables, seed number and seed mass. These functional traits were integrated in a species*traits matrix, hereafter "Q matrix".

Ungulate population densities

The local densities of the three ungulates species were provided by the French hunting institute (ONCFS), and were expressed through the number of animals killed, which, although highly imperfect, is the best approximation available to us for population sizes. For wild boar, data were available for each year from 1993 to 2007 and per administrative municipality. For roe deer, data were available for 1985, 1993, 1998, 2002 and 2007, per municipality. For red deer, data were available for 1985, 1988, 1991, 1995, 2000 and 2005, per unit of hunting management. Since roe deer and wild boar were present over our entire study area since 1985, we average all the densities per municipality over the years. Yet, red deer was not present over our entire study area in 1985. In order to avoid any over- or underestimation of this species' densities, we averaged the densities of three years: the two years on both side of the year of vegetation sample and the corresponding year. We then attributed to each plot of vegetation sample the density of the municipality (for wild boar and roe deer) or the density of the unit of hunting management in which it was located.

Forest stand description on the plot

For each plot of vegetation sample, four variables describing the forest stand in the plot were also provided by the IGN: total basal area (G, in m²); maximum stand height, which corresponded to the high of the taller tree in the stand (H0, in m); averaged tree diameter (Dg, in cm); and the number of trees per hectare (N).

Landscape description

We calculated four indices of landscape configuration with Arcgis.10. We recorded the percentage of forested area within a buffer of 2.5 kilometers around each plot, which correspond to the mean distance covered by the three animal species over 48 hours (unpublished data). We also computed the averaged surface (in hectares) of all the forested areas which intersected the buffer, the coefficient of variation of these forested areas, and the distance of the plot from the nearest ancient woodland. Ancient woodland corresponded to forested areas existing since 1744. We included ungulate densities, habitat composition and landscape structure into a site*environmental variables matrix, hereafter “R matrix”.

Statistical analyses

We used an RLQ multivariate analysis to relate environmental variables (R matrix) with plant traits (Q matrix) through the site*species matrix (L matrix) (Dolédec et al., 1996; Dray and Legendre, 2008). The RLQ analysis is a three step analysis. First, we analyzed each matrix separately, with a principal component analysis (PCA) for R matrix, a correspondence analysis (CA) for L matrix, and a Hill and Smith analysis (HS) for Q matrix. We subsequently related the L and R, and the L and Q matrices with co-inertia analyses, and used Monte-Carlo permutations to assess their robustness. Eventually, the RLQ analysis allowed to relate the two co-inertia analyses. All statistical analyses were performed using R 3.1 software (R Development Core Team 2012) and the ade4 library (Dray and Legendre, 2008).

RESULTS

CA, L matrix

We retained the first two components of the CA, explaining respectively 6.6 % and 5.4 % of the total variability of the site*species matrix. The low amount of variance explained by each axis is probably due to the large number of species and the high variability of plant community composition across sites. However, fir and oak forest were clearly separated in the CA space, reflecting the known separation of dominant tree species within the study area (see Material and Methods, Figure 2). The second axis could represent an altitudinal gradient, since plots dominated by fir were mainly located at altitudes from 300 to 1300 m, in Vosges Mountains, while oak forests were in plains (< 300 m).

PCA, R matrix

We retained the first three components of the PCA, which explained respectively 27.3 %, 16.4 % and 14.8 % of the total variance. The first axis corresponded to a gradient of forest cover, with a high percentage of forested area and large trees (high Dg) toward negative values, and a more fragmented forest habitat toward positive values (high coefficient of variation of forest area) (Figure 3). The second axis had a less clear interpretation ; we therefore did not consider it further. All ungulate population densities were correlated with the third axis.

HS, matrix Q

We retained the first two components of the Hill and Smith analysis, which explained 70 % of the total variance. The first axis segregated plants mainly dispersed by birds toward positive values, from those dispersed by wind, wild boar, domestic animals and all epizoochorous species toward negative values. Dispersal by birds was further correlated with heavy seeds, those embedded in fruits and phanerophytes. Dispersal by wind and wild boar or domestic animals was associated with disc or needle shaped seeds, bearing elongated or flat appendages, or possessing balloon structures. The second axis separated dispersal by invertebrates toward negative values, from endozoochory by red deer and roe deer toward positive values. Dispersal by invertebrates was correlated with seeds with elaiosome and cryptophytes, while endozoochorous dispersal was associated with high seed numbers (Figure 4).

Co-inertia analysis

The link between L and R matrices (p=0.001) was stronger than the link between L and Q matrixes (p=0.053), suggesting that plant composition was better explained by environmental variables than by plant and seed traits.

RLQ analysis

We retained the two first components of the RLQ. The first and second axes of the RLQ were respectively correlated with the first and third axes of the PCA. The first axis thus reflected a gradient of forest cover, ranging from fragmented (positive values) to continuous forest cover (negative values). The second axis opposed high wild boar and red deer densities (negative values) to high number of trees per hectare (positive values), reflecting ungulate's preference for open forest stands. Population densities of roe deer were uncorrelated to those of the two other ungulates and contributed more to the first axis, in accordance with the species' preference for forests (Figure 5). Endozoochorous dispersal was located close to the centroid of the RLQ space, showing that its contribution to plant community composition was low (Figure 6).

The relation between the R and Q matrices (Figures 7 and 8) showed that forest habitats and high roe deer densities (negative values of axis 1) were correlated with dispersal by wild boar and domestic animals, and to a lesser extent with epizoochory. High population densities of wild boar and red deer (negative values of axis 2) were correlated with a broad spectrum of functional traits, with both traits usually associated with epizoochory (elongated appendages, disc- or needle-shaped seeds, high seed number), and traits and characteristics which refer to anemochory (flat appendages, balloon structures, wind as dispersal vector).

DISCUSSION

Our results showed that plant community composition is structured at the scale of North-Eastern France by the distinct influences of forest cover and wild ungulate densities. However, functional composition was hardly structured by these gradients, suggesting that the processes relating habitat and ungulates to plant assembly are unrelated to the ecological traits incorporated in our analysis.

Forest cover and fragmentation accounted for a large amount of the RLQ total variance while local stand characteristics had a lower effect, which suggests that landscape gradients can overcome the effects of local habitat structure in shaping the composition of forest plant communities (Hunter and Price, 1992; Turner, 1989).

Wild ungulates population densities had a significant influence on the RLQ space, albeit smaller than that of landscape features. This result is in line with the usually predicted hierarchy of assembly processes within which environmental filters dominate large-scale patterns of community assembly, while biotic processes have more local, although sometimes stringent effects (Pearson and Dawson, 2003). Although competition has traditionally been considered as the main biotic assembly process structuring communities (Cody and Diamond, 1975; Tilman, 1994), plant-animal interactions may alter dramatically local plant taxonomic and functional composition particularly through herbivory and zoochory (Vellend et al., 2006). High ungulate abundances are known to reduce forest plant diversity due to overgrazing (Boulanger et al., 2009), with indirect implications for the structure of forest animal communities (e.g. birds; Ferry and Frochot, 1974). Our results accordingly show that ungulate densities have a strong influence on forest plant communities, and that this influence is not accompanied with a functional trait structure suggesting an effect of zoochory. Hence, the patterns reflected in our RLQ space more likely reveal large-scale effects of herbivory, which is further supported by the low dietary specialization of the three ungulates included in our study. Few other herbivores are likely to influence plant communities in the study area, most of them being small-sized animals foraging on low quantities and within small home ranges. However, we may have overlooked the effects of alternative zoochory vectors including granivorous birds (Herrera et al., 1994), although the trait structure of our RLQ does not support this hypothesis. Bird or insect-mediated dispersal may however not involve seed quantities similar to those ingested by ungulates, and their effects on plant community composition may thus operate at local scales well beyond that of our data. Hence, herbivory by wild ungulates is probably the dominant biotic process influencing plant community composition in the temperate forests of north-eastern France.

Looking deeper into the influence of the three ungulates revealed that their contributions to plant communities differed, especially with respect to ecological traits. Wild boar and red deer frequent more open habitats than roe deer (Kuijper et al., 2009), which could explain their positive correlation with epizoochory and anemochory, both associated to open-habitat plant species (Ozinga et al., 2004). Additionally, red deer is known to reduce or slow down forest regeneration, and thus to maintain forest openness (Augustine and Mcnaughton, 2004; Olff and Ritchie, 1998), which could favor colonization of forest areas by anemochorous plants.

Conclusion

Our results support the prediction that plant-animal interactions add up with environmental filters to shape plant community composition in temperate forests. We interpret the absence of any clear functional signal as the outcome of generalist grazing by the three most common ungulates present within our study area. The dynamics of plant metacommunities may thus be influenced by the joint effects of landscape changes and the dynamics of large herbivores, which could overcome more specialized plant-animal interactions with more local or more diffuse effects. The biotic filter imposed by ungulate to plant communities may however itself be spatially heterogeneous and depend on dominant forest types, topology and human hunting and forestry. The transferability of our results therefore remains to be assessed by further analyses of the community-level outcomes of plant-herbivore interactions at other spatial scales and compared with other environmental gradients. Nevertheless, our results provide a first large-scale outlook of how herbivores shape plant community composition. This broad-scope view shows that even in temperate areas where they are often overlooked, plant-animal interactions may contribute to assembly processes over large spatial scales.

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FIGURES

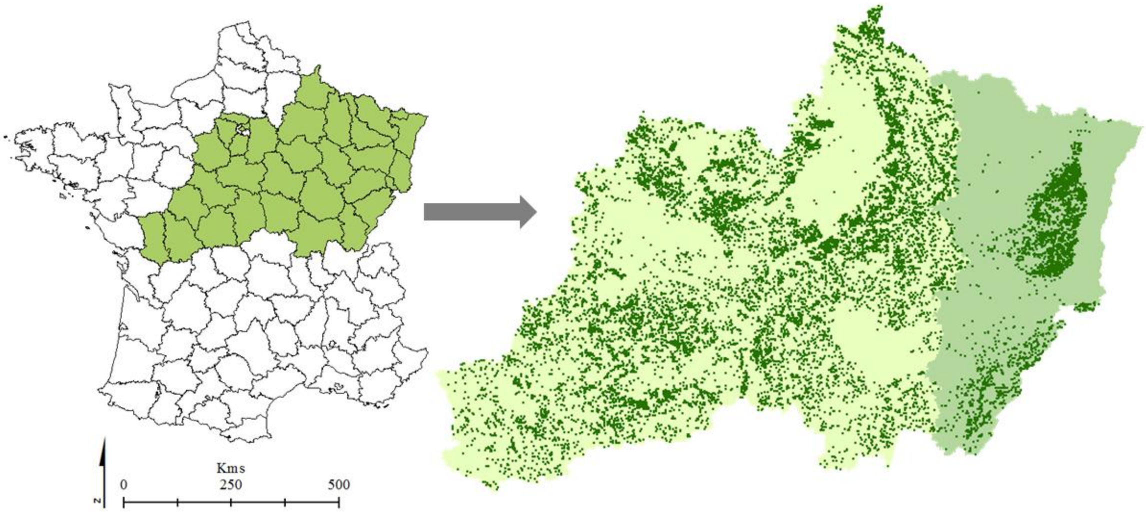

Figure 1: The study area, with fir forest in dark green and oak forest in light green. Green points correspond to the community-plots sampled of vegetation.

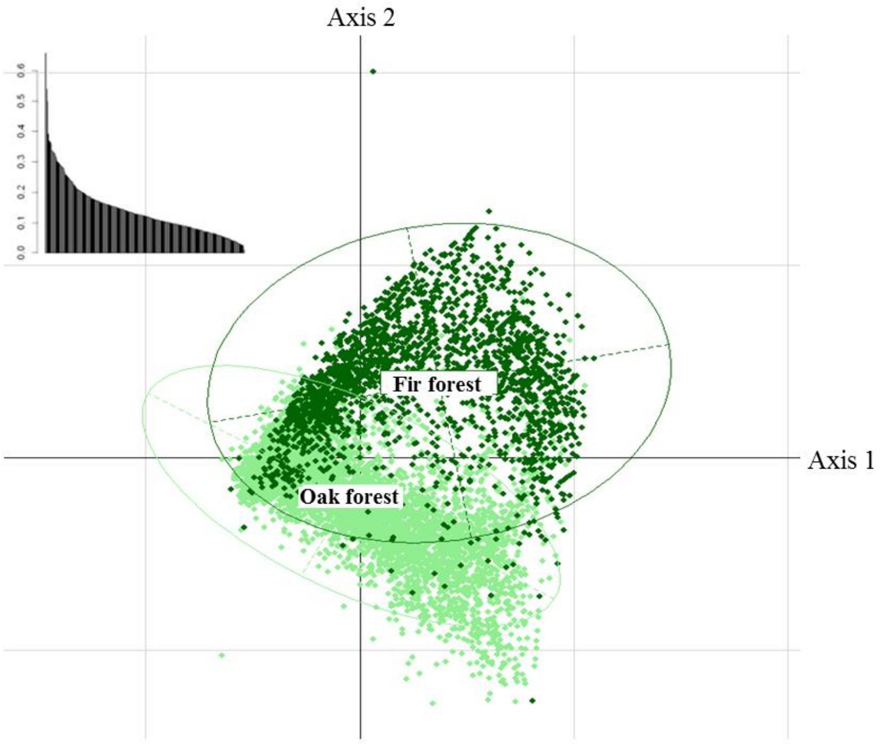

Figure 2: AFC realized on the matrix L, distinguishing fir and oak forest.

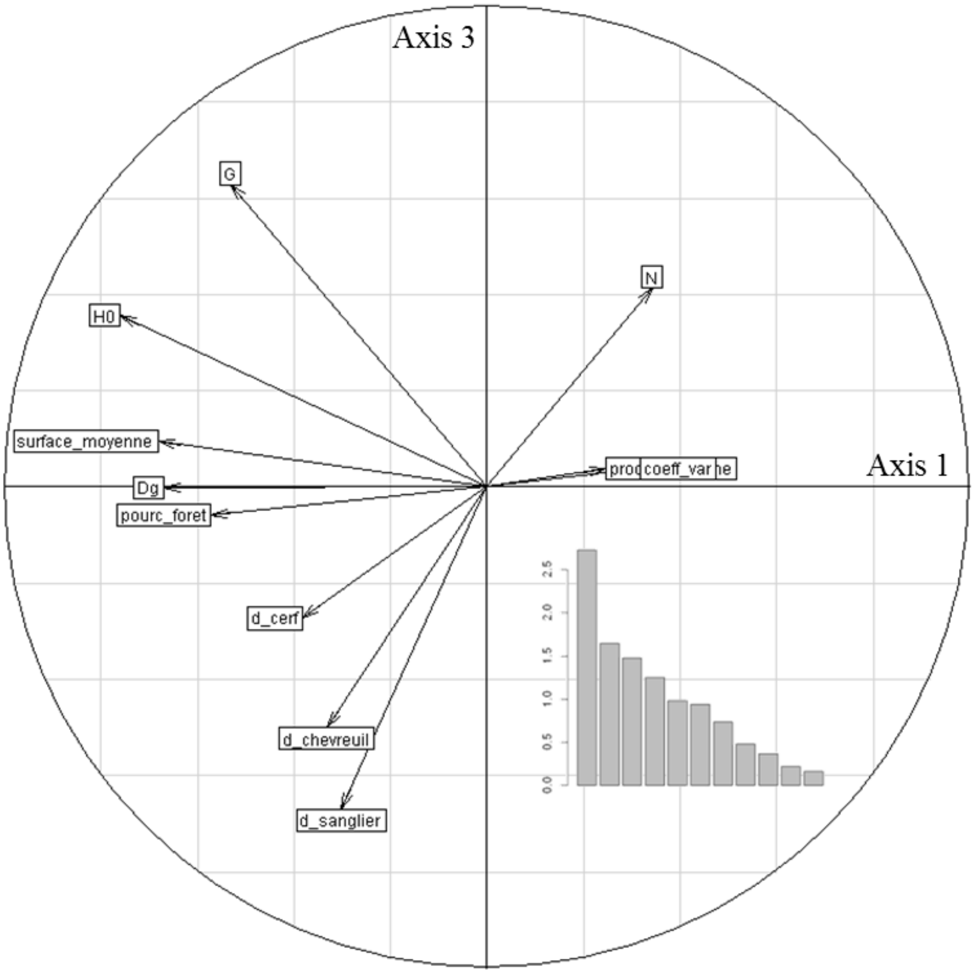

Figure 3: Correlation circle issued from the ACP realized on the matrix R, and distinguishing landscape variables (Axis 1) from ungulates population densities (Axis 3).

