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Dispersion épizootique des graines par les ongulés sauvages dans des paysages changeants : le cerf élaphe comme étude de cas

Ushma Shukla

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INRAE Val de Loire, UR Écosystèmes Forestiers

THÈSE présentée par **Ushma SHUKLA**

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**Epizoochorous seed dispersal
by wild ungulates in changing landscapes
the red deer as a case study**

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Epizoochorous seed dispersal by wild ungulates in changing landscapes : the red deer as a case study

Summary

Epizoochory is one mode of plant dispersal, where seeds are conveyed externally on animals. It mostly concerns forbs and graminoids, shrubs and trees relying more on endozoochory or abiotic vectors. Epizoochory is considered a strong biotic filter that shapes local plant assemblages from the regional pool of species. Abundant populations of large-bodied ungulates and their home range movements provide frequent 'mobile links' among habitat patches. For my thesis, I was interested in assessing the role of wild ungulates, especially red deer, in epizoochorous seed dispersal. I addressed 1) the role of ungulates in structuring local plant communities with respect to dispersal-related plant traits, 2) the effect of landscape composition on movement decisions made by individual red deer on subsequent seed dispersal kernels, and 3) the complementarity of ungulate-mediated dispersal modes and their overall influence on local plant communities. I used a combination of empirical field data and ecological modeling to address these questions. I found that zoochory presents a weak signal in structuring plant communities compared to other abiotic factors, but that dispersal-enabling traits were good predictors. I demonstrated the importance of accounting for home ranging behavior in range-resident ungulates in the seed dispersal kernel, which prevents from over-estimating dispersal distances. Moreover, I underlined how considering the total seed load dispersed by individual red deer is crucial and reveals the complementarity of dispersal modes in the total dispersal kernel. Finally, I highlighted the underrated role of ungulates in spreading invasives as a real threat to biodiversity.

Keywords: seed dispersal kernel, functional traits, complementarity, changing landscapes, plants-ungulate interactions

Dispersion épizoochore des graines par des ongulés sauvages dans des paysages changeants : le cerf élaphe comme étude de cas

Résumé

L'épizoochorie définit la dispersion des plantes véhiculées sur le corps des animaux. Elle concerne herbacées et graminées, arbres et arbustes étant dispersés par endozoochorie et vecteurs abiotiques. Filtre biotique sélectif, elle façonne les communautés végétales locales à partir du pool régional d'espèces. Les populations abondantes d'ongulés sauvages et leurs longs déplacements créent ainsi de fréquents "liens mobiles" entre patchs d'habitat. J'ai ainsi étudié le rôle de ces animaux, notamment du cerf élaphe, comme vecteurs de dispersion épizoochore dans la structuration des communautés végétales locales en tenant compte des traits des plantes favorisant la dispersion. Puis, j'ai évalué comment structure et composition du paysage affectaient les déplacements individuels du cerf, les distances de dispersion et le site de dépôt des graines. Finalement, j'ai comparé différents modes de dispersion à l'échelle du vecteur individuel. Pour répondre à ces questions, j'ai combiné données empiriques de terrain et approches de modélisation écologique. J'ai constaté que la zoochorie constitue un signal faible, par rapport aux facteurs abiotiques, dans la structuration des communautés végétales, mais les traits facilitant la dispersion sont de bons prédicteurs. J'ai montré l'importance de tenir compte du domaine vital individuel pour ne pas surestimer les distances de dispersion. En outre, j'ai démontré qu'il fallait considérer la charge totale en graines véhiculées car elle révèle la complémentarité des modes de dispersion. Pour finir, j'alerte sur le rôle sous-estimé des ongulés sauvages et domestiques dans la propagation des plantes exotiques, réelle menace pour la biodiversité

Mots clés : dispersion des graines, traits fonctionnelles, complémentarité, paysages changeants, interactions plantes-ongulés



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CHAPTER 1

Introduction

(version française)

La dispersion est le mouvement qui sépare le lieu de naissance du lieu de reproduction (Matthysen, 2012). Pour les organismes sessiles comme les plantes, d'autres vecteurs abiotiques (comme le vent et l'eau) et biotiques (comme les vertébrés et les invertébrés) sont essentiels pour permettre ce mouvement. La dispersion des graines connecte les populations de plantes génétiquement isolées ; permet aux graines d'échapper à la prédation et à la mortalité densité-dépendante du fait de la compétition intraspécifique. Elle permet aussi de coloniser de nouveaux habitats favorables (Howe et Smallwood, 1982). A l'échelle locale, la disponibilité des graines a une incidence sur la taille et le taux de croissance de la population. À l'échelle régionale, le frein à la dispersion affecte la répartition des espèces (Münzbergová et Herben, 2005). La dispersion des graines est donc un processus écologique crucial qui dicte la structuration spatiale des populations de plantes (Nathan et Muller-Landau, 2000).

Alors que la plupart des graines tombe à proximité de la plante mère elle-même, quelques-unes se déplacent sur de grandes distances, aboutissant naturellement à des distributions de dispersion leptokurtiques. La dispersion à longue distance (DLD) est importante pour la propagation et la migration des plantes, en particulier dans un contexte de changements globaux des paysages (McConkey et al., 2012).

La dispersion des graines par les animaux (i.e. zoochorie)

Le processus de dispersion primaire des graines (Fig.1.1) commence par la production de fruits et de graines disponibles sur la plante-mère, la prise en charge ultérieure des graines par le vecteur de dispersion puis le dépôt des graines dans des habitats propices à leur germination (Wang et Smith, 2002). Concernant la dispersion assistée par les animaux, cette interaction mutualiste est bénéfique à la plante qui se disperse spatialement, et pour l'animal qui en retire une compensation nutritive. Cependant, pour les graines dispersées de manière externe sur le corps des animaux, le processus est passif par nature (Sorensen, 1986). Le succès de la dispersion ou l'efficacité du vecteur de dispersion dépendent à la fois des composantes quantitative et qualitative de la dispersion (Schupp et al., 2010). La zoochorie est un des modes privilégiés de dispersion à longue distance. Elle comprend principalement deux modes de dispersion primaire, l'épizoochorie, c'est-à-dire la dispersion par attachement sur une partie de l'animal ; et l'endozoochorie, c'est-à-dire la dispersion de graines ingérées, qui subissent le transit digestif et sont libérées à distance. Nous discutons ces deux modes à la suite.

L'épizoochorie

L'épizoochorie concerne donc le transport des graines par adhésion sur le corps de l'animal. Les graines peuvent être véhiculées dans le pelage et les sabots (chez les ongulés), dans le plumage ou encore les pattes. Les graines ou encore les plantes dont elles sont issues, qui ont des caractéristiques comme la présence d'appendices crochus pour adhérer au pelage, une hauteur de libération des graines élevée, ou bien une préférence écologique pour les milieux ouverts sont connues pour être préférentiellement dispersées par transport externe (Albert et al., 2015a). Les études sur l'épizoochorie sont

moins fréquentes que celles concernant l'endozoochorie, principalement du fait de contraintes méthodologiques pour observer et comptabiliser directement les graines sur les vecteurs de dispersion. Les études ont généralement impliqué la pose de graines sur des animaux habitués, le brossage d'individus morts à la chasse ou par accident, des prototypes pour secouer mécaniquement en laboratoire des graines attachées à des peaux d'animaux, ou bien par des simulations basées sur des données et observations empiriques.

L'épizoochorie a été étudiée dans le pelage des mammifères : chez les souris (Agnew et Flux, 1970; Sorensen, 1986) ; les ongulés domestiques comme les moutons, les chèvres, les chevaux et les ânes (Ansong et Pickering, 2013; Bläß et al., 2010; Couvreur et al., 2004; Fischer et al., 1996; Kaligarič et al., 2016; Mouissie et al., 2005; Shmida et Ellner, 1983) ; les ongulés sauvages comme les sangliers, chevreuils et cerfs élaphe (Dovrat et al., 2012; Heinken et Raudnitschka, 2002a; Picard et Baltzinger, 2012; Schmidt et al., 2004) ; les chiens (Graae, 2002; Heinken, 2000; Hernández et Zaldívar, 2013), ou encore les primates (Chen et al., 2018). Cependant, certains auteurs ont aussi étudié l'épizoochorie chez les oiseaux, comme les oiseaux d'eau (Brochet et al., 2010) et les passereaux en migration (Costa et al., 2014).