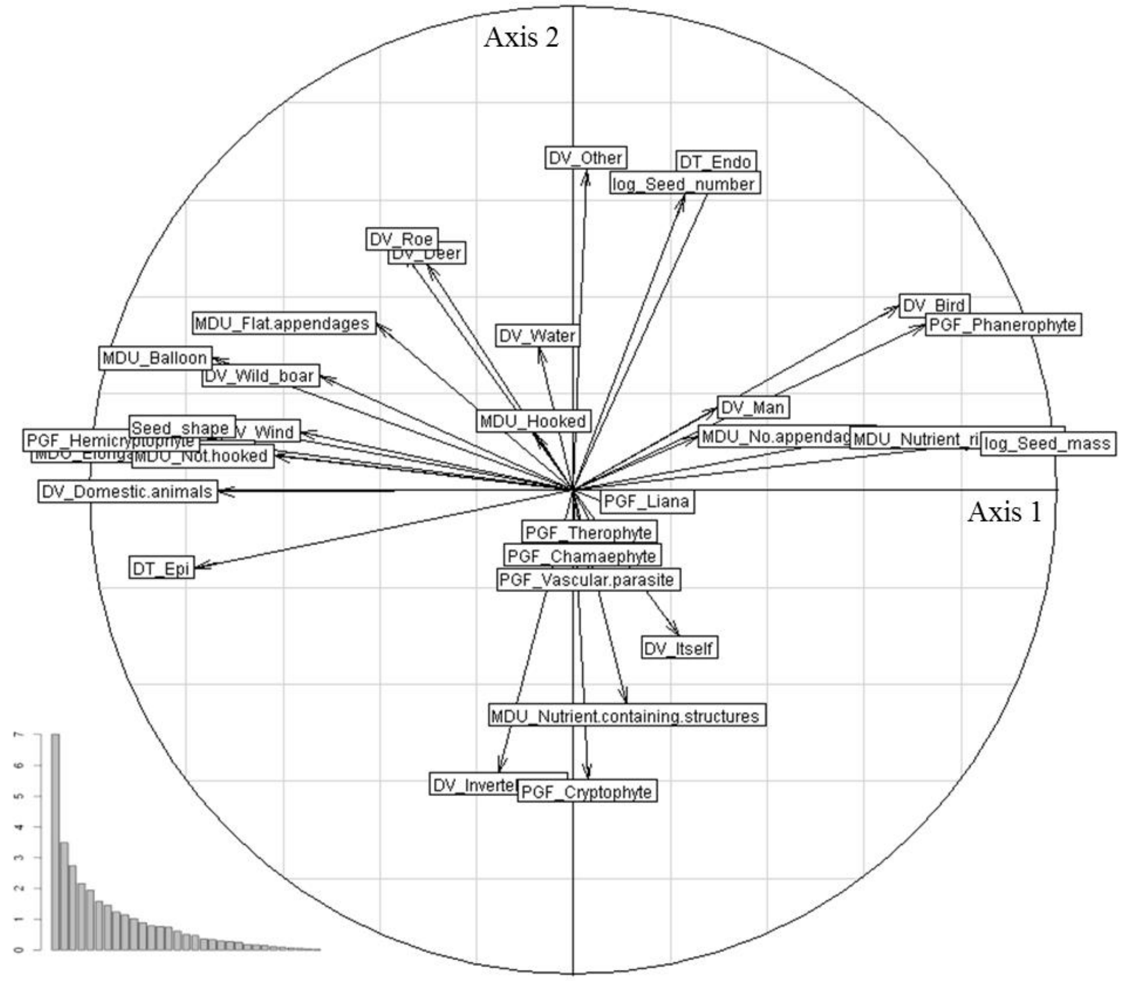

Figure 4: Correlation circle issued from the Hill and Smith realized on the matrix Q.

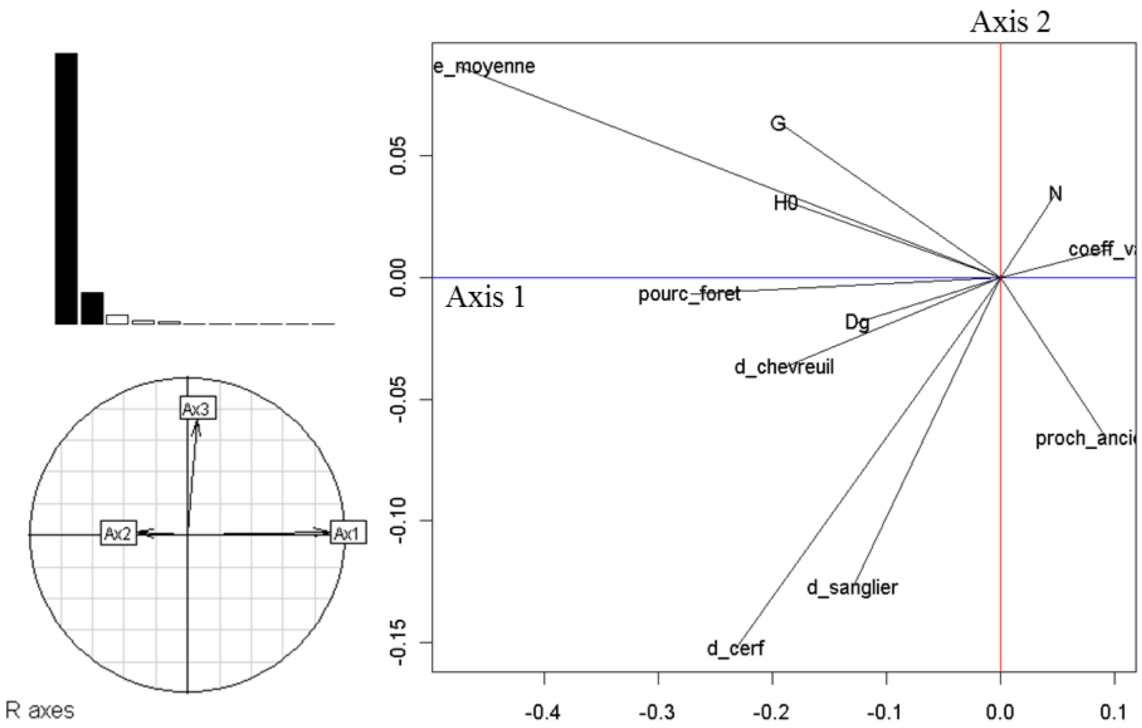

Figure 5: RLQ analysis for the link between L and R matrixes.

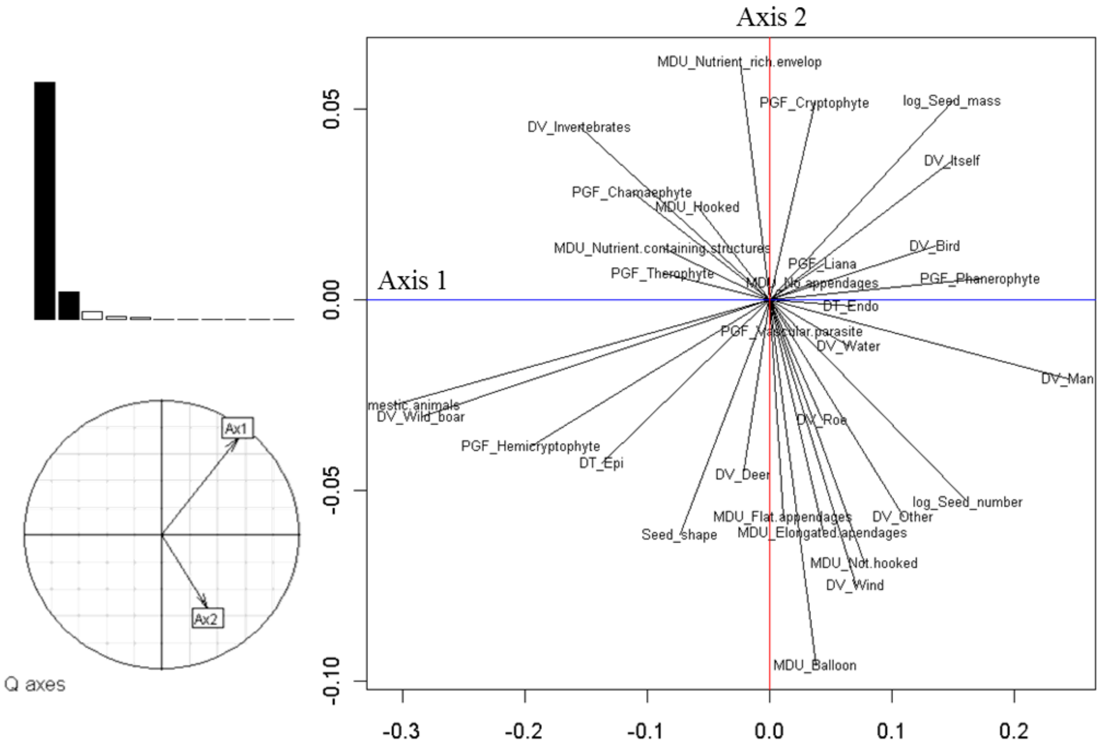

Figure 6: RLQ analysis for the link between L and Q matrixes.

TABLES

Table 1: Plant and seed traits used in our analyses.

Traits	**Modalities**
Dispersal vector (DV)	The plant itself (i.e., autochory) Wind Water Invertebrates (ants) Birds Domestic animals (sheep, cow, horse) Red deer Roe deer Wild boar Man Others
Dispersal type (DT)	Endozoochory Epizoochory
Mophology of dispersal unit (MDU)	No appendages Flat appendages Elongated appendages Balloon structure Nutrient containing structure (elaiosome) Nutrient rich envelop (pulp) Hooked Not hooked
Plant growth form (PGF)	Phanerophyte Hemicryptophyte Chamaephyte Cryptophyte Therophyte Liana Vascular parasite
Seed number (SN)	log (seed number)
Seed mass (SM)	log (seed mass)
Seed shape (SS)	seed shape (corresponding to Vs. From 0: round, to 0.2: disc- or needle-shaped)

APPENDICES

Appendix 1: List of the 232 plant species present in our study area.

Plant species (names are given accroding to TAXREF_V5.0)	Plant family
Achillea millefolium L. 1753	Asteraceae
Actaea spicata L. 1753	Ranunculaceae
Aegopodium podagraria L. 1753	Apiaceae
Agrimonia eupatoria L. 1753	Rosaceae
Agrimonia procera Wallr. 1840	Rosaceae
Agrostis capillaris L. 1753	Poaceae
Aira caryophyllea L. 1753	Poaceae
Ajuga reptans L. 1753	Lamiaceae
Alliaria petiolata (M.Bieb.) Cavara & Grande 1913	Brassicaceae
Allium schoenoprasum L. 1753	Alliaceae
Allium ursinum L. 1753	Alliaceae
Lysimachia arvensis (L.) U.Manns & Anderb.	Primulaceae
Anemone nemorosa L. 1753	Ranunculaceae
Anemone ranunculoides L. 1753	Ranunculaceae
Angelica sylvestris L. 1753	Apiaceae
Anthericum ramosum L. 1753	Anthericaceae
Anthoxanthum odoratum L. 1753	Poaceae
Anthyllis vulneraria L. 1753	Fabaceae
Aquilegia vulgaris L. 1753	Ranunculaceae
Arabis turrita L. 1753	Brassicaceae
Arum maculatum L. 1753	Araceae
Betula nana L. 1753	Betulaceae
Brachypodium sylvaticum (Huds.) P.Beauv. 1812	Poaceae
Briza media L. 1753	Poaceae
Bromus erectus Huds. 1762	Poaceae
Bromus racemosus L. 1762	Poaceae
Calamagrostis arundinacea (L.) Roth 1788	Poaceae
Calamagrostis epigejos (L.) Roth 1788	Poaceae
Caltha palustris L. 1753	Ranunculaceae
Calystegia sepium (L.) R.Br. 1810	Convolvulaceae
Campanula glomerata L. 1753	Campanulaceae
Campanula trachelium L. 1753	Campanulaceae
Cardamine amara L. 1753	Brassicaceae
Cardamine flexuosa With. 1796	Brassicaceae
Cardamine impatiens L. 1753	Brassicaceae
Cardamine pratensis L. 1753	Brassicaceae
Carex acutiformis Ehrh. 1789	Cyperaceae
Carex brizoides L. 1755	Cyperaceae
Carex digitata L. 1753	Cyperaceae
Carex elongata L. 1753	Cyperaceae
Carex flacca Schreb. 1771	Cyperaceae

Carex hirta L. 1753	Cyperaceae
Carex panicea L. 1753	Cyperaceae
Carex pilosa Scop. 1772	Cyperaceae
Carex pilulifera L. 1753	Cyperaceae
Carex remota L. 1755	Cyperaceae
Carex riparia Curtis 1783	Cyperaceae
Carex sylvatica Huds. 1762	Cyperaceae
Carex umbrosa Host 1801	Cyperaceae
Centaurea jacea L. 1753	Asteraceae
Centaurea scabiosa L. 1753	Asteraceae
Centaurium erythraea Raf. 1800	Gentianaceae
Chaerophyllum temulum L. 1753	Apiaceae
Chelidonium majus L. 1753	Papaveraceae
Chrysosplenium alternifolium L. 1753	Saxifragaceae
Lactuca alpina (L.) Benth. & Hook.f. 1876	Asteraceae
Cirsium arvense (L.) Scop. 1772	Asteraceae
Cirsium palustre (L.) Scop. 1772	Asteraceae
Cirsium rivulare (Jacq.) All. 1789	Asteraceae
Convallaria majalis L. 1753	Convallariaceae
Conyza canadensis (L.) Cronquist 1943	Asteraceae
Cornus sanguinea L. 1753	Cornaceae
Corydalis solida (L.) Clairv. 1811	Papaveraceae
Corylus avellana L. 1753	Betulaceae
Crepis paludosa (L.) Moench 1794	Asteraceae
Dactylis glomerata L. 1753	Poaceae
Danthonia decumbens (L.) DC. 1805	Poaceae
Daucus carota L. 1753	Apiaceae
Deschampsia cespitosa (L.) P.Beauv. 1812	Poaceae
Deschampsia flexuosa (L.) Trin. 1836	Poaceae
Dianthus superbus L. 1755	Caryophyllaceae
Digitalis purpurea L. 1753	Plantaginaceae
Digitaria ischaemum (Schreb.) Schreb. ex Mühl. 1817	Poaceae
Epilobium hirsutum L. 1753	Onagraceae
Epilobium montanum L. 1753	Onagraceae
Epipactis helleborine (L.) Crantz 1769	Orchidaceae
Erica tetralix L. 1753	Ericaceae
Eupatorium cannabinum L. 1753	Asteraceae
Euphorbia amygdaloides L. 1753	Euphorbiaceae
Euphrasia stricta D.Wolff ex J.F.Lehm. 1809	Orobranchaceae
Festuca altissima All. 1789	Poaceae
Festuca gigantea (L.) Vill. 1787	Poaceae
Festuca ovina L. 1753	Poaceae
Festuca rubra L. 1753	Poaceae
Filipendula ulmaria (L.) Maxim. 1879	Rosaceae
Filipendula vulgaris Moench 1794	Rosaceae
Fragaria vesca L. 1753	Rosaceae
Fritillaria meleagris L. 1753	Liliaceae
Galanthus nivalis L. 1753	Amaryllidaceae

Galeopsis tetrahit L. 1753	Lamiaceae
Galium aparine L. 1753	Rubiaceae
Galium glaucum L. 1753	Rubiaceae
Galium mollugo L. 1753	Rubiaceae
Galium odoratum (L.) Scop. 1771	Rubiaceae
Galium palustre L. 1753	Rubiaceae
Galium sylvaticum L. 1762	Rubiaceae
Galium verum L. 1753	Rubiaceae
Geranium robertianum L. 1753	Geraniaceae
Geranium sanguineum L. 1753	Geraniaceae
Geranium sylvaticum L. 1753	Geraniaceae
Geum rivale L. 1753	Rosaceae
Geum urbanum L. 1753	Rosaceae
Helianthemum nummularium (L.) Mill. 1768	Cistaceae
Helleborus foetidus L. 1753	Ranunculaceae
Anemone hepatica L. 1753	Ranunculaceae
Heracleum sphondylium L. 1753	Apiaceae
Hieracium laevigatum Willd. 1803	Asteraceae
Hieracium pilosella L. 1753	Asteraceae
Hieracium umbellatum L. 1753	Asteraceae
Holcus lanatus L. 1753	Poaceae
Holcus mollis L. 1759	Poaceae
Hydrocotyle vulgaris L. 1753	Apiaceae
Hypericum hirsutum L. 1753	Hypericaceae
Hypericum humifusum L. 1753	Hypericaceae
Hypericum montanum L. 1755	Hypericaceae
Hypericum perforatum L. 1753	Hypericaceae
Hypericum pulchrum L. 1753	Hypericaceae
Ilex aquifolium L. 1753	Aquifoliaceae
Impatiens noli-tangere L. 1753	Balsaminaceae
Impatiens parviflora DC. 1824	Balsaminaceae
Inula conyza DC. 1836	Asteraceae
Juncus bufonius L. 1753	Juncaceae
Juncus conglomeratus L. 1753	Juncaceae
Juncus effusus L. 1753	Juncaceae
Lamium album L. 1753	Lamiaceae
Lamium maculatum (L.) L. 1763	Lamiaceae
Lamium purpureum L. 1753	Lamiaceae
Lapsana communis L. 1753	Asteraceae
Lathyrus pratensis L. 1753	Fabaceae
Lathyrus sylvestris L. 1753	Fabaceae
Lathyrus vernus (L.) Bernh. 1800	Fabaceae
Leucanthemum vulgare Lam. 1779	Asteraceae
Leucojum vernum L. 1753	Amaryllidaceae
Lilium martagon L. 1753	Liliaceae
Kalmia procumbens (L.) Gift Kron & P.F.Stevens 2002	Ericaceae
Lotus corniculatus L. 1753	Fabaceae
Lunaria rediviva L. 1753	Brassicaceae