L'endozoochorie

L'endozoochorie comprend l'ingestion des graines, et leur dépôt à distance après digestion. Les études sur l'endozoochorie, en particulier la frugivorie, dominent la littérature sur la zoochorie, du fait de la possibilité de mesurer le temps de passage des graines dans le transit digestif sur des oiseaux habitués et d'autres animaux en leur donnant les graines à consommer et en mesurant les temps associés de défécation. Ces

études sont surreprésentées pour les oiseaux et les primates en milieu tropical (Corlett, 1998). Cependant, d'autres groupes taxonomiques sont impliqués dans la dispersion des plantes. Par exemple, Corlett (1998) a réalisé une revue de littérature concernant la frugivorie par différents vertébrés dans les forêts humides d'Asie, il a ainsi identifié 2 familles de reptiles, 17 d'oiseaux et 12 de mammifères avec un régime alimentaire essentiellement frugivore. Les frugivores de grande taille comme les civettes, les ours et les cervidés consomment des fruits à larges graines et les dispersent sur de longues distances (Spiegel et Nathan, 2007; Sridhara et al., 2016). La probabilité d'être dispersé par endozoochorie est favorisée pour les graines arrondies (Albert et al., 2015a), de petite taille (Pakeman et al., 2002), avec un tégument résistant à la digestion (Traveset, 1998), autant de caractéristiques qui favorisent aussi leur persistance dans la banque de graines du sol (Grime, 2007; Pakeman et al., 2002).

La dispersion des graines par les ongulés

Dans les écosystèmes tempérés, les grands herbivores, notamment les ongulés, ont contribué à maintenir les milieux ouverts, paysages dominés par les graminées, par le pâturage depuis plus de 1.8 million d'années (Pärtel et al., 2005). Les ongulés du fait de leur grande taille corporelle, de leurs domaines vitaux de plusieurs kilomètres carrés et de leurs mouvements journaliers, le tout généralement associé à des populations abondantes, peuvent constituer des agents mobiles importants entre patches d'habitat (Couvreur et al., 2004) en tant que vecteurs de dispersion à longue distance. Par ailleurs, les cervidés sont aussi connus pour leur forte fidélité spatiale (e.g. cerf et chevreuil ; Richard et al., 2014). Ils sont aussi considérés comme des ingénieurs de l'écosystème qui contribuent à l'hétérogénéité spatiale de la structure physique (e.g. en piétinant et en

se baugeant) et de la composition chimique (e.g. par dépôt d'urine et de fèces) des sols. Ils consomment et dispersent la végétation de façon sélective, et se nourrissent aussi de l'écorce des arbres (e.g. écorçage par le cerf).