Luzula campestris (L.) DC. 1805	Juncaceae
Luzula luzuloides (Lam.) Dandy & Wilmott 1938	Juncaceae
Luzula multiflora (Ehrh.) Lej. 1811	Juncaceae
Luzula pilosa (L.) Willd. 1809	Juncaceae
Lycopus europaeus L. 1753	Lamiaceae
Lysimachia vulgaris L. 1753	Primulaceae
Lythrum salicaria L. 1753	Lythraceae
Maianthemum bifolium (L.) F.W.Schmidt 1794	Convallariaceae
Melampyrum arvense L. 1753	Orobranchaceae
Melampyrum pratense L. 1753	Orobranchaceae
Melampyrum sylvaticum L. 1753	Orobranchaceae
Melica nutans L. 1753	Poaceae
Melica uniflora Retz. 1779	Poaceae
Mentha arvensis L. 1753	Lamiaceae
Mercurialis perennis L. 1753	Euphorbiaceae
Milium effusum L. 1753	Poaceae
Moehringia trinervia (L.) Clairv. 1811	Caryophyllaceae
Molinia caerulea (L.) Moench 1794	Poaceae
Loncomelos pyrenaicus (L.) Hrouda 1988	Hyacinthaceae
Oxalis acetosella L. 1753	Oxalidaceae
Paris quadrifolia L. 1753	Trilliaceae
Pedicularis sylvatica L. 1753	Orobranchaceae
Petasites hybridus (L.) P.Gaertn. B.Mey. & Scherb. 1801	Asteraceae
Phalaris arundinacea L. 1753	Poaceae
Phragmites australis (Cav.) Trin. ex Steud. 1840	Poaceae
Phyteuma spicatum L. 1753	Campanulaceae
Plantago lanceolata L. 1753	Plantaginaceae
Plantago media L. 1753	Plantaginaceae
Poa nemoralis L. 1753	Poaceae
Poa pratensis L. 1753	Poaceae
Poa trivialis L. 1753	Poaceae
Polygala vulgaris L. 1753	Polygalaceae
Polygonatum multiflorum (L.) All. 1785	Convallariaceae
Polygonatum odoratum (Mill.) Druce 1906	Convallariaceae
Polygonatum verticillatum (L.) All. 1785	Convallariaceae
Persicaria bistorta (L.) Samp. 1913	Polygonaceae
Potentilla erecta (L.) Räusch. 1797	Rosaceae
Potentilla recta L. 1753	Rosaceae
Potentilla sterilis (L.) Garcke 1856	Rosaceae
Primula elatior (L.) Hill 1765	Primulaceae
Primula veris L. 1753	Primulaceae
Primula vulgaris Huds. 1762	Primulaceae
Pulicaria dysenterica (L.) Bernh. 1800	Asteraceae
Pyrola minor L. 1753	Ericaceae
Ranunculus acris L. 1753	Ranunculaceae
Ranunculus ficaria L. 1753	Ranunculaceae
Ranunculus repens L. 1753	Ranunculaceae
Rhinanthus minor L. 1756	Orobranchaceae

Ribes rubrum L. 1753	Grossulariaceae
Ribes uva-crispa L. 1753	Grossulariaceae
Rubus caesius L. 1753	Rosaceae
Rubus idaeus L. 1753	Rosaceae
Rubus saxatilis L. 1753	Rosaceae
Rumex acetosa L. 1753	Polygonaceae
Rumex acetosella L. 1753	Polygonaceae
Rumex obtusifolius L. 1753	Polygonaceae
Rumex sanguineus L. 1753	Polygonaceae
Sagina procumbens L. 1753	Caryophyllaceae
Salvia pratensis L. 1753	Lamiaceae
Saponaria officinalis L. 1753	Caryophyllaceae
Saxifraga granulata L. subsp. granulata	Saxifragaceae
Scirpus sylvaticus L. 1753	Cyperaceae
Scrophularia nodosa L. 1753	Scrophulariaceae
Jacobaea vulgaris Gaertn. 1791	Asteraceae
Silene dioica (L.) Clairv. 1811	Caryophyllaceae
Silene nutans L. 1753	Caryophyllaceae
Silene vulgaris (Moench) Garcke 1869	Caryophyllaceae
Solanum dulcamara L. 1753	Solanaceae
Solidago virgaurea L. 1753	Asteraceae
Stachys officinalis (L.) Trévis. subsp. officinalis	Lamiaceae
Stachys sylvatica L. 1753	Lamiaceae
Stellaria graminea L. 1753	Caryophyllaceae
Stellaria holostea L. 1753	Caryophyllaceae
Stellaria media (L.) Vill. subsp. media	Caryophyllaceae
Stellaria nemorum L. 1753	Caryophyllaceae
Succisa pratensis Moench 1794	Dipsacaceae
Teucrium scorodonia L. subsp. scorodonia	Lamiaceae
Thymus serpyllum L. subsp. serpyllum	Lamiaceae
Trifolium campestre Schreb. 1804	Fabaceae
Trifolium medium L. 1759	Fabaceae
Trollius europaeus L. 1753	Ranunculaceae
Tussilago farfara L. 1753	Asteraceae
Urtica dioica L. 1753	Urticaceae
Vaccinium myrtillus L. 1753	Ericaceae
Vaccinium vitis-idaea L. 1753	Ericaceae
Valeriana dioica L. 1753	Valerianaceae
Verbascum nigrum L. 1753	Scrophulariaceae
Verbascum thapsus L. 1753	Scrophulariaceae
Veronica chamaedrys L. 1753	Plantaginaceae
Veronica montana L. 1755	Plantaginaceae
Veronica officinalis L. 1753	Plantaginaceae
Viburnum opulus L. 1753	Caprifoliaceae
Vicia cracca L. 1753	Fabaceae
Vicia sepium L. 1753	Fabaceae
Viola palustris L. 1753	Violaceae

DISCUSSION

I. Rappel des résultats

Mon travail visait dans un premier temps à comprendre les interactions plantes-animaux dans le cadre de la dispersion zoochore, pour ensuite étudier la résultante de cette interaction en termes de composition fonctionnelle à échelle des communautés de plantes dispersées.

J’ai montré que la dispersion zoochore a un effet filtre sur les espèces transportées et leurs traits. L’interaction entre les traits du vecteur et des graines semble peu influer sur la probabilité de transport des graines, notamment dans le cas de l’endozoochorie, qui est apparu comme un processus peu sélectif. En revanche, l’interaction entre les traits des graines et du vecteur influe sur les durées de rétention qui déterminent les distances de dispersion. Les graines dispersées par endozoochorie possèdent une large gamme d’attributs morphologiques analogue à celle de la flore régionale, mais la zoochorie filtre les espèces en sélectionnant l’assemblage d’espèces dispersées en fonction de l'habitat dans lequel se nourrit le vecteur. De plus, l’endozoochorie impose un coût élevé aux plantes transportées, là encore modulé par l’interaction entre les traits des plantes et des vecteurs. Toutefois, à grande échelle spatiale, les patrons de diversité des communautés semblent peu affectés par la zoochorie, en particulier l’endozoochorie, relativement aux effets d’autres processus incluant les gradients environnementaux, l’herbivorie et les autres modes de dispersion.

II. Implications des résultats

Compromis coûts-bénéfices de la zoochorie

Si la dispersion endozoochore confère un avantage aux plantes, elle impose aussi un coût (Article 1). L'herbivorie, à travers la consommation et la destruction de parties entières de la plante voire des graines, crée de la mortalité locale ; mais en contrepartie, elle est à l'origine de flux de gènes, par la dispersion des graines (Vellend et al., 2006). On peut alors se demander quel est le coût de l'herbivorie relatif à l'avantage d'être dispersé et de coloniser de nouveaux habitats. Vellend et al. (2006) ont montré que ce compromis dépend de l'abondance des vecteurs. En effet, les taux de migration et donc de dispersion de *Trillium grandiflorum* sont maximum pour des taux d'herbivorie inférieurs à 15 %. Il existe donc une abondance optimale de vecteurs au-delà de laquelle l'effet de l'herbivorie dépasse celui de la dispersion. Toutefois, si les vecteurs sont très sélectifs concernant leur habitat, la dispersion dirigée prédomine et la probabilité que les graines transportées soient déféquées dans un habitat favorable augmente (Wenny and Levey, 1998). De plus, j'ai montré que la durée du transport, et donc la distance de dispersion implique un coût qui se traduit par une réduction de la probabilité de germination. Ainsi, il existe un compromis entre l'avantage de pouvoir coloniser un nouvel environnement et le coût lié à la faible probabilité de germination. Des adaptations morphologiques réduisent ce coût, notamment les téguments imperméables qui résistent bien aux attaques des enzymes digestives et qui permettent aux graines d'être viables et aptes à germer après avoir transité longtemps dans le tube digestif. La dispersion zoochore implique donc deux catégories de compromis. En premier lieu, les compromis liés à l'abondance et à la spécialisation des vecteurs font varier la probabilité qu'une graine soit transportée et déféquée dans un habitat adéquat, donc colonisable. D'autre part, les compromis liés au coût du transport lui-même influent principalement sur la viabilité des graines après leur immigration.

Distribution locale des populations de plantes

Mes travaux montrent que l'endozoochorie en particulier pourrait contribuer à modifier les patrons locaux de distribution, en particulier en favorisant l'intrusion des espèces de milieux ouverts dans les espaces forestiers. En effet, j'ai montré que les ongulés sauvages dispersent préférentiellement des espèces de milieux ouverts (Article 3). Etant donné que ces animaux sont inféodés au milieu forestier, il est probable que des quantités importantes de graines d'espèces de milieux ouverts soient disséminées au sein du milieu forestier. De plus, les espèces dispersées sont souvent celles qui possèdent une banque de graines à longévité élevée (Mouissie et al., 2005; Pakeman et al., 2002). Ainsi, bien qu'étant dispersées dans un habitat à priori défavorable, avec peu de luminosité, les espèces de milieux ouverts pourraient tirer profit des bords de chemin forestiers, des troués dans la canopée, ou encore des coupes pour l'exploitation forestière, pour s'établir dans des milieux intra-forestiers. Afin de mieux comprendre les implications de tels processus sur les dynamiques de populations des espèces de milieux ouverts, il est nécessaire de mieux étudier la manière dont les interactions plantes-animaux (hors herbivorie, déjà bien étudiée) affectent les patrons de distribution des plantes.

Modèles de distribution à échelle biogéographique

La plupart des modèles qui visent à prédire les distributions futures des espèces face à des modifications de leur environnement (réchauffement climatique, changement d'usage des sols) sont presque exclusivement basés sur des variables abiotiques (climat) et/ou liées à l'utilisation des sols (Guisan and Thuiller, 2005; Thuiller et al., 2008). De précédents travaux ont montré qu'introduire la dispersion améliorait nettement la capacité prédictive de ces modèles (Boulangeat et al., 2012), assez logiquement d'ailleurs car on sait que les flux d'individus sont critiques dans l'établissement des marges d'aires de distribution (Sexton et al., 2009) et la structure spatiale des populations à l'intérieur de ces aires (Hanski, 1998). Cependant, la dispersion n'a été pour l'instant incorporée dans les modèles de distribution que sous la forme de fonctions kernel de la distance entre populations, non explicites quant aux processus sous-jacents (Boulangeat et al., 2012). De plus, les interactions interspécifiques commencent seulement à être introduites dans ces modèles, le plus souvent sous la forme de matrices de cooccurrence entre espèces compétitrices (Boulangeat et al., 2014; Heikkinen et al., 2007). Mes résultats suggèrent que l'endozoochorie, comme l'épizoochorie (Picard and Baltzinger, 2012), modifient la structure des assemblages de graines dispersées par rapport à la flore régionale, et donc que l'influence de la dispersion sur les patrons de distribution des plantes varie selon le ou les mode(s) de dispersion impliqué(s), l'échelle spatiale et les vecteurs disponibles. Si les modèles qui prennent en compte la dispersion et la compétition sont clairement un progrès par rapport à la première génération de modèles de distribution, une nouvelle étape cruciale pour améliorer leur qualité prédictive serait de prendre en compte explicitement l'existence d'une interaction entre le processus de dispersion et la coexistence entre une plante et ses vecteurs. L'utilisation de modèles prédictifs de la distribution des plantes, à partir des relations entre les traits et les capacités/distances de dispersion connues, pourrait être une solution. L'ajustement de ces modèles pourrait ensuite être testé sur des communautés réelles, et permettrait sans doute de mieux mettre en valeur le signal de la dispersion à échelle des communautés.

Effet filtre de la zoochorie sur l'assemblage des communautés

A chacune des étapes de la dispersion, ce ne sont pas les mêmes traits animaux et végétaux qui interviennent. Lors de l'émigration, ce sont l'architecture et la phénologie de la plante mère, la morphologie et l'abondance des graines et les préférences alimentaires et d'habitat du vecteur qui déterminent la probabilité de prise en charge des graines (voir Introduction). Lors du transfert, la plante mère n'intervient plus et c'est la forme et la taille des graines, ainsi que la masse corporelle et le mode de digestion du vecteur qui déterminent le temps de rétention (Article 1). En effet, j'ai montré que l'interaction entre les traits des graines et des vecteurs influence le temps de rétention des graines. Enfin, c'est la viabilité des graines excrétées, en interaction avec les conditions biotiques et abiotiques sur le microsite d'excrétion, qui détermine si l'immigration se termine ou non par la germination des graines (voir Introduction). Ainsi, une modélisation mécaniste du processus de dispersion devrait distinguer les différentes étapes du processus, leurs influences relatives et les facteurs qui les modulent.

A l'échelle des assemblages locaux de graines, l'effet filtre de l'endozoochorie est bien marqué, puisque les vecteurs tendent à sélectionner les espèces de milieux ouverts et que l'interaction entre les traits des graines et des vecteurs influe sur les temps de rétention, qui eux-mêmes influent sur les distances de dispersion (Articles 1 à 3). Cependant, à grande échelle et dans les communautés de plantes, la zoochorie ne semble pas avoir d'effet (Article 5). Dans le contexte de l'étude de la dispersion, le fait de ne s'intéresser qu'à un mode de dispersion en particulier est peut-être trop réducteur. Isoler le processus de dispersion zoochore permet de mieux comprendre ses mécanismes, notamment l'effet de l'interaction plante-animal ; mais la dispersion zoochore seule ne permet pas d'expliquer la variabilité observée dans les patrons de composition des communautés végétales. Ces résultats laissent penser que d'autres filtres agissent sur les assemblages des communautés après l'événement de dispersion, sur l'établissement des plantules et les plantes adultes. En effet, les filtres environnementaux, d'autres interactions biotiques (compétition, prédation, mutualisme) et d'autres modes de dispersion influent également sur les patrons de composition des communautés végétales (Nathan et al., 2002; Ricklefs, 2004). Une étude de la composition de la banque de graines permettrait probablement d'observer un signal plus marqué de la zoochorie, car les processus cités précédemment n'auraient pas encore agit.

Plusieurs événements de dispersion peuvent avoir lieu en parallèle pour les graines d'une même plante, ou bien se succéder : d'abord la dispersion primaire, puis la dispersion secondaire. Afin de déterminer de façon optimale la distribution des graines qui résulte de la dispersion, il faudrait prendre en compte la séquence entière des événements de dispersion (Roth and Vander Wall, 2005; Figure 13).

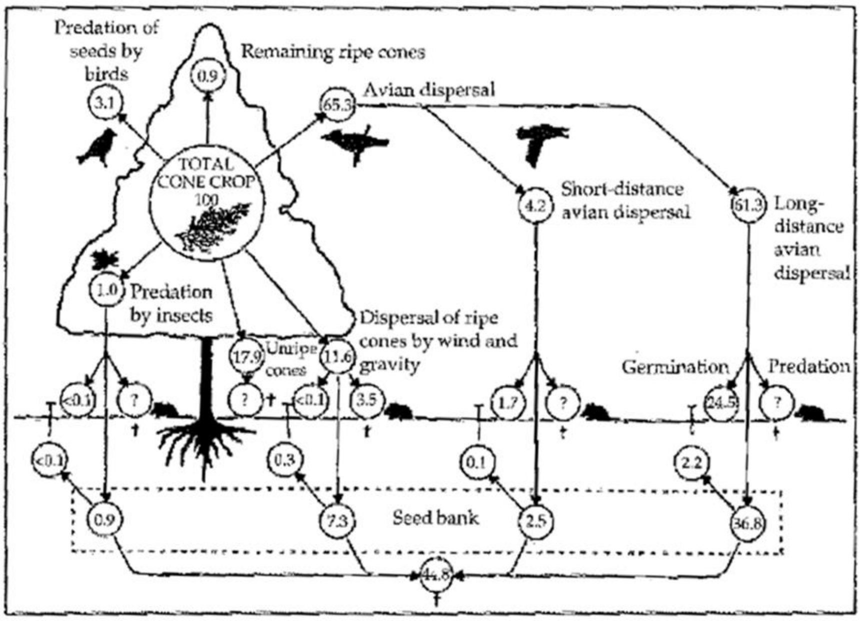

Figure 13 : Exemple d'un réseau de dispersion, dans le cas de *Juniperus virginiana*. (D'après Roth et Vander Wall 2005).

III. Développements futurs

J’ai montré que l’interaction entre les traits du vecteur et des graines influe sur les durées de rétention qui déterminent les distances de dispersion. Nous avons également calculé les distances de dispersion associées aux temps de rétention des graines. Toutefois, nous n’avons pas étudié les conséquences de ces distances de dispersion en termes de distribution spatiale de la banque de graines dispersée. Dans cet objectif, les données obtenues suite à mon travail de thèse (distributions des temps de rétention et des distances de dispersion) pourraient servir à calibrer un modèle de dispersion qui prenne en compte l'effet des traits des vecteurs et des plantes (Will and Tackenberg, 2008) (voir Figure 14). Ce travail de modélisation permettrait de visualiser la distribution spatiale des graines dispersées, les fréquences de distribution des distances de dispersion (définition de fonctions kernel de dispersion) et les fréquences d’immigration des graines dans les différents types d’habitats (voir par exemple D’hondt et al., 2012). Grace à la modélisation, il est aussi possible de faire varier les conditions d’habitat, comme par exemple le degré de fragmentation d’un habitat donné, pour étudier l’effet de la configuration paysagère sur la distribution des graines dispersées et leur habitat d’immigration. Le modèle envisagé serait individu-centré, l’individu étant l’animal vecteur, et basé sur des sources multiples de graines, c’est-à-dire sur les graines de différentes espèces, disponible dans l’habitat de nourrissage du vecteur animal (voir Figure 14). Le principal challenge des approches de modélisation réside avant tout dans la mise à l’épreuve du modèle, faute de données spatialisées à la résolution adéquate permettant de caractériser les banques de graines : des collaborations étroites entre modélisateurs et opérateurs de terrain seraient ici plus que jamais nécessaires.

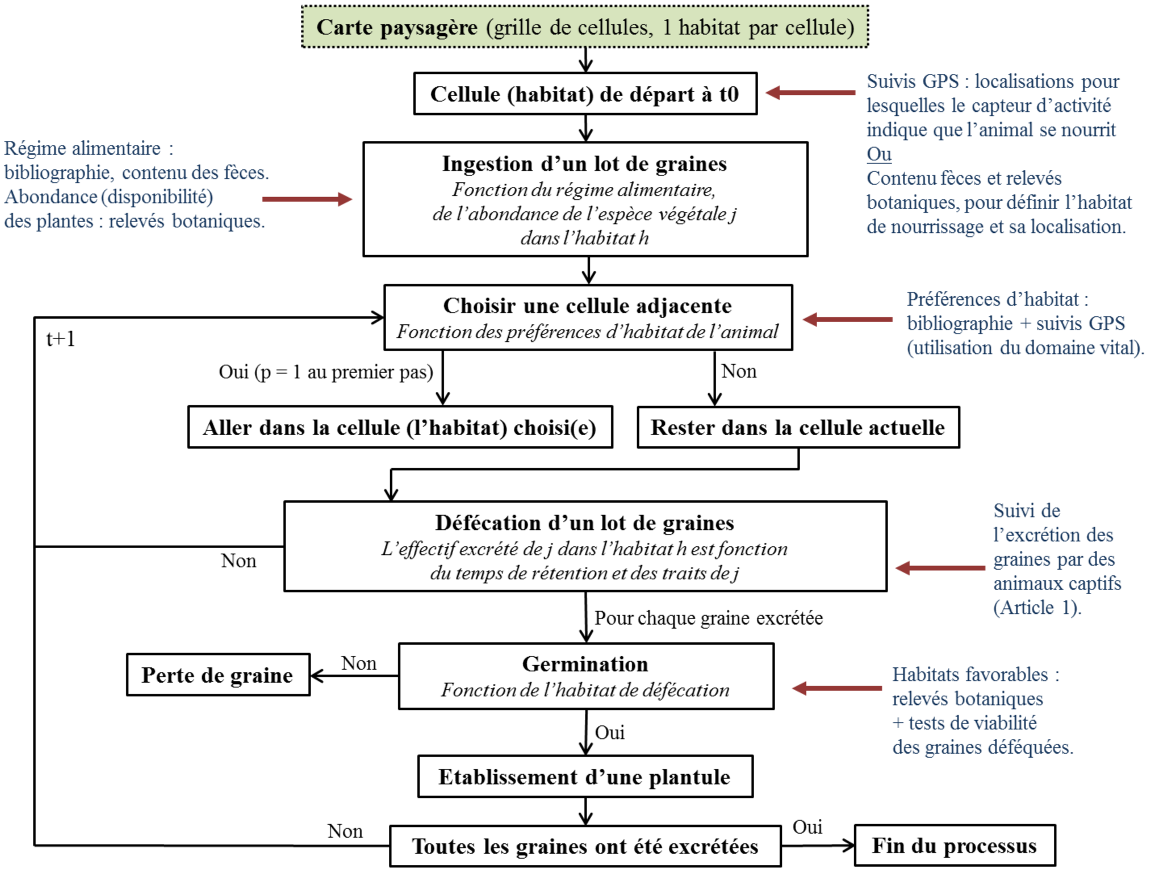

Figure 14 : Exemple de schéma de modèle. La carte paysagère peut correspondre à un paysage réel ou fictif, sur lequel serait apposée une grille, avec un type d'habitat attribué à chaque cellule, et pour chaque type d'habitat, une valeur de préférence ou de résistivité pour l'animal vecteur. Le texte en bleu et les flèches rouges indiquent les données nécessaires à la calibration du modèle.

Les activités humaines peuvent affecter les processus de dispersion. En Europe, l'instauration de plans de chasse, qui fixent des quotas de prélèvement des ongulés sauvages, a finalement conduit, avec d'autres facteurs (passerelles à gibier et baisse de la moralité routière, augmentation de la fréquence des hivers doux) à l'augmentation des densités de populations d'ongulés (Figure 11), influant ainsi sur la quantité de vecteurs disponibles pour les plantes, la dynamique des liens entre sous populations de plantes, mais impliquant aussi les conséquences négatives sur leur fitness dues à l'herbivorie (Vellend et al., 2006). Avec l'abandon de l'agriculture traditionnelle et du pâturage extensif (transhumances par exemple), le potentiel de dispersion a en revanche nettement diminué dans les milieux prairiaux (Poschlod et al., 1998), c'est pourquoi les ongulés domestiques comme les chevaux, les ânes, les vaches, les moutons ou les chèvres sont de plus en plus utilisés en tant qu'agents de dispersion permettant la restauration et le maintien des populations végétales (Couvreur et al., 2004; Poschlod et al., 1998; Rico et al., 2014; et voir Annexe 3, Article 7). Cependant, la disponibilité accrue des vecteurs peut aussi favoriser la dispersion d'espèces exogènes. Par exemple, le sanglier peut disperser des espèces en provenance des terres agricoles ou des zones urbaines au sein d'une réserve (Dovrat et al., 2012) ; tandis que des espèces introduites peuvent être dispersées dans le milieu forestier ou sur de longues distances par les grands herbivores comme les cervidés ou les vaches (Bartuszevige and Endress, 2008; Eschtruth and Battles, 2009; Vavra et al., 2007). Ainsi, en manipulant les densités de vecteurs et leurs possibilités de mouvement sur de plus ou moins longues distances, les activités humaines influencent les flux de graines dispersées. L'Homme disperse également des graines, et ce sur des distances de dispersion répertoriées comme étant plus longues que pour n'importe quel autre vecteur animal (Auffret et al., 2014; Vittoz and Engler, 2007; Tableau 1).

Autre perspective :

L'endozoochorie est peu sélective dans nos sites d'étude en milieu tempéré, on peut donc se demander s'il en est de même en milieu tropical, où les espèces végétales et animales frugivores sont plus nombreuses (Hillebrand, 2004). Jordano (1987) a montré que la spécificité moyenne entre une plante et son disperseur est plus forte en présence d'une forte diversité d'espèces. On pourrait donc tester la prédiction selon laquelle plus on s'éloigne des tropiques, moins la zoochorie a d'effet sur la composition fonctionnelle des communautés végétales. On peut s'attendre à des disperseurs généralistes comme les ongulés européens en milieu tempéré *versus* des mutualismes plus spécifiques sous les tropiques. On pourrait donc tenter de comparer l'importance évolutive de la zoochorie et/ou la force des interactions plantes-animaux entre différents biomes.

CONCLUSION

La dispersion zoochore, et en particulier l'interaction entre les traits des graines et des vecteurs, influe sur les distances de dispersion, et par conséquent sur les dynamiques des métapopulations et des métacommunautés. La dispersion est aussi le processus par lequel les espèces répondent aux changements de leur environnement.

Les perturbations environnementales, qu'elles soient ou non le fait de l'Homme, affectent les capacités de dispersion des espèces (Hanski, 1998). La dispersion est à la fois le processus qui permet aux espèces de faire face aux modifications de l'environnement, *via* l'extension ou le décalage de leur aire de répartition ; et le processus par lequel s'effectue la sélection sur les traits associés à la capacité de dispersion. La dispersion est donc à la fois sujet et objet de sélection (Starrfelt and Kokko, 2012), et est un processus central dans la dynamique des populations, et dans la capacité des espèces à faire face aux changements globaux.

Dans le contexte actuel des changements globaux, et notamment du réchauffement climatique, la question de la composition taxonomique et fonctionnelle des communautés végétales du futur reste largement ouverte. Les réponses aux changements climatiques sont largement idiosyncratiques, et les disparités entre espèces ont notamment été liées à leurs différences de capacité de dispersion (Devictor et al., 2012; Ricklefs, 2004). Les fourmis de feu (*Solenopsis invicta*), originaire d'Amérique du Sud, ont envahi les forêts de Géorgie (Etat du Sud-Est des Etas-Unis) (Ness, 2004). Elles sont particulièrement nombreuses dans les forêts fragmentées, où elles dispersent de plus grandes quantités de graines que les fourmis indigènes, mais sur des distances beaucoup plus courtes (< 10 cm), qui ne permettent pas aux jeunes plantules d'échapper à la compétition avec la plante mère (Ness, 2004). Cet exemple montre comment l'arrivée d'une nouvelle espèce au sein d'une communauté peut avoir des effets délétères sur les distances de dispersion des graines et les interactions entre les plantes et les espèces animales indigènes. Des différences de capacités de dispersion entre espèces devraient par conséquent mener à de nouveaux types d'interactions et à la construction de communautés non analogues (Blondel, 2012).

A travers cette thèse, j'ai tenté de montrer comment un processus particulier influence les dynamiques des espèces et des communautés. Sur le plan méthodologique, j'ai mis en valeur la nécessaire complémentarité entre approches expérimentales et corrélatives, l'une et l'autre répondant à une partie de ma question, mais ni l'une, ni l'autre ne pouvant y répondre isolément. Sur le plan conceptuel, j'ai montré que la dispersion n'est pas un processus unique, mais un ensemble de processus modulé par les interactions interspécifiques, et dont les conséquences dépendent de l'échelle spatiale. Ainsi, je dépasse la traditionnelle hiérarchie entre les filtres d'assemblage des communautés, pour proposer un cadre de travail où les filtres (c'est-à-dire les processus) eux-mêmes sont en interaction. Enfin, sur le plan appliqué, j'ai montré que les ongulés peuvent avoir un effet sur les communautés de plantes au-delà de l'herbivorie, mais dont la complexité et la dépendance aux échelles spatiales et aux assemblages régionaux d'espèces limite la capacité des modèles actuels à prédire l'effet.

Ainsi, ma thèse contribue à suggérer que l'étude des processus qui influent sur la dynamique des communautés de plantes, et donc sur notre capacité à prédire les dynamiques futures, doit impliquer non seulement une succession de processus parmi lesquels les interactions plantes-animaux, les filtres environnementaux et la dispersion, mais aussi les relations entre ces multiples processus.

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ANNEXES

ANNEXE 1

Article 6

Hitch-hiking in the wild: should seeds rely on ungulates?

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Abstract

Background – Seed dispersal appears to be a key process in maintaining plant population and community dynamics, even more so in the current context of global warming and landscape fragmentation. Wild ungulates, due to their capacity to cover long distances in a large variety of habitats, are potential vectors of long-distance dispersal for plants.

Methods – In order to estimate their role as seed dispersal vectors, we conducted a cross-species comparative approach on three common wild ungulates: roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*). We brushed the fur and hooves of animals shot in Loiret forests during the hunting season and counted and identified the seeds transported on the animals' bodies.

Results – We found seeds from 41 different plant species, 24% of which were found in the cleft of the hoof. Wild boar transported 85% of the species identified (versus 34% and 7% for roe and red deer respectively). More seeds from plants representing a greater variety of dispersal modes were carried by wild boar. Less than 50% of the transported plants were epizoochorous species. Moreover, the plants transported were mainly non forest or periforest light-demanding species. We also showed that wild boar is a vector for plants not specifically adapted to external dispersal, whereas red and roe deer are more prone to move epizoochorous species.

Conclusion – Globally, our naturalist approach confirmed that common large ungulates are indeed effective vectors plants can rely on. Moreover, since many types of seeds are concerned, ungulates' specific role in plant dispersal should be reconsidered.

Key words – Seed dispersal, epizoochory, dispersal mode, *Sus scrofa*, *Capreolus capreolus*, *Cervus elaphus*.

INTRODUCTION

Seed dispersal is a key process in determining plant populations and community dynamics. Particularly, long-distance dispersal events (> 100 m for plants, Cain et al. 2000), though rare, are crucial to maintaining the connectivity between isolated populations necessary for plant species to survive at the regional scale (Will & Tackenberg 2008). Long-distance dispersal by large herbivores also accounted for the plant migration rates during the Holocene (Pakeman 2001). Understanding long-distance dispersal mechanisms and their consequences is critical in a context of rapidly changing environments under the effects of global change (Shupp et al. 2010). Because plants are fixed, their mobility relies on vectors that may be abiotic like wind (anemochory) and water (hydrochory), or biotic (zoochory) (Ridley 1930). Wind and water disperse few species over long distances (Mouissie et al. 2005, Schmidt et al. 2004) and wind is ineffective inside forest stands (Howe & Smallwood 1982). Birds and mammals are therefore the main vectors for long-distance seed dispersal within and among forest areas. While birds seem to disperse specific plants according to their diet (endozoochory), large herbivores, compared to small-bodied rodents, might be able to disperse many plant species in their fur due to a larger surface available for hitching seeds. For example, the role of roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) in the expansion of Green Hound's-tongue (*Cynoglossum germanicum* Jacq.) through external dispersal has recently been highlighted (Boulanger et al. 2011).

Wild ungulates provide useful models for the study of long-distance plant dispersal and distributional dynamics under changing landscapes. First, roe deer, red deer and wild boar

(*Sus scrofa*) populations have been increasing in Europe, and particularly in France, since the 1970's. The number of animals killed by hunting has increased ninefold over the last forty years, reaching over 500,000 individuals for both roe deer and wild boar and 50,000 for red deer in 2010 (Source: 'Réseau Ongulés sauvages ONCFS-FNC-FDC').
Second, due to their large home ranges and high travel speed, wild ungulates move over long distances and through a wide diversity of open and closed habitats (Heinken et al. 2002).

In this study, our aim is to highlight the role of these three wild forest ungulates as potential long-distance seed dispersers, by external transport on their body, i.e. epizoochory. Zoochory has generally been studied using information gathered in floras or based on seed attributes, or sometimes even common sense. We deliberately chose a naturalist approach. We identified seeds directly collected on the wild animals' bodies (on fur and in the clefts of hooves) so as to address the following three questions:

(1) Do the three studied ungulates differ in their ability to move seeds? We hypothesized that large-bodied animals would be more effective due to more available hitching-hiking surface for seeds. We therefore expected a higher number of seeds to be transported by red deer than by roe deer.
(2) Which plant traits might enhance dispersal probability? First, epizoochorous diaspores have adapted morphologically to catch on animals’ fur. We therefore expected to collect a higher proportion of epizoochorous seeds on the animals studied. What is more, such seeds should be more numerous on the fur than in the hooves, and more numerous on deer species than on wild boar, for which external dispersal should mainly rely on their wallowing activities (a muddy crust is often visible on wild boar fur).
(3) Do the collected seeds originate from both closed and open areas? Wild ungulates' home ranges are composed of diverse habitats and this should increase the diversity of the seeds identified.

The answers we obtained to these questions have helped us to better determine the influence of animal and seed traits on the dispersal process, and consequently on the distributional patterns of plants.

MATERIALS AND METHODS

Animal species and hunting areas

We used a cross-species comparative approach on the three most common wild forest ungulates in France and Europe, which are easily accessible through the practice of hunting: the roe deer, a browser ruminant species; the red deer, a browser/grazer ruminant species (Hoffman 1989); and the wild boar, an omnivorous-frugivore non-ruminant species. Comparing these three species is pertinent due to their ecological differences in terms of body size, fur structure, home range and diet (see table 1), all of which may influence the dispersal process. Samples were collected on animals shot in Loiret forests (France) (fig. 1): the Domaine des Barres and the Forêt de Montargis, inhabited by both roe deer and wild boar, and the Massif de Lorris where red deer are present. The forests were chosen for the presence/absence of red deer and for variations in the abundance of both roe deer and wild boar. The Domaine des Barres and the Forêt de Montargis are dominated by sessile oak (*Quercus petraea* (Matt.) Liebl.) and hornbeam (*Carpinus betulus* L.) stands and the Massif de Lorris is composed of sessile oak and Scots pine (*Pinus sylvestris* L.) in pure and mixed stands.

Assessing epizoochorous transport

We collected seeds transported by 51 animals (29 roe deer, five red deer and seventeen wild boar) shot from October 2009 to February 2010 in the three forests (appendix 1). Killed animals were placed on a tarp. We removed all debris from the hooves with a toothbrush and brushed out the fur entirely with a louse comb (tooth space 0.3 mm). For large animals (> 30 kg) which had been dragged through the woods after being killed, seeds may have been lost or gained after death. In that case, to limit the over- or underestimation of the number of transported seeds, we did not brush the part of the body which had been dragged on the soil. The diaspores collected were dissected under a stereo microscope for seed counting and identification according to morphological characteristics (length, width, shape, colour, surface reflection…) from Cappers et al. (2006) and Pujol et al. (2007) and reference photographs. We estimated the mean number of seeds and plant species transported by each animal species both on the fur and in the hooves.

Comparison between transported plants and the local flora

Plant species observed in all the districts belonging to the three forests were considered to be the local flora. The list of plant species present in each district was obtained from the Conservatoire Botanique National du Bassin Parisien (available online at http://cbnbp.mnhn.fr/cbnbp/observatoire/collTerrForm.jsp). Authorship for each species is given in appendix 2. For each plant species identified, from the list of local flora or transported by the animals, the main dispersal mode and the main habitat were obtained from Julve (1998) and the L-Ellenberg index from Ellenberg et al. (1991) (see appendix 2 for transported species). The main dispersal modes were anemochory (by wind), autochory (by the plant itself), barochory (by gravity), diszoochory (lost by animals), endozoochory (internally by animals), epizoochory (externally by animals), hydrochory (by water) and myrmecochory (by ants). The main habitats defined were forest (for woodlands, undergrowth and creeper patches), periforest (for perennial waste lands, forest edges, glades and moors), open (for annual waste lands, grasslands, meadows and cultivated lands) or hygrophile (for marshes). We defined two class ranges based on the L-Ellenberg index: from 1 to 5 for shade-loving plants which do not require much light to grow, and from 6 to 9 for light demanding species, which require high quantities of light. For certain plants only determined to genus level, we attributed the ecological trait value when it was shared by all the species within the same genus present in the local flora (see above). Plants for which the ecological traits could not be obtained (NA in appendix 2) were discarded from the analyses.