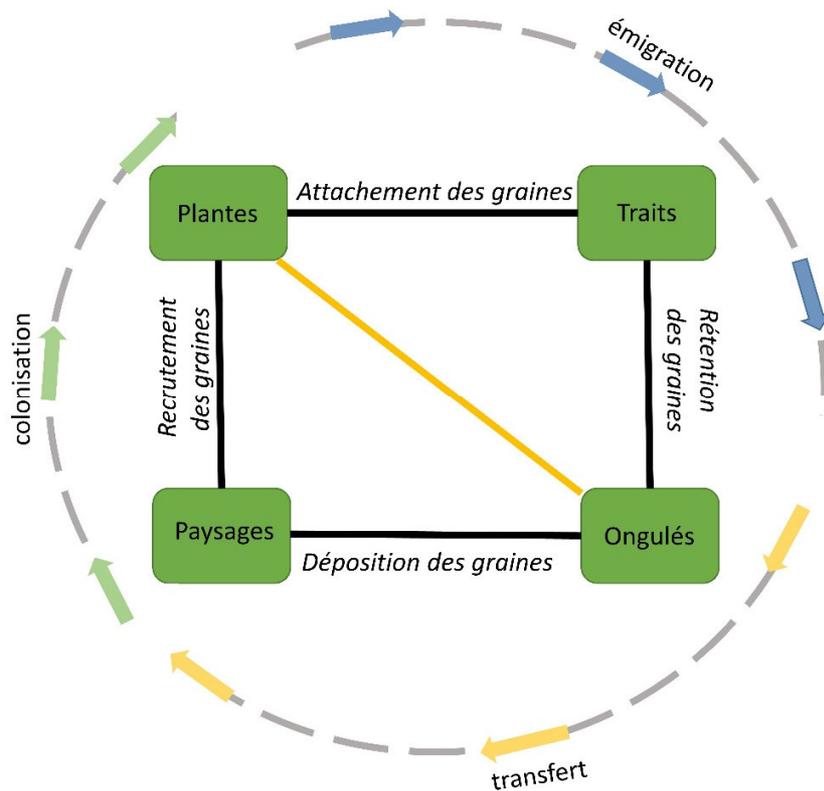


Figure 1.1: Cycle dispersion des plantes assistée par les animaux (adapté de Wang et Smith, 2002). Les étapes de la dispersion (Baguette et Van Dyck, 2007) sont représentées sur le cercle externe, chacune identifiée par des flèches de couleur unique.

De plus, la prise en charge des graines dépend des traits à la fois des plantes et de leurs vecteurs. Les traits comme la taille de l'animal, la taille de sa gueule (pour l'endozoochorie) et le type de pelage (pour l'épizoochorie) d'une part, et la hauteur de

libération des graines, la présence d'appendices d'accrochage d'autre part, contribuent à augmenter les chances de contact entre les plantes et leurs vecteurs et la prise en charge. La dispersion des graines a été étudiée chez les ongulés sauvages (comme le chevreuil, le cerf et le sanglier ; Dovrat et al., 2012; Heinken et al., 2002; Heinken et Raudnitschka, 2002a; Pellerin et al., 2016; Picard et al., 2015; Picard et Baltzinger, 2012; Schmidt et al., 2004) et les ongulés domestiques (comme les chèvres et les moutons ; Benthien et al., 2016) en régions tempérées. Nous discutons plus précisément le rôle des ongulés dans la dispersion des plantes dans la revue de littérature réalisée dans le chapitre 2.

Les kernels de dispersion

La façon la plus commune de caractériser la dispersion des graines consiste à estimer le kernel de dispersion, i.e. la probabilité de densité de dispersion des graines en fonction de la distance à la plante mère (Nathan et Muller-Landau, 2000).

Alors que le *seed shadow* ne se réfère quant à lui qu'aux distances de dispersion des graines issues d'une seule plante (Nathan and Muller-Landau 2000), ces termes kernels de dispersion et *seed shadow* sont utilisés de façon interchangeable dans la littérature (Cousens et al., 2010).

L'évaluation du kernel de dispersion requiert une fonction de probabilité, le plus souvent gaussienne, ou lognormale (Bullock et al., 2017). Estimer le kernel de dispersion dans sa forme la plus simple nécessite deux paramètres, la distance parcourue par le vecteur en un temps donné et la distribution des temps de rétention des graines, que ce soit par transit digestif (endozoochorie) ou sur le corps de l'animal (épizoochorie). La trajectoire de l'animal est déterminante et dépend du comportement fin de déplacement (Russo et

al., 2006; Westcott et al., 2005). Quand, pourquoi, où et comment les animaux se déplacent, dépendent des besoins intrinsèques de chaque individu et des caractéristiques de son environnement (Nathan et al., 2008). Chacun de ces éléments peut influencer la forme et l'amplitude du kernel de dispersion considéré. Alors qu'il est très fréquent de décrire le kernel de dispersion en incluant un ou quelques vecteurs de dispersion, un pan de recherche reste ouvert considérant chaque plante comme potentiellement dispersée par plusieurs vecteurs et par plusieurs modes de dispersion (ce que l'on nomme le kernel total de dispersion, Rogers et al. (2019).

La dispersion des graines dans les paysages changeants

Dans les habitats qui changent rapidement, l'importance de processus écosystémiques fondamentaux comme la pollinisation ou la dispersion des graines paraît plus qu'évidente. Notamment quand ces habitats favorables s'amenuisent, les animaux couvrent des distances plus faibles (Tucker et al., 2018) réduisant ainsi les distances potentielles de dispersion. De plus, le changement de composition de la matrice paysagère environnante augmente la probabilité que les graines véhiculées soient libérées dans des habitats défavorables, et ne puissent n'y germer et n'y s'installer dans ces nouveaux sites de dépôt. Le défaut de dispersion est considéré comme une contrainte majeure à l'aptitude des plantes à atteindre de nouveaux habitats, prérequis nécessaires pour qu'elles puissent maintenir le rythme des changements climatiques en cours.