Statistical analyses

Within- and among-species variations in animals -- In the Domaine des Barres, we were only able to obtain data for roe deer, though wild boar is also present in this forest. Red deer only occurs in the Massif de Lorris. We therefore used Kruskall-Wallis tests to compare the number of transported plant species and diaspores among roe deer, red deer and wild boar in the Massif de Lorris, and between roe deer and wild boar in the Forêt de Montargis separately. We also used the same approach to compare intra-specific variations for roe deer among all 3 studied forests. In case of significant differences among animal species or study sites, we used Kruskall-Wallis tests to conduct pairwise comparisons.

Ecological traits of transported plants -- To determine whether or not epizoochorous species were more dispersed than other plant species, we compared epizoochorous species in our samples to those present in the local flora of the Loiret. In addition, we compared the number of epizoochorous species on fur vs. hooves, and in cervidae vs. wild boar, through pairwise comparisons relying on Fisher's exact test (Crawley 2005). The whole analysis was carried out using the R software (R Development Core Team 2010, stats package), with a $p = 0.05$ threshold.

RESULTS

Altogether we identified 651 diaspores corresponding to 41 plant species. Ten percent of the seeds could not be identified. Only certain plant species (24%) were found in the cleft of the hoof. The five most abundant species identified in fur were, in decreasing order, *Chenopodium* sp., *Betula pendula*, *Rubus fruticosus*, *Brachypodium sylvaticum* and *Geum urbanum*, and they were essentially dispersed by wild boar. *Betula pendula* was the only species encountered on all three animal species, both on the fur and in the hooves. Ninety-four percent of the wild boar sampled carried seeds on their fur and 88% carried seeds in their hooves, thus revealing that wild boar is an important dispersal vector. When we pooled all the samples, wild boar transported 85% of the 41 species identified, while roe deer transported 34% and red deer only 7%.

Within- and among-species variations in animals

The species most frequently found on red and roe deer were similar, with first Poaceae species and then *Betula pendula*. However, we obtained a different pattern for wild boar: *Betula pendula* was the most frequent species, followed in decreasing order by *Chenopodium* sp., *Geum urbanum* and the Poaceae species. We identified fourteen different plant species on roe deer: ten in the Domaine des Barres, three in Lorris and four in Montargis with only one species common to Lorris and Montargis. There were no significant differences either in the number of species or in the number of diaspores carried by roe deer among the three sites ($\chi^2_{(2)} < 3.69$ for number of species, number of diaspores both on fur and in hooves).

We identified 35 different plant species on wild boar, sixteen in Lorris and 28 in Montargis, nine of which occurred on both sites. In Montargis, 29 different species were described, four on roe deer and 28 on wild boar, with three plant species common to both ungulates. Of the nineteen different species identified in Lorris, red and roe deer carried three species each, with one in common to both cervidae. Wild boar carried sixteen plant species, two of which were also carried by deer.

Differences exist for seeds dispersed on fur among the three animal species, both in terms of number of plant species and number of seeds (table 2). Wild boar appeared to be the best disperser in both cases, with seeds not only on fur but also in hooves (fig. 2). Roe deer and red deer did not differ significantly (table 2). Wild boar transported on average 6.4 ± 4.4 plant species and 34.4 ± 40.6 seeds on their fur, versus 2.4 ± 1.0 species and 3.2 ± 1.5 seeds for red deer and 1.2 ± 1.3 species and 1.7 ± 2.0 seeds for roe deer.

Ecological traits of transported plants

The majority of transported plants were epizoochorous (n = 19), while other modes of dispersal were less represented (see table 3). We found no significant differences in the number of epizoochorous species dispersed among the three animal species (Fisher Exact tests: Cc vs. Ce p = 0.27, Cc vs. Ss p = 0.89 and Ce vs. Ss p = 0.31). Among these epizoochorous species, the majority was found on the animals' fur. Other plant species dispersed by wild boar belonged to more varied modes of dispersal (n = 5 modes, epizoochory, barochory, anemochory, endozoochory, hydrochory) than the ones found on roe deer (n = 3) and red deer (n = 2). The proportion of epizoochorous species was higher in our samples than in the local flora (transported plants vs. local flora, Fisher Exact tests: p = 0.00079). In terms of main habitat and L-Ellenberg index, plant species were dispersed according to their representation in the local flora (transported plants vs. local flora, Fisher Exact tests: main habitat p = 0.70, L-Ellenberg p = 1; table 3). In our samples, light-demanding plant species and those from non forest and periforest dominated. The few forest-specific species that we encountered in our samples were essentially tree species such as *Betula pendula*, *Carpinus betulus* and *Pinus sylvestris*.

DISCUSSION

Our naturalist approach based on field observations allowed us to highlight the potential of common wild ungulates as seed vectors and should also help to update information on species dispersal modes. Former studies rarely considered seeds on fur and in hooves separately, even though this distinction can help to test relevant hypotheses. Moreover, our cross-species comparative approach helped us to understand which characteristics affected their potential as seeds vector the most.

We found that roe deer, red deer and, especially, wild boar moved a great number of plant species and seeds externally. Our results are in agreement with Heinken & Raudnitschka (2002), who found 55 plant species on roe deer and wild boar bodies under similar forest conditions during the hunting season.

Methodological insights

The methodology we chose allowed us to determine seeds that were effectively transported on the animal's body. This method proves to be efficient and not very time consuming. However, our seed counts were probably biased due to the difficulty in identifying all the seeds. We have therefore planned to place the seeds collected in growth chambers under controlled conditions and will later transplant the seedlings into greenhouses (Cosyns 2004) to confirm the species identified under stereo microscope and to identify the unknown species. This second process will involve much more time and require more expensive equipment. However, combining microscopic observations and germination tests will no doubt improve the identification process, even though all the seeds are not likely to germinate and an underestimation of the number of dispersed seeds will still remain.

Within- and among-species variations in animals

We found differences among animal species in their ability to move seeds but, contrary to what we expected, red deer and roe deer were very similar both in the number of species and diaspores transported. Moreover, in the Massif de Lorris, roe deer and red deer had one species in common, *Betula pendula*, even though they only carried three different species each. Thus, relative to our first hypothesis, it seems that roe deer is more efficient than red deer as a seed vector. As we globally identified a greater variety of seeds on roe deer than on red deer, we may assume that smaller animals optimize their contact with the lower stratum of the vegetation.

However, like Heinken et al. (2002), we found that wild boar is the most effective disperser, with more species and more seeds dispersed, both on fur and in hooves. Moreover, wild boar seems to be more involved in epizoochory than roe deer and red deer, as Heinken & Raudnitschka (2002) suggested. Its long-bristled fur and thick undercoat of curly hair make adhesion of seeds easier than the short, sleek fur of roe and red deer. The wallowing activity of wild boar apparently increases the number of seeds that stick to the animal’s fur; we found mud crusts containing many different seeds with different dispersal modes.

Obviously, we found a much greater diversity of species transported by wild boar both in comparison with roe deer in Montargis and with red and roe deer in Lorris. This also resulted in a very low overlap between wild boar and deer species.

Ecological traits of transported plants

The most dispersed plant species we found are similar to those in other studies: *Betula pendula*, *Rubus fruticosus*, *Brachypodium sylvaticum*, *Geum urbanum*, *Galium odoratum*, *Deschampsia flexuosa*. *Betula pendula* was the only species transported by all three animal species, even though its main dispersal mode is anemochory. For this species, epizoochorous transport acts as a secondary dispersal mode. *Betula pendula* was also the species most frequently found on wild boar individuals, followed by *Chenopodium* sp. and *Geum urbanum*. Epizoochorous species, like Poaceae, were the plants most frequently transported by red and roe deer. As expected, the plant species we found on ungulates’ bodies were mainly epizoochorous (Poaceae, *Geum urbanum*, *Deschampsia flexuosa*…) and were more frequent on fur than in the hooves.

Both results clearly show that epizoochorous species have been selected for external dispersal. However, contrary to what we hypothesized, globally wild boar transported a greater number of epizoochorous species than cervidae did. Moreover, there were no significant differences among animal species concerning the proportion of epizoochorous species that were transported. Due to their different fur structure and behaviour (wallowing activity), wild boar may stock seeds longer than cervidae where species turn over may be higher.

However, species with other modes of dispersal were also transported by the animals we brushed, particularly in the hooves (*Amaranthus* sp., *Chenopodium* sp.…). Indeed, we identified seeds from nearly all dispersal classes (epizoochory, barochory, anemochory, endozoochory, hydrochory) and, again, these seeds were mainly found on wild boar, followed by roe deer. Our results agree with Fischer et al. (1995) and Mrotzek et al. (1999) who demonstrated that plant species are more easily carried when they produce small seeds rather than large ones. Therefore, we supposed that any type of seed could be dispersed in hooves and wild ungulates could play a role in the distribution of the entire flora even though epizoochorous species should be more dispersed than other plant species.

Our final hypothesis was that the diversity of the seeds collected on hunted individuals should reflect the diversity of the habitats present within their home range. Our results are in contradiction with that statement. We mainly collected light-demanding plant species that originated from periforest and non forest habitats. This result agrees with the fact that woodland plants are only rarely dispersed (Heinken & Raudnitschka 2002). Indeed, most woodland species do not possess morphological adaptations and generally produce few seeds (Bierzychudek 1982); this negatively affects the likelihood that they will be dispersed by animals. The fact that wild ungulates more actively search for food in open areas may also enhance the likelihood that ruderal and grassland species will be transported.

Consequences for plant population dynamics

A large number of seeds are transported by wild ungulates, but probably only a few germinate and establish, and even fewer are efficiently dispersed over long distances.

However, a seed from an open landscape species might very well thrive in forest gaps or along forest roads. Inversely, examples of shrub encroachment tend to show that woody species can establish very well in open areas (Eldridge et al. 2011), just as they do under the forest canopy. Common wild ungulates appear to be relevant seed vectors in the fragmented landscapes common today. They might help to maintain connectivity between isolated plant populations but also to penetrate suitable new habitats in a rapidly changing environment.

Our study confirms that large ungulates are indeed effective vectors plants can rely on. Moreover, since many different types of seeds are concerned, ungulates' specific role in plant dispersal should be reconsidered. Wild ungulates like deer or wild boar, whose population levels are regulated by hunting, could become potential management tools to maintain plant population dynamics.

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TABLES

Table 1 -- Principal characteristics of the three animal species studied (from the Association Nationale des Chasseurs de Grand Gibier, available online at http: //www.ancgg.org/).

	Cervus elaphus	*Capreolus capreolus*	*Sus scrofa*
Withers	to 1,30 m	60 to 80 cm	90 to 95 cm
Body mass (kg)	♀ : 90 to 130 ♂ : to 250	♀ and ♂ : 20 to 25	♀ : 60 to 80 ♂: 50 to 150
Fur texture	short and sleek fur	short and sleek fur	long bristles combined with a thick undercoat of curly hair
Home range (ha)	♂ : 2000 to 5000 ♀ : 500	30 to 60	♀ + offspring: 500 to 1000 ♂ : 1000 to 2000
Diet	herbivore: grass, foliage, conifer branchs, fern rhizomes, crops	herbivore: leaves, grass, shrubs, blackberry bush, seedlings of conifers, acorn, cultivated land	omnivorous-frugivore: forest fruits, corne and maize, roots, nightcrawlers

Table 2 -- Summary of the comparisons (Kruskall-Wallis tests) among animal species for the total number of plant species and seeds dispersed both on the fur and in hooves, in the Massif de Lorris and the Forêt de Montargis.

Massif de Lorris

Capreolus capreolus (Cc), *Cervus elaphus* (Ce) and *Sus scrofa* (Ss)

		Plant species			Total number of seeds		
		χ^2	df	p	χ^2	df	p
Fur	Cc-Ce-Ss	15.3	2	0.0005	15.5	2	0.0004
	Ce-Ss	5.7	1	0.02	7.1	1	0.008
	Cc-Ss	12.3	1	0.0005	12.7	1	0.0004
	Cc-Ce	4.3	1	0.04	3.1	1	0.08
Hooves	Cc-Ce-Ss	6.0	2	0.05	5.2	2	0.07

Table 3 -- Number of species by (A) main dispersal mode and (B) main habitat, and L-Ellenberg index for plant species both transported by the brushed animals and present in the local flora**.** Plants for which the ecological traits could not be obtained were not used in the analyses.

A.

Main dispersal mode

	A	**Au**	**B**	**D**	**En**	**Ep**	**H**	**M**
Transported plants	6	0	9	0	1	19	3	0
Local flora	219	3	202	11	62	187	55	45

A: anemochory, Au: autochory, B: barochory, D: diszoochory, En: endozoochory, Ep: epizoochory, H: hydrochory, M: myrmecochory.

B.

	Main habitat				L-Ellenberg index	
	Forest	**Peri-forest**	**Open**	**Hygrophile**	**1 to 5**	**6 to 9**
Transported plants	5	11	20	2	6	33
Local Flora	103	229	359	91	124	602

FIGURES

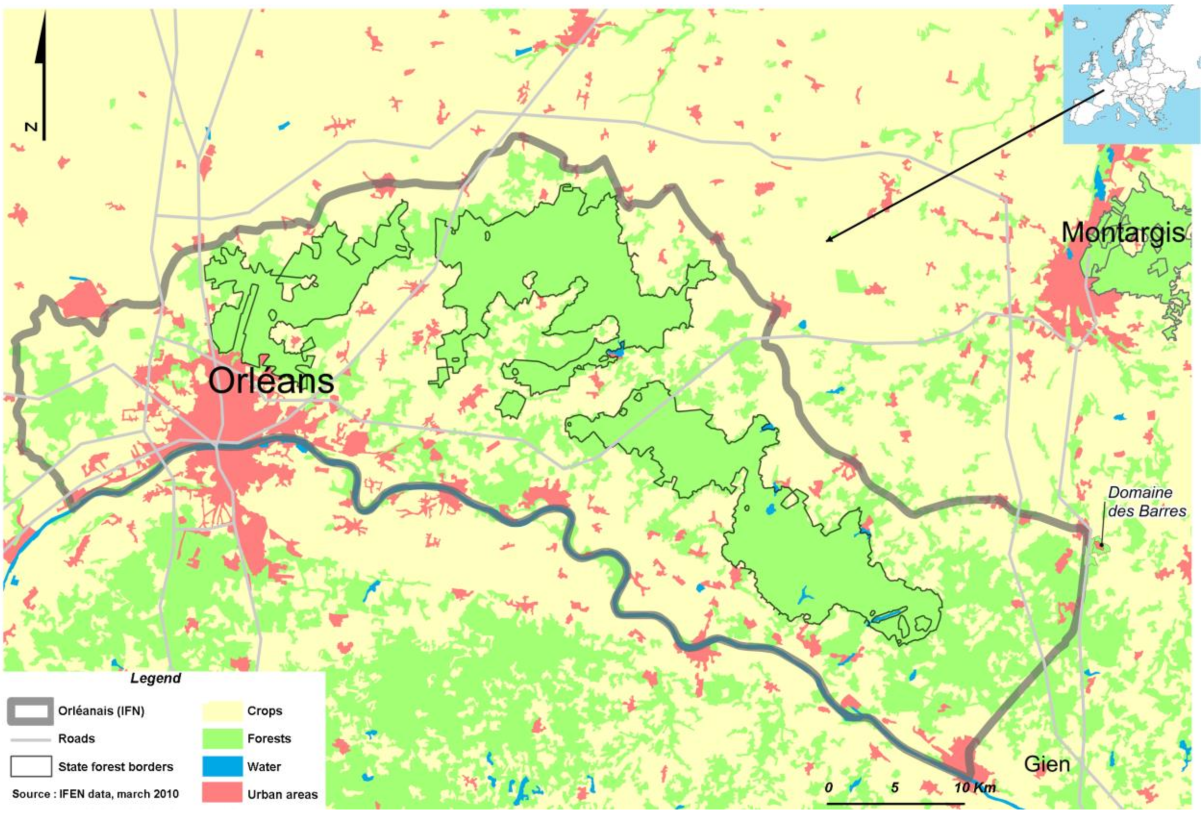

Figure 1 -- Location of the three forests where the animals were shot: Domaine des Barres, Forêt de Montargis and Massif de Lorris, Loiret, France.