Un des principaux challenges des écosystèmes forestiers européens est aussi la croissance des populations d'ongulés sauvages à des niveaux jamais atteints par le passé. Ces fortes abondances questionnent à plusieurs titres, notamment via

l'homogénéisation biotique et la propagation de plantes exotiques, qui affectent la composition des communautés végétales et la persistance des plantes locales.

Dans ce contexte, cette thèse cherche à évaluer le rôle des ongulés sauvages, et notamment du cerf élaphe, dans le processus de dispersion épizoochore des graines dans les écosystèmes forestiers tempérés.

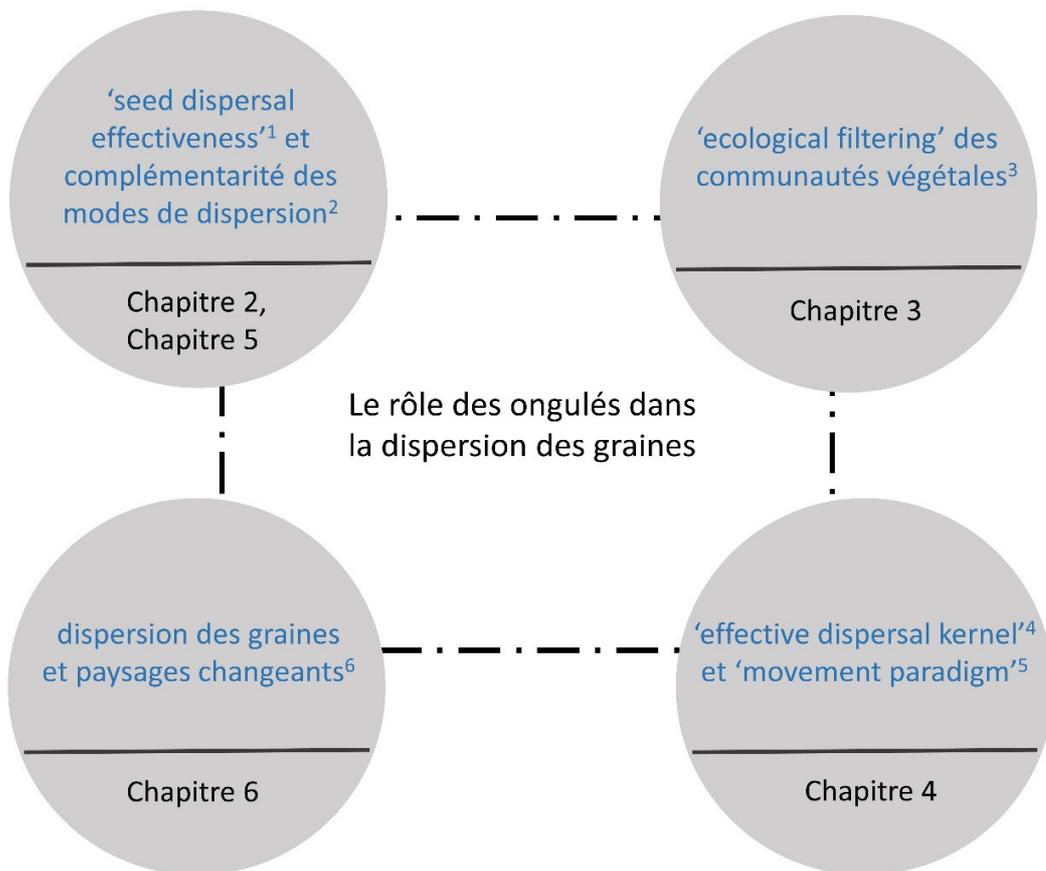


Figure 1.2: Structure de la thèse avec les concepts théoriques majeurs de la dispersion des graines, en font bleu pour chaque chapitre. Sources: 1. Schupp et al. (2010), 2. Couvreur et al. (2005), 3. revue par Albert et al. (2015), 4. Nathan et Muller-Landau (2000), 5. Nathan et al. (2008) and 6. revue par McConkey et al. (2012).