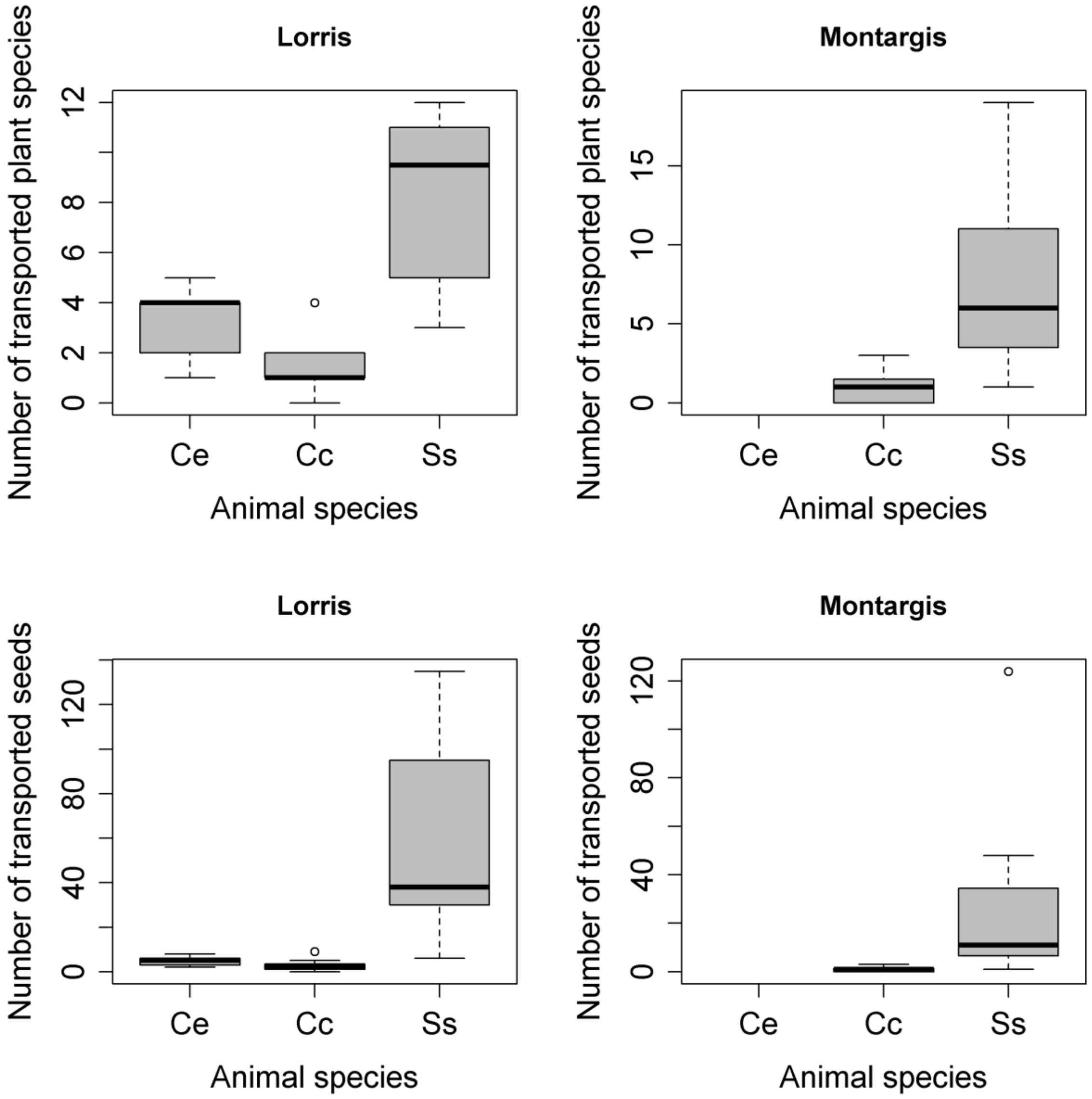

Figure 2 -- Number of plant species (top) and seeds (bottom) transported by one animal, for each animal species (Cc = *Capreolus capreolus*, Ce = *Cervus elaphus* and Ss = *Sus scrofa*) in the Massif de Lorris (left) and the Forêt de Montargis (right).

APPENDICES

Appendix 1: Table summarizing data concerning the brushed animals

N°	**Animal species**	**Sex**	**Body mass (kg)**	**Forest**	**Date**	**Fur**	**Hooves**
1	Ss	NA	30	Montargis	oct 2009	yes	4
2	Ss	NA	30	Montargis	oct 2009	yes	4
3	Cc	NA	NA	Barres	oct 2009	yes	4
4	Ss	male	> 80	Montargis	oct 2009	yes	0
5	Ss	female	50-60	Montargis	oct 2009	yes	4
6	Ss	NA	NA	Montargis	oct 2009	yes	4
7	Cc	female	NA	Barres	nov 2009	yes	3
8	Cc	male	NA	Barres	nov 2009	yes	1
9	Ss	female	80	Montargis	nov 2009	yes	4
10	Ss	male	80	Montargis	nov 2009	yes	0
11	Ss	male	NA	Montargis	nov 2009	yes	4
12	Cc	male	NA	Montargis	dec 2009	yes	4
13	Cc	female	NA	Montargis	dec 2009	yes	4
14	Ss	male	75	Montargis	dec 2009	yes	4
15	Cc	male	NA	Barres	dec 2009	yes	4
16	Cc	female	NA	Barres	dec 2009	yes	4
17	Ss	male	30	Montargis	jan 2010	yes	4
18	Ss	male	50	Montargis	jan 2010	yes	0
19	Ce	female	99	Lorris	jan 2010	yes	0
20	Cc	female	15	Lorris	jan 2010	yes	4
21	Cc	male	15	Lorris	jan 2010	yes	4
22	Cc	male	10	Lorris	jan 2010	yes	4
23	Cc	female	20	Montargis	feb 2010	yes	4
24	Cc	male	20	Montargis	feb 2010	yes	4
25	Cc	male	25	Lorris	feb 2010	yes	4
26	Cc	female	< 20	Lorris	feb 2010	yes	4
27	Cc	male	NA	Lorris	frb 2010	yes	4
28	Cc	female	23	Lorris	feb 2010	yes	4
29	Ce	female	98	Lorris	feb 2010	yes	4
30	Ss	NA	44	Lorris	feb 2010	yes	4
31	Ce	female	75	Lorris	feb 2010	yes	4
32	Ss	male	80	Lorris	feb 2010	yes	4
33	Cc	male	< 20	Lorris	feb 2010	yes	4
34	Ce	female	100	Lorris	feb 2010	yes	4
35	Cc	female	NA	Montargis	feb 2010	yes	4
36	Cc	male	NA	Montargis	feb 2010	yes	4
37	Cc	female	NA	Montargis	feb 2010	yes	4
38	Ce	male	75	Lorris	feb 2010	yes	4
39	Ss	NA	29	Lorris	feb 2010	yes	4
40	Cc	male	< 20	Lorris	feb 2010	yes	4

N°	Animal species	Sex	Body mass (kg)	Forest	Date	Fur	Hooves
41	Cc	male	NA	Lorris	feb 2010	yes	4
42	Cc	female	NA	Lorris	feb 2010	yes	4
43	Cc	female	NA	Lorris	feb 2010	yes	4
44	Cc	male	12	Lorris	feb 2010	yes	4
45	Cc	male	12	Lorris	feb 2010	yes	4
46	Cc	male	24	Lorris	feb 2010	yes	4
47	Cc	female	NA	Lorris	feb 2010	yes	4
48	Ss	male	NA	Lorris	feb 2010	yes	4
49	Ss	male	NA	Lorris	feb 2010	yes	4
50	Ss	female	71	Lorris	feb 2010	yes	4
51	Cc	male	NA	Barres	mar 2010	yes	4

Sample number, animal species: Cc = *Capreolus capreolus*, Ce = *Cervus elaphus* and Ss = *Sus scrofa*, sex, body mass, forest, date of brushing, yes when all the fur was brushed, and the number of hooves brushed.

Appendix 2: Ecological traits of the plant species identified as being transported by the animals sampled

Plant species (http://www.ipni.org)	Main mode of dispersal	Main habitat	L-Ellenberg index
Agrostis sp.	NA	NA	7
Amaranthus sp.	NA	Open	8
Asperula cynanchica L.	Barochory	Open	7
Avena fatua L.	Epizoochory	Open	6
Betula pendula Roth	Anemochory	Forest	7
Bidens tripartita L.	Epizoochory	Open	8
Brachypodium sylvaticum (L.) P.Beauv.	Epizoochory	Peri-forest	3
Bromus sp.	Epizoochory	NA	5
Calluna vulgaris (L.) Hull	Anemochory	Peri-forest	8
Carpinus betulus L.	Anemochory	Forest	4
Chenopodium sp.	Barochory	Open	6
Clematis v italba L.	Anemochory	Forest	7
Deschampsia flexuosa (L.) Trin	Epizoochory	Peri-forest	6
Digitaria ischaemum (Schreb.) Muhl.	Barochory	Open	7
Echinochloa crus-galli (L.) P.Beauv.	Epizoochory	Open	6
Erica cinerea L.	Barochory	Peri-forest	7
Festuca arundinacea Schreb.	Epizoochory	Open	8
Festuca rubra L.	Epizoochory	Open	NA
Galium odoratum (L.) Scop.	Epizoochory	Forest	2
Galium sp.1	NA	Open	6
Galium sp.2	NA	NA	6
Geum urbanum L.	Epizoochory	Peri-forest	4
Holcus lanatus L.	Epizoochory	Open	7
Hydrocotyle vulgaris L.	Hydrochory	Hygrophile	7
Juncus sp.	Epizoochory	Open	6
Lapsana communis L.	Barochory	Peri-forest	5
Lycopus europaeus L.	Hydrochory	Hygrophile	7
Mentha aquatica L.	Hydrochory	Open	7
Orobanche amethystea Thuill.	Barochory	Peri-forest	8
Picris hieracioides L.	Anemochory	Peri-forest	8
Pinus sylvestris L.	Anemochory	Forest	7
Polygonum persicaria L.	Barochory	Open	6
Rubus fruticosus L.	Endozoochory	Peri-forest	NA
Rumex obtusifolius L.	Epizoochory	Peri-forest	7
Setaria sp.	Epizoochory	Open	7
Teucrium scorodonia L.	Barochory	Peri-forest	6
Thymus pulegioides L.	Epizoochory	Open	8
Torilis arvensis (Huds.) Link	Epizoochory	Open	7
Trifolium campestre Schreb.	Epizoochory	Open	8
Vulpia bromoides (L.) Gray	Epizoochory	Open	9
Vulpia myuros (L.) C.C.Gmel.	Epizoochory	Open	8

Plant species, main mode of dispersal: Anemochory, Barochory, Endozoochory, Epizoochory, Hydrochory; main habitat: Forest, Peri-forest, Open or Hygrophile; and L-Ellenberg index: 1 to 5 = sciaphile plants and 6 to 9 = heliophile plants. NA = Not Available.

ANNEXE 2

Article 7

Using basic plant traits to predict ungulate seed dispersal potential

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Soumis à *Ecography*

Abstract

Habitat fragmentation contributes to the decline of plant species by decreasing gene flow among populations. Restoring connectivity among habitat patches is therefore a major issue for plant conservation. But, deciding where to focus restoration efforts requires identifying suitable dispersers for each target plant species. We collected data from the literature on wild and domesticated ungulates, known to be effective seed dispersers, and on the plants they dispersed in Europe via epi- and/or endozoochory. We performed a systematic literature review to identify plant and animal traits relevant for seed dispersal. We first modeled the relationships between epi- or endozoochory and a priori selected plant traits (diaspore releasing height, length, shape and morphology, and habitat openness). The differences we underlined between the two dispersal mechanisms justified splitting our analyses accordingly. Then, for each dispersal mechanism, we asked whether basic plant traits could be used to predict specific traits of ungulates as endozoochorous or epizoochorous seed dispersers. We modeled the relationships between a priori selected ungulate traits for epizoochory (habitat openness, shoulder height, hair curliness, and hair length) and for endozoochory (habitat openness, body mass, feeding type and digestive system) and plant traits. Plant habitat openness and diaspore morphology were the predictors that most often explained differences among ungulates for epizoochory, whereas plant habitat openness and diaspore releasing height most often explained differences for endozoochory. Our trait-based predictive models can help improve our ability to propose more precise management decisions for the conservation of plant populations worldwide by taking into account ungulate dispersers.

Keywords: seed dispersal; ungulates; epizoochory; endozoochory; predictive models; phylogenetic generalized linear mixed models

Habitat fragmentation may contribute to the decline of plant species by increasing functional isolation among populations (Anderson and Jenkins 2006). Agricultural intensification and the physical barriers created by both urbanization and the increased density of the transportation network have reduced functional connectivity at the landscape scale (EEA and FOEN 2011, McRae et al. 2012). Populations in small, isolated fragments are more prone to extinction due to inbreeding depression or environmental stochastic events (Anderson and Jenkins 2006, Krosby et al. 2010). Guaranteeing seed dispersal among spatially disjunct populations thus becomes critical for the maintenance of regional-scale populations; this is particularly true for species lacking seed dormancy (Cain et al. 2000).

The conservation of plant species in isolated populations may be achieved by restoring the functional connectivity among habitat patches (Anderson and Jenkins 2006). This could be done by increasing matrix permeability—that is, by restoring and managing the matrix vegetation—and/or by creating ecological corridors—to provide structural connections between habitats (Castellón and Sieving 2005). For animal populations, these practices have proven to be efficient conservation strategies: they increase the gene flow between communities and help maintain species richness and diversity (Banks and Lindenmayer 2014, Gilbert-Norton et al. 2010, Haddad et al. 2003). For plant communities, corridors have also been shown to facilitate seed dispersal and increase species richness in the linked habitat fragments (Damschen et al. 2006, Tewksbury et al. 2002). The efficiency of landscape restoration could be further improved by considering processes related to plant-animal interactions. For example, by knowing which animal species is likely to disperse a target plant species present in a fragment, corridors could be created according to the disperser's habitat use.

Even where restoration of connectivity is not feasible, plant species conservation may be achieved by using domesticated animals as 'dynamic ecological corridors' or 'mobile links' (Bonn and Poschlod 1998, Cosyns et al. 2005, Couvreur et al. 2004a). Indeed the transport of domesticated ungulates from one grazing area to another may help reconnect isolated plant populations (Couvreur et al. 2004a).

In human-influenced landscapes, ungulates are known to be efficient seed dispersers (Boulanger et al. 2011, Milton and Dean 2001, Mouissie et al. 2005c, Welch 1985) and useful in restoring plant diversity (Cosyns et al. 2005, Couvreur et al. 2004a, Wessels-de Wit and

Schwabe 2010). Either wild or domesticated ungulates are abundant in most countries (Fritz and Loison 2006, Kenward and Putman 2011, Prins and Gordon 2008). These rather large animals (Groot Bruinderink et al. 2003) forage on numerous and varied plant species (e.g., in Europe: *Cervus elaphus* (Gebert and Verheyden-Tixier 2001); *Dama dama* (Nugent 1990); *Sus scrofa* (Schley and Roper 2003); *Capreolus capreolus* (Tixier and Duncan 1996); *Ovis aries* (Kuiters and Huiskes 2010)). They can travel rapidly—thereby bringing about long-distance seed dispersal (i.e., > 100 m; Cain et al. 2000, Heinken et al. 2002, Mouissie et al. 2005a)—and they use a wide variety of habitats (Bakker et al. 2008, Heinken et al. 2002, Kuiters and Huiskes 2010, Nugent 1990).

Consequently, particular plant traits might feasibly be used to predict the characteristics of an optimal animal dispersal vector. Indeed, we know that certain animal traits improve plant dispersal and, conversely, that plant traits influence their dispersal by animals. Successful ungulate epizoochory has often been associated with relatively small diaspores with long and/or hooked appendages, which release at low to medium height. Survival after endozoochory has been correlated with persistent, small, rounded diaspores with a hard seed coat (see Table 1 for references). In fact, zoochory may have acted as a selection pressure for the evolution of morphological adaptations that increase the probability of dispersal via the animal gut or fur (Cousens et al. 2008). In our review, we considered a trait to be ‘a well-defined property of organisms measured at the individual level and used comparatively across species’ (McGill et al. 2006).

We carried out a systematic literature review (Pullin and Stewart 2006) and subsequently performed a meta-analysis (i) to test whether basic plant traits were associated with seed dispersal by ungulates and (ii) to predict, for a large number of plant species, the characteristics of the most probable seed disperser among various ungulate species. We aimed to build predictive models that could be applied worldwide—i.e., even in countries where ungulate and plant species differ from those in Europe and where dispersal information is scarce. This goal naturally oriented us toward a trait-based, rather than a species-based, approach. Highlighting specific animal traits would then make it possible to identify the most probable disperser among the specific local pool of ungulates. Furthermore, we included both wild and domesticated ungulates in our review as both may be relevant vectors for seed dispersal (Bartuszevige and Endress 2008, Malo et al. 2000, Milton and Dean 2001). We also distinguished between epizoochory and endozoochory because these two dispersal mechanisms may complement each other (Couvreur et al. 2005a) and act at different spatial scales even on a given individual. We used a European data set to build our models simply because most seed dispersal studies on ungulates have been performed in Europe.

We tackled the following questions:

(Q1) Is there any difference between plant traits associated with epi- and endozoochory?

(Q2) Can basic plant traits predict ungulate disperser traits in the European context?

(Q3) Are predictive models based on European data valid for ungulate seed dispersal in other regions of the world?

MATERIAL AND METHODS

Data selection

We used the guidelines provided by Pullin and Stewart (2006) for systematic literature reviews to study which plant species are dispersed by various ungulate species via epi- or endozoochory. We did not pre-publish our protocol as suggested by these authors, but instead made it available directly in the article (Supplementary material Appendix A). We collected information from both published and unpublished sources (Supplementary material Appendix B) related to plants dispersed by wild or domesticated ungulates; the sources were based on presence-absence data, seed and/or seedling numbers or frequency in the study samples (Supplementary material Appendix C). Because we aimed to study natural seed dispersal, we did not include data from studies where the targeted plant species were fed to ungulates, where seeds were placed in the rumen, or where seeds were artificially attached to the ungulates' fur. In total, we collected data from 52 European studies (Supplementary material Appendix D). For non-European data, we initially collected 30 studies, but due to missing data preventing the use of predictive models (see Methods), only 21 studies (5 and 16 studies of epi- and endozoochory respectively) were retained. We used the Taxonomic Name Resolution Service (Boyle et al. 2012, The Taxonomic Name Resolution Service 2012) and the Plant List (2010)—which complies with the Angiosperm Phylogeny Group taxonomy—to standardize plant and family names across studies.

We queried various databases (Supplementary material Appendix B) to collect data for both plant and animal species on easily measurable characteristics (hereafter called 'basic traits') usually related to seed dispersal. Due to the limited availability of standardized data for some traits (e.g., animal behavior, seed coat thickness, diaspore retention time and seed production), they were not included in our analysis, although they are known to be relevant for zoochorous seed dispersal. We standardized plant traits according to LEDA trait standards (Knevel et al. 2005) (Supplementary material Appendix E).

For ungulate traits (Supplementary material Appendix F), we collected data about habitat openness, body mass and shoulder height from seed dispersal papers (Supplementary material Appendix B) or from Montulet (1984), data on hair curliness and length from Debrot et al. (1982), data on feeding type from Hofmann (1989), and data on the digestive system from Feldhamer et al. (2007).

Data exploration and trait selection

Prior to analysis, we checked for multi-collinearity among traits. Variance Inflation Factors (VIF) were calculated using the vif function in the HH package (Heiberger 2013) in R v 3.0.1 (R Development Core Team 2013). The traits with the highest VIF values were removed until all VIF values were below three (Zuur et al. 2010). We retained five plant traits (Table 2): plant habitat openness, diaspore releasing height, length, shape (measured as variance in dimensions (Vs); Bekker et al. 1998), and morphology (i.e. balloon structure, presence and shape of appendages, and presence of elaiosome or pulp) (Supplementary material Appendix E). The diaspore shape was calculated as follows:

$$Vs = \Sigma\ (xi - \text{mean}\ (x))2/n$$

with $n = 3$ and $x1 = \text{length}/\text{length} = 1$, $x2 = \text{height}/\text{length}$ and $x3 = \text{width}/\text{length}$

We considered the diaspore to be the dispersal unit. We retained four ungulate traits; for epizoochory: animal habitat openness, shoulder height, hair curliness and hair length; and similarly four traits for endozoochory: animal habitat openness, body mass, feeding type and digestive system (Supplementary material Appendix F). For each ungulate trait, we defined categories (Table 2) based on intervals rather than continuous data so that our models would be less sensitive to phenotypic variation in animal species. We defined categories such as the number of species was balanced among them. Each category was coded as a binary variable. For plant trait, plant releasing height, a continuous variable, was divided into categories, each being coded as a binary variable. Thus, we did not lose the information relative to the range of releasing heights associated with the dispersal by ungulates. We removed from the analysis the plant species for which at least one trait was missing.

Plant traits exclusively associated with either epizoochory or endozoochory

We fitted phylogenetic generalized linear mixed models (PGLMM) based on the European sample, for epi- and endozoochory dispersal mechanisms. We used PGLMMs since they are phylogenetic logistic regressions that take into account phylogeny (i.e., we can use them in case of non-independent values among species) and that we can build with binary dependent variables (Ives and Garland Jr. 2010). Thus phylogenetically related species tend to have the same value of the dependent variable (Ives and Garland Jr. 2010). We based our PGLMMs on the Phylomatic tree R20120829 for plants (Webb et al. 2008, Webb and Donoghue 2005). To highlight any difference between the two mechanisms, we looked for traits exclusively linked with one or the other. Consequently, we only took into account the plant species that are exclusively dispersed via one mechanism (65 species via epizoochory and 298 via endozoochory) (Supplementary material Appendix D). We used the phyloglm function of the phylolm package (Ho and Ané 2014) in R, with plant traits as explanatory variables (i.e., predictors). We transformed quantitative dispersal data (i.e., studies with number of seeds/seedlings, frequencies) into a binary variable: presence-absence. This enabled us to harmonize data across studies without excluding any study from the analyses. However, the same weight was thus given to all plant species, whether they were rarely or frequently dispersed. To limit this bias, we only took into account species for which dispersal was observed for at least two seeds/seedlings in each study. One should note that the studies based on presence-absence data only recorded species that had dispersed several diaspores. We performed model selection among the list of candidate models using the Akaike Information Criterion adjusted for small sample size (AICc, Burnham and Anderson 2002).When the difference between the minimum AICc value and the AICc values of other models was < 2, we retained the most parsimonious model by removing uninformative parameters (Arnold 2010, Burnham and Anderson 2002), i.e., our ‘best’ model. Then, when several models could be defined as ‘best’ models, we averaged the estimates (Burnham and Anderson 2002).

Plant traits associated with ungulate traits

We randomly split our European sample into two parts: a training sample and a test sample. Based on the European training sample (158 plant species for epizoochory and 391 for endozoochory), we fitted PGLMMs for each of the basic ungulate traits entered as a binary response variable. We used plant traits as explanatory variables, as in the analysis explained above. We performed the model selection among the list of candidate models using the AICc ranking and parsimony. Since epizoochory and endozoochory were associated with different plant traits (see above), we separately fitted models for each dispersal mechanism.

Model validation using European and non-European data

We used our resulting predictive models to calculate the probability for each ungulate trait of being associated with the dispersal of each plant species in the European test sample (50 plant species for either epi- or endozoochory) and in the non-European sample (13 plant species for epizoochory and 42 for endozoochory). We used the code published by Thomson et al. (2010).

Several methods have been previously used to assess the model prediction accuracy on test sample data: for instance, the area under the receiver operating characteristic (AUC or ROC) or Pearson/Spearman correlations. However, we chose not to use either of these methods because they have major drawbacks when modeling presence-absence data, in particular when absences are uncertain (i.e., pseudo-absences occur). Indeed, the data from our training sample were not comprehensive because the studies included had focused on specific ungulates; therefore, dispersal data for some non-target ungulate species were lacking. Moreover, a given plant species lacking in the study area would obviously not be dispersed, simply because it was absent. The main flaw of AUC and correlation methods is that they take into account all the conditions the model might potentially operate in: true positive rate (sensitivity), true negative rate (specificity), false positive rate (commission errors), and false negative rate (omission errors) (Lobo et al. 2007). In our case, specificity (and commission errors) could not be used because they were likely to be biased by pseudo-absences. That is why we based our validation for each model only on sensitivity (and omission errors) rather than on a global measurement such as the AUC. Our choice was further justified because we were only interested in which ungulate was able to disperse a given plant, and not in the ungulate's inability to disperse it. We deemed the accuracy of our models good when they predicted a trait better than chance (prediction > 0.5) with a sensitivity of > 80% to limit biases due to omission errors.

RESULTS

Data selection

In all, 547 plant species (58 plant families) in European or non-European studies were found to be dispersed by ungulates, of which 63 species were dispersed exclusively via epizoochory, 326 exclusively via endozoochory and 158 via both dispersal mechanisms (Supplementary material Appendices D and F). Most of these plant species (68.1 %) prevail in open habitats (grasslands, scrublands, open wetlands, croplands), while very few (5.8 %) were typical of closed habitats (forest, forested wetlands). The most represented families were Poaceae (94 species), Asteraceae (49 species), and Caryophyllaceae (36 species).

Plant traits exclusively associated with either epizoochory or endozoochory

The most parsimonious model based on AICc ranking showed that epizoochory and endozoochory differed according to the plant releasing height, the diaspore shape and the type of appendage on the diaspore. Thus rounded diaspores released below 20 cm and with a flat appendage were likely to be exclusively dispersed via endozoochory, whereas elongated diaspores released above 20 cm, and with a hooked appendage were likely to be exclusively dispersed via epizoochory (Table 3 and Supplementary material Appendix G).

Plant traits associated with ungulate traits

For epizoochory, five out of 10 ungulate traits were associated with several of the five plant traits we retained in our analysis, each association being unique (Table 3 and Supplementary material Appendix G). Hair curliness (straight category) was associated with only one predictor. Plant habitat openness and diaspore morphology were the most frequent predictors (N=5 and 4 respectively) of differences among ungulate traits for epizoochory. Ungulate shoulder height (< 100 cm), hair curliness (Curly) and hair length (Medium and Long) were not associated with any of the studied plant traits (Table 3 and Supplementary material Appendix G).

For endozoochory, eight out of nine ungulate traits were associated with several of the five plant traits we retained in our analysis, each association being unique (Table 3 and Supplementary material Appendix G). The most common predictors were plant habitat openness (N=7) and diaspore releasing height (N=8). Only ungulates < 100 kg were not associated with any of the studied plant traits.

Model validation

Only two out of the six non-null models tested performed well for epizoochory and four out of eight for endozoochory, similarly for the European and the non-European test samples (Table 4). They correctly predicted epizoochorous seed dispersal by ungulates able to live in forests, and ungulates bearing straight hair (Table 4). Endozoochorous seed dispersal was correctly predicted for the following categories: ungulates able to live in forests, ungulates with a body mass > 300 kg, intermediate mixed feeders, or foregut fermenters. The model for grass and roughage eaters also provided good predictions for the European test sample but was just below the 80% threshold (i.e. 74, Table 4).

DISCUSSION

Plant traits exclusively associated with either epizoochory or endozoochory

We found that basic plant traits can be used to distinguish between epi- and endozoochorous plant dispersal by ungulates. Diaspore releasing height was associated with ungulate seed dispersal, with contrasting patterns for epi- and endozoochory. Diaspores with a releasing height above 20 cm were likely to be exclusively dispersed via epizoochory. This is in accordance with the results from other studies that have shown that seeds are unlikely to be retained in the short straight hair covering the ungulates' shanks (below 20 cm), whereas they are mostly retained in the fur of the ungulate flanks (De Pablos and Peco 2007, Dutoit et al. 2003). Conversely, diaspores with a releasing height below 20 cm were likely to be solely dispersed via endozoochory since they are very likely to be ingested by herbivores, mainly grazers.

Elongated diaspores were more likely to be dispersed via epizoochory. An elongated diaspore may be able to burrow more deeply inside an animal's fur, thus improving its adhesion, this is particularly likely for unhooked diaspores (Mouissie et al. 2005b, Pakeman et al. 2002). On the other hand, and in accordance with other studies (Mouissie et al. 2005b, Pakeman et al. 2002), rounded diaspores were more likely to be dispersed via endozoochory. Indeed, a low variance in dimension has sometimes been related to better seed survival, because rounded diaspores are less susceptible to be damaged by chewing and often pass the digestive tract faster (Gardener et al. 1993a, Janzen 1984).

As expected, hooked diaspores do seem to be exclusively dispersed via epizoochory. This morphological adaptation specifically helps the diaspore to cling to animal fur (Couvreur et al. 2004b, Heinken et al. 2006, Mouissie et al. 2005a). Furthermore, we found that hooked diaspores were unlikely to survive digestion. Bruun and Poschlod (2006) proposed that diaspores with hooked appendages may become attached to coarse material during the digestion process, thus slowing down their progression in the gut. Longer gut retention increases the seeds' exposure time to gastric fluids thus decreasing their survival rate (Traveset and Verdú 2002). On the other hand, and unexpectedly, diaspores with a flat appendage were unlikely to be dispersed via epizoochory. A flat appendage probably prevents the diaspore from penetrating deeply inside the hair entanglement. Moreover, a flat appendage is usually more adapted to anemochory (van der Pijl 1982).

Epizoochory: plant traits associated with ungulate traits

For epizoochory, plant habitat openness and diaspore morphology were frequently related to the difference among ungulate trait categories. Plant habitat openness is an expected predictor for ungulate habitat openness since plants and ungulates must be at the same place to interact. Indeed, in our study, ungulates able to live in forests were more likely to disperse forest plant species. In addition, we observed that ungulates with a shoulder height above 100 cm or ungulates bearing straight or wavy hair dispersed forest plant species. Open habitat plants are generally well adapted to epizoochory (Heinken and Raudnitschka 2002), that's the reason why we were logically more prone to detect differences among ungulates with forest plant species.

Considering diaspore morphology, diaspores with an elongated appendage were more associated with epizoochorous dispersal by ungulates with a shoulder height between 100 and 130 cm or ungulates with short hair, the latter being also less likely than other ungulates to disperse hooked diaspores. Ungulates with wavy hair were less susceptible than other ungulates to disperse diaspores with flat appendage. Hooked diaspores were exclusively associated with epizoochory for all ungulates. Therefore, another morphological diaspore attributes, such as the presence of an elongated appendage known to improve attachment (Couvreur et al. 2004b) or a balloon structure, may be necessary to distinguish among ungulates.

Other traits were less frequently related to differences among ungulate trait categories. For instance, the shortest diaspores were more likely to be dispersed by the largest ungulates (shoulder height > 130 cm) or ungulates with short hair. This is in accordance with some

European studies showing a negative relationship between diaspore size and epizoochory (Couvreur et al. 2004b, Römermann et al. 2005).

Ungulates able to live in forests were more likely to disperse elongated diaspores. As forest plants are typically less adapted to epizoochory (Heinken and Raudnitschka 2002), only those with elongated diaspores (a shape which improves adhesion to the fur, see results) are able to take advantage of external dispersal. The largest ungulates were also more likely than others to disperse elongated diaspores. Moreover, dispersal by the smallest ungulates and ungulates with medium and long curly hair (e.g., sheep) were not associated with any studied plant trait, which may have several explanations, including that these ungulates may be able to externally disperse any plant species, regardless of their traits.

Finally, we observed that ungulates with wavy hair were less likely than others to disperse diaspores released between 100 and 200 cm. This is possibly due to a sampling bias. Indeed, only *Capreolus capreolus* and *Cervus elaphus* are wavy-haired in our European dataset. The roe deer dispersed more than twice as many species as the larger red deer (49 and 23 species respectively). This may have oriented the results towards diaspores with lower releasing heights.

Endozoochory: plant traits associated with ungulate traits

For endozoochory, the most frequent predictors for the difference among ungulate trait categories were plant habitat openness and diaspore releasing height. Once again, it is not surprising that plant habitat openness was often a good predictor of ungulate traits for endozoochory, as was the case for epizoochory. Here again, ungulates able to live in forests were more likely to disperse forest plant species. Then, most ungulates feed in open areas (Jaroszewicz et al. 2008, Malo et al. 2000, von Oheimb et al. 2005) and thus mainly ingest and disperse open habitat plant species. This may explain why the distinction among ungulates was more obvious for forest plant species. The difference related to plant species from open habitats was related to ungulates intermediate in size, grass and roughage eaters, intermediate mixed feeders and foregut fermenters. This was expected since the diet of grass and roughage eaters and intermediate mixed feeders includes a large proportion of grasses (Gebert and Verheyden-Tixier 2001), which are mostly predominant in open habitats. Moreover, in our sample, all intermediate mixed feeders were also foregut fermenters, which may explain the paired results obtained for the two categories. In the same line, all ungulates intermediate in size were either grass and roughage eaters or intermediate mixed feeders.

Diaspore releasing height also accurately distinguished among ungulate species for endozoochory. Given that ungulate mass and shoulder height are closely related (Supplementary material Appendix F), the latter has to be taken into account when analyzing our results. We observed that ungulates able to live in forests were more likely to disperse diaspores released between 100 and 200 cm. This is probably due to the highest density of tall plants in forests compared to open areas. Moreover, we found that very tall plants (200-500 cm high) were unlikely to be dispersed by the largest ungulates, contrary to intermediate plants (40-60 cm). This result was expected given the range of their shoulder height (100-180 cm). The dispersal of very tall plants was also unlikely for grass and roughage eaters and foregut fermenters. Indeed, the diet of grass and roughage eaters made them unlikely to disperse very tall plant species. In the same line, intermediate mixed feeders were less prone to disperse diaspores released between 100 and 500 cm. Hindgut fermenters were also more unlikely than others to disperse plants above 5 m. This was expected given that all hindgut fermenters, in our analysis, were grass and roughage eaters. Concentrate selectors and hindgut fermenters were more prone to disperse diaspores released between 60 and 100 cm above ground. Indeed, concentrate selectors tend to forage higher than ground level. On the other hand, grass and roughage eaters avoided diaspores released between 40 and 60 cm above ground because they preferentially eat at ground level.

Other traits were less frequently related to the difference among ungulate trait categories for endozoochory. The largest ungulates and concentrate selectors were more likely to disperse small diaspores, in agreement with previous studies (Cosyns and Hoffmann 2005, Gardener et al. 1993a, Pakeman et al. 2002).

We found that the dispersal of elongated diaspores was more likely to be associated with the largest ungulates, concentrate selectors and ungulates able to live in forests. Given that rounded diaspores were highly associated with endozoochory (exclusive dispersal for all ungulates), the difference among ungulates is more obvious when looking at the dispersal of elongated diaspores.

Intermediate mixed feeders were unlikely to disperse fleshy fruits. This was expected since fleshy fruits are not usually associated with dispersal by herbivores but mainly by birds (Couvreur et al. 2005a, van der Pijl 1982). In the same line, concentrate selectors and grass and roughage eaters were unlikely to disperse diaspores bearing an elaiosome. Indeed, these diaspores are known to be mainly dispersed by ants (Lengyel et al. 2010). Moreover, we found that hooked diaspores were unlikely to be dispersed by concentrate selectors. Indeed, we showed that hooked diaspores were usually not dispersed via endozoochory. Finally, hindgut fermenters were more likely than other ungulates to disperse diaspores with a long appendage. This may be due to the consumption by hindgut fermenters (all grass and roughage eaters in our study) of a large quantity of Poaceae which include a high number of species bearing a long appendage (Supplementary material Appendix F).

Model applicability and conclusions

When populations of a particular plant are declining, conservation managers may be able to promote the functional reconnection of habitat patches by improving seed dispersal. Then, there are two main questions we have to answer: (i) what kind of animal could contribute to the seed dispersal of the given plant species? And (ii) where could we create effective corridors?

Our analysis shows that some ungulate dispersers' traits can be predicted from easily measurable plant traits. The manager can combine the results given by our epizoochory and endozoochory models to determine the traits describing the "generalist" ungulate species the best able to disperse the target plant via both epi- and endozoochory.

We have shown that several null models were the 'best' ones (according to AICc and parsimony) and that predictive models for only certain traits performed well. For null models and the less performing models, we propose four explanations. 1) Some important variables may have not been taken into account in the analysis. Although most null models were observed for epizoochory, this explanation is more likely for endozoochory. Indeed seed coat thickness or diaspore retention time were not taken into account into the analysis due to the poor availability of data (see Methods). 2) There may have been no differences in the dispersal processed by various ungulates characterized by different categories of a given trait, such as shown by Eycott et al. (2007). This is likely for ungulates with various heights and hair lengths since models for every category of height and hair length were either null or performed poorly. 3) Our predictive models may have been valid only for the training sample, not for the test sample. However, this is unlikely since the European training and test samples were created randomly from the same dataset. 4) Data may have been less abundant for the traits related to less well performing models. This is probably true for epizoochory. Indeed, the mediocre performance of most predictive models may stem from a high rate of omission errors (i.e., false negative rate). This simply means that the test sample did not contain any case where the given combination of plant traits was associated to the given ungulate trait. This association may have existed but may not have been observed in the studies included in our analysis. A more comprehensive test sample would probably have limited this bias and the occurrence of null models as 'best' models. A larger sample would also have allowed us to use the number of seeds instead of presence-absence data and to make more precise predictions. We are confident that our models will improve as more data will become available.

Our models globally performed equally well for non-European and European flora. This suggests that the models may be applicable to other data sets throughout the world. Finally, our models show which ungulate is the most probable disperser of a given plant species, but to ensure effective connections among habitat patches, they should be combined with models predicting dispersal distances (e.g., Couvreur et al. 2008).

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Supplementary material: Appendix A-F.

TABLES

Table 1. Description of the different plant and ungulate traits known to be involved in epi- and endozoochory.

		Trait	Source
Epizoochory			
	Plant	Diaspore releasing height	Fischer et al. (1996), Hughes et al. (1994), Wessels et al. (2008)
		Diaspore size	Couvreur (2005), Rosas et al. (2008), Willson et al. (1990)
		Presence of adhesive appendages	Couvreur et al. (2004b), Römermann et al. (2005), Tackenberg et al. (2006)
		Size of appendages	Couvreur et al. (2004b)
		Seed production	Bruun and Fritzbøger (2002)
	Ungulate	Hair length	Couvreur et al. (2004b), Couvreur et al. (2005b)
		Hair curliness	Couvreur et al. (2004b), Couvreur et al. (2005b)
		Specific behaviors	De Pablos and Peco (2007), Fischer et al. (1996)
Endozoochory			
	Plant	Diaspore size	Cosyns and Hoffmann (2005), Iravani et al. (2011), (Pakeman et al. 2002)
		Diaspore shape	Mouissie et al. (2005b)
		Permeability/thickness of the seed coat	Gardener et al. (1993a), Gardener et al. (1993b), Razanamandranto et al. (2004)
		Seed longevity	Mouissie et al. (2005b), Pakeman et al. (2002)
		Seed production	Malo and Suarez (1995)
	Ungulate	Diet/feeding type	Clauss et al. (2002), Cosyns and Hoffmann (2005)
		Digestive system	Lowry (1997)
		Seed retention time	Lowry (1997)
		Body mass	Clauss et al. (2003), Weyenberg et al. (2006)

Table 2. Description of the different categories for each plant and ungulate trait used to model ungulate dispersers' traits. ^{e} exclusive variable; $^{n-e}$ non-exclusive variable.

	Traits	Categories	Comments
Plants	Habitat openness (PH) $^{n-e}$	Open, Forest	Open: grasslands, scrublands, open wetlands, cropland Forest: forest, forested wetlands
	Releasing height (DRH) $^{n-e}$	[0;20[, [20;40[, [40;60[, [60;100[, [100;200[, [200;500[, ≥ 500 cm	Intervals included between minimum and maximum values
	Diaspore length (DL)		Continuous variable
	Diaspore shape (DS)	Variance of diaspore dimension (Vs)	Continuous variable; values ranging from 0 (spherical) to 0.2 (needle-like or thin disk)
	Diaspore morphology (DM) $^{n-e}$	Balloon structure Flat appendage, elongated appendage, small appendage, long appendage, hook, elaiosome, pulp	See Knevel et al. (2005) for the definition of morphological categories
Ungulates	Habitat openness (Habitat) $^{n-e}$	Open, Forest	Open: grasslands, scrublands, open wetlands, cropland Forest: forest, forested wetlands
	Shoulder height (Height)^{e}	[0;100[, [100;130[, ≥ 130 cm	Mean value
	Body mass (Mass)^{e}	[0;100[, [100;300[, ≥ 300 kg	Mean value
	Hair curliness (H.curl)^{e}	Straight (St), Wavy (Wa), Curly (Cu)	
	Hair length (H.length)^{e}	[0;30[(S), [30;50[(M), ≥ 50 (L) mm	Mean value. S = small, M = medium, L = long
	Feeding type (Diet) ^{e}	Concentrate selector (CS), Grass and roughage eater (GRE), Intermediate mixed feeder (IMF)	Classification including only herbivore species (i.e., not wild boars). See Hofmann (1989) for details.
	Digestive system (Dig) ^{e}	Foregut fermenter (FF), Hindgut/Colon fermenter (HF)	See Feldhamer et al. (2007) for details.

Table 3. Estimated parameter values for the 'best' PGLMMs predicting epi- and endozoochory, and ungulate traits for each dispersal mechanism. Ungulate habitat openness (Habitat): F = forest, O = open; ungulate shoulder height (Height): S < 100 cm, M = 100-130 cm, L > 130 cm; ungulate body mass (Mass): S < 100 kg, M = 100-300 kg, L > 300 kg; ungulate hair curliness (H.curl): St = straight, Wa = wavy, Cu = curly; ungulate hair length (H.length); ungulate feeding type (Diet): CS = concentrate selector, GRE = grass and roughage eater, IMF = intermediate mixed feeder; ungulate digestive system (Dig): FF = foregut fermenter. HF = hindgut/colon fermenter.

Response variable	Predictor (plant trait)					Predictor (detailed category)	Coefficient (±SE)	N
	Plant habitat	Diaspore releasing height	Diaspore length	Diaspore shape	Diaspore morphology			
Q1 Epizoochory								362
		x				[0;20[cm	- 1.963 ± 0.367	
				x			13.066 ± 3.088	
					x	Flat appendage	- 1.792 ± 0.607	
					x	Hooked appendage	2.418 ± 0.561	
Q2 Epizoochory								
Habitat_F	x					Forest	1.960 ± 0.500	158
				x			4.098 ± 4.045	
					x	Ballon structure	0.234 ± 0.404	
Height_S								158
Height _M	x					Forest	0.394 ± 0.459	158
			x				- 0.197 ± 0.078	
				x			4.519 ± 5.782	
					x	Elongated appendage	1.204 ± 0.482	
Height _L	x					Forest	0.996 ± 0.372	158
			x				- 0.202 ± 0.071	
				x			14.417 ± 4.906	
H.curl_St	x					Forest	1.693 ± 0.407	158
H.curl_Wa	x					Forest	1.372 ± 0.400	158
		x				[100;200[cm	- 1.221 ± 0.446	
					x	Flat appendage	- 1.581 ± 0.828	
H.curl_Cu								158
H.length_S			x				- 0.267 ± 0.124	158
					x	Elongated appendage	1.637 ± 0.641	
					x	Hooked appendage	- 1.884 ± 1.504	
H.length_M								158

H.length_L									158
Q2 Endozoochory									
Habitat_F	x					Forest		0.475 ± 0.470	391
		x				[100;200[cm		0.298 ± 0.481	
				x				12.128 ± 4.016	
Mass_S									391
Mass _M	x					Forest		1.458 ± 0.272	391
	x					Open		1.150 ± 0.476	
		x				[200;500[cm	-	1.660 ± 0.554	
Mass _L		x				[40;60[cm		0.177 ± 0.245	391
		x				[200;500[cm	-	0.591 ± 0.682	
			x				-	0.091 ± 0.034	
				x				10.804 ± 2.724	
Diet_CS	x					Forest		1.620 ± 0.264	391
		x				[60;100[cm		0.492 ± 0.377	
			x				-	0.100 ± 0.060	
				x				5.426 ± 4.560	
					x	Elaiosome	-	0.905 ± 0.895	
					x	Hooked appendage	-	0.195 ± 0.558	
Diet _GRE	x					Forest		1.376 ± 0.280	391
	x					Open		0.589 ± 0.661	
		x				[40;60[cm	-	0.511 ± 0.231	
		x				[200;500[cm	-	0.044 ± 1.630	
			x				-	0.010 ± 0.024	
					x	Elaiosome	-	0.195 ± 0.405	
Diet _IMF	x					Forest	-	0.123 ± 0.243	391
	x					Open		1.661 ± 0.489	
		x				[100;200[cm	-	0.141 ± 0.275	
		x				[200;500[cm	-	0.223 ± 0.469	
					x	Pulp	-	0.264 ± 0.535	
Dig_FF	x					Forest		1.410 ± 0.775	391
	x					Open		2.130 ± 0.930	
		x				[200;500[cm	-	3.785 ± 0.656	
Dig_HF	x					Forest		1.189 ± 0.231	391
		x				[60;100[cm		0.543 ± 0.224	
		x				≥ 500 cm	-	2.512 ± 1.568	
					x	Long appendage		0.558 ± 0.246	

Table 4. Sensitivity of the ‘best’ PGLMMs (according to AICc ranking and parsimony) (see Table 3) predicting associations between each ungulate trait and plant traits via epizoochory and endozoochory for European and Non-European samples. Ungulate habitat openness (Habitat): F = forest; ungulate shoulder height (Height) and ungulate body mass (Mass): S = small, M = medium, L = large; ungulate hair curliness (H.curl): St = straight, Wa = wavy, Cu = curly; ungulate hair length (H.length); ungulate feeding type (Diet): CS = concentrate selector, GRE = grass and roughage eater, IMF = intermediate mixed feeder; ungulate digestive system (Dig): FF = foregut fermenter. HF = hindgut/colon fermenter. N = number of plant species; - = no data (no ungulate from the medium height in the non-European sample; or model null was the ‘best’ model). Good predictions (prediction > 0.5 and sensitivity > 80%) are in bold.

	Epizoochory			Endozoochory	
	Europe	Non-Europe		Europe	Non-Europe
N	50	13		50	42
Habitat_F	**97**	**100**	Habitat_F	**100**	**100**
Height_S	**-**	**-**	Mass_S	**-**	**-**
Height_M	35	-	Mass_M	48	14
Height_L	24	0	Mass_L	**94**	**100**
H.curl_St	**100**	**100**	Diet_CS	13	0
H.curl_Wa	22	0	Diet_GRE	74	41
H.curl_Cu	**-**	**-**	Diet_IMF	**97**	**100**
H.length_S	0	0	Dig_FF	**98**	**86**
H.length_M	-	-	Dig_HF	19	0
H.length_L	-	-			

ANNEXE 3 : Listes de communications autres que les articles scientifiques effectuées pendant la thèse

Communications orales :

Picard, M., Lalouette P., Mårell A., Chevalier R. and Baltzinger C. Influence of endozoochory on processes of plant community assembly in agro-forested landscapes. *BES-SFE Joint Annual Meeting*, Lille, France, 11/12/2014.

Picard, M. et Baltzinger, C. Les ongulés sauvages contribuent-t-ils à la dispersion des plantes ? *ECOVEG 7,* Lausanne, Suisse, 30/03/2011.

Conférences « invité » :

Picard M. Conséquences du transport endozoochore par trois ongulés sauvages sur les patrons de distribution de la flore. *Rencontre IRSTEA-INRA*, Toulouse, France, 06/01/2012.

Picard M. Conséquences du transport endozoochore par trois ongulés sauvages sur les patrons de distribution de la flore. *Réunion d'unité EFNO*, Nogent-sur-Vernisson, France, 14/11/2011.

Workshops :

Picard M., Pellerin M. and Baltzinger C. Consequences of endozoochorous seed dispersal by three wild ungulates on plant distribution patterns. *Workshop "Seed dispersal by large ungulates: Do they act as ecological filters?"*, Nogent-sur-Vernisson, France, 05/09/2013.

Picard M. Conséquences du transport endozoochore par trois ongulés sauvages sur les patrons de distribution de la flore. *Réunion du Groupe Chevreuil*, Chizé, France, 24/10/2012.

Posters :

Picard M. and Baltzinger C. 2013. Wild ungulates shape plant distributions in fragmented landscape: an experimental approach to endozoochorous dispersal. *IAVS 2013*, Tartu, Estonia, 26-30/06/2013.

Picard M. 2012. Influence de la dispersion endozoochore par les ongulés sauvages sur la distribution de la flore en paysage fragmenté. *ECOVEG 8*, Nancy, France, 28-30/03/2012.

Pellerin M., **Picard M.**, Saïd S., Baubet E. et Baltzinger C. 2012. Variations saisonnières du potentiel de dispersion des plantes par les ongulés sauvages. *ECOVEG 8*, Nancy, France, 28-30/03/2012.

Publications dans des revues techniques :

Picard M., Virfollet D., Bohême C., Pellerin M., Baltzinger C. et Ballon P. 2013. DIspersion des PLantes par les Ongulés forestiers - DIPLO. *Covalences* n°89 p.13.

Baltzinger C., **Picard M.**, Virfollet D., Bourdin L., Pellerin M., Saïd S. et Baubet E. 2013. Dispersion des plantes par les ongulés sauvages - DIPLO. *Lettre d'information du réseau « Ongulés sauvages »* n°17 p.25- 27.

ANNEXE 4 : Affiliations des co-auteurs

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Influence de la dispersion endozoochore sur la composition des communautés végétales : une approche fonctionnelle basée sur trois ongulés sauvages

La dispersion est un processus clé dans les dynamiques de populations. Chez les organismes à dispersion passive, dont les plantes, la dispersion de la banque de graines fait appel à un vecteur biotique ou abiotique. En particulier, la zoochorie influence les patrons spatiaux de distribution et de diversité des plantes à travers une interaction entre les traits écologiques du vecteur animal et de la plante transportée. Ma thèse vise à étudier l'effet de cette interaction sur la composition taxonomique et fonctionnelle des communautés floristiques. Je me concentre sur trois questions principales : (1) Comment les traits écologiques des plantes et des vecteurs influencent-ils le processus de dispersion endozoochore? ; (2) La zoochorie constitue-t-elle un filtre d'assemblage sur les traits fonctionnels des plantes dispersées? ; (3) La zoochorie imprime-t-elle un signal sur les patrons spatiaux de diversité? J'adopte à cet effet une approche expérimentale, en me concentrant sur la flore d'Europe de l'Ouest et sur les trois ongulés sauvages les plus communs dans cette région : le cerf (*Cervus elaphus*), le chevreuil (*Capreolus capreolus*) et le sanglier (*Sus scrofa*). Je montre que l'interaction entre les traits des plantes et des vecteurs influe sur les durées de rétention des graines, qui influencent les distances de dispersion. L'endozoochorie modifie la composition de l'assemblage d'espèces dispersé par rapport à la flore régionale en imposant un filtre fonction de l'habitat dans lequel se nourrit le vecteur animal, mais indépendant des traits morphologiques des graines. A échelle des communautés, l'effet de la zoochorie est cependant réduit relativement aux autres processus abiotiques et biotiques tels que les filtres liés à l'habitat ou l'herbivorie. Compte tenu de ces résultats, je propose de prendre en compte l'influence de la dispersion dans les modèles prédictifs de distributions des plantes, afin d'améliorer notre compréhension des dynamiques d'aires et leur prédiction en lien avec les scénarios de changements climatiques. Il apparaît en particulier nécessaire de mieux quantifier la contribution de la dispersion zoochore aux patrons de diversité et de composition des communautés végétales, relativement aux autres processus qui résultent d'interactions plantes-animaux et aux autres modes de dispersion des graines.

Mots clés : Dispersion, Ongulés, Zoochorie, Communautés, Traits.

Influence of endozoochorous dispersal on the composition of plant communities: a functional approach based on three wild ungulates

Dispersal is a key process shaping population dynamics. In passive dispersers like plants, the dispersal of the seed bank relies on biotic or abiotic vectors. Among the wide range of passive dispersal, zoochory influences spatial plant diversity and distribution patterns through an interaction between the ecological traits of dispersed plants and their animal vectors. In this work, I investigate the outcomes of this interaction on the taxonomic and functional composition of plant communities. I address three main questions: (1) How do the ecological traits of dispersed plants and their vectors influence the dynamics of endozoochorous dispersal? ; (2) Does zoochory affect the functional traits of dispersed species as a community assembly filter? ; (3) What is the imprint of zoochory on spatial patterns of plant diversity? I frame my work within an experimental approach focused on the West-European flora and on the three most common wild ungulates in this area: red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and wild boar (Sus scrofa). I show that interactions between plant and vector traits influence dispersal distances by modulating seed retention times. Endozoochory modifies the composition of dispersed plant assemblages as compared with that of the regional pool by filtering species according to the feeding habitats of the vectors. At a community level, zoochory has a limited influence relative to other abiotic or biotic processes including habitat and herbivory. On the basis of these results, I suggest to include dispersal in predictive models of plant distributions to improve our understanding of range dynamics and their prediction especially within the framework of current global changes. My results further suggest that the contribution of zoochorie to plant diversity and community composition patterns needs to be better quantified and compared with other plant-animal interactions and other dispersal modes.

Keywords: Dispersal, Ungulates, Zoochory, Communities, Traits.

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