Je me suis d'abord intéressée à comprendre le rôle des ongulés et des services de dispersion qu'ils pourvoient dans la structuration des communautés végétales, en tenant compte des traits des plantes qui favorisent la dispersion. Par la suite, j'ai étudié les effets de la structure et de la composition du paysage sur les décisions de déplacement des animaux, et leurs conséquences sur les kernels de dispersion des graines (Cf. Fig.1.2 pour les détails sur la structure de la thèse)

Structure et panorama de la thèse

Chapitre 2: Cette revue de littérature aborde les différents modes de dispersion par lesquels les ongulés distribuent les graines à l'échelle du paysage. Nous avons recueilli 27 jeux de données recouvrant 23 études pour l'endozoochorie, 7 jeux de données issus de 6 études sur l'épizoochorie et finalement 17 jeux de données couvrant 11 études qui ont abordé endozoochorie et épizoochorie sur le même site. Nous évaluons et discutons l'ensemble des modes de dispersion dans lesquels les ongulés sont impliqués, trois modes de dispersion primaire et trois de dispersion secondaire. Nous discutons la complémentarité des vecteurs de dispersion (au moins deux espèces d'ongulés dispersant les plantes sur un même site) et celle des modes de dispersion (un même vecteur dispersant des graines par différents modes de dispersion). Nous discutons ces différents aspects au sein du cadre conceptuel d'efficacité de la dispersion des graines (Schupp et al. 2010) et évaluons au final, le rôle de la diversité fonctionnelle des ongulés au sein des écosystèmes, à partir des traits affectant la dispersion des plantes.

Nous montrons que les ongulés offrent une plus grande diversité fonctionnelle et des services de dispersion plus complets qu'estimé auparavant par des études monospécifiques. Cependant, le manque de standardisation dans les protocoles de mise

en germination rend difficile la comparaison des résultats entre études. Pour ce qui concerne les applications en terme de gestion des milieux naturels (comme la pratique du réensauvagement par exemple), nous suggérons d'introduire des espèces d'ongulés de régime alimentaire et de type de pelage diversifiés pour optimiser l'efficacité des services de dispersion dont bénéficient les plantes.

Chapitre 3: Ici, nous nous sommes intéressés au rôle des traits des plantes liées à la dispersion dans leur réponse à la présence des ongulés. Nous avons utilisé 105 espèces (pour un total de 403 espèces de plantes identifiées dans 156 relevés de végétation dans le Domaine National de Chambord, centre de la France) et un modèle hiérarchique de distribution conjointe des espèces pour évaluer la réponse des espèces de plantes à la présence des ongulés, ainsi qu'à d'autres variables environnementales et d'habitat – distance à la route la plus proche, hauteur de la canopée, indice d'humidité dérivé de données de télédétection. Pour chaque espèce de plante, nous avons aussi utilisé des traits pour mieux évaluer la réponse des plantes à la présence des ongulés. Globalement, l'indice de présence des ongulés ne permet pas de prédire la distribution des plantes. Ceci pourrait être dû à la surabondance ancienne des ongulés sur le site d'étude, ainsi qu'à l'indice de présence des ongulés finalement assez simpliste et à un taux d'échantillonnage trop faible.

Chapitre 4: Nous avons utilisé ici, une approche de simulation basée sur des données de localisation par GPS pour essayer d'évaluer comment les comportements fins de déplacements des cerfs affectent le kernel de dispersion d'une plante épizoochore, *Xanthium strumarium*, et cela sur un pas de temps court (i.e. 5 jours). Temps pendant lequel, nous estimons que chaque individu est en mesure de traverser son domaine vital

au moins une fois. Nous avons utilisé la distribution des temps de rétention estimée par Liehrmann et al. (2018) pour *Xanthium strumarium*, et des localisations de biches équipées de collier GPS dans le Domaine National de Chambord, en France et dans le parc national de la forêt bavaroise en Allemagne. Nous avons spécifiquement testé l'effet 1) de se déplacer au sein d'un domaine vital, 2) de la préférence d'habitat au sein du domaine vital et 3) de caractéristiques de déplacement dépendant de l'habitat sur la distance de dispersion et l'habitat de libération des graines transportées. Globalement, nos résultats soulignent l'importance de tenir compte des limites du domaine vital pour estimer les kernels de dispersion. Aussi, les graines issues des habitats peu représentés dans la matrice paysagère (comme les milieux ouverts dans nos sites d'étude) semblent bénéficier de la dispersion assistée par le cerf.

Chapitre 5: Nous avons évalué la complémentarité fonctionnelle et taxonomique des modes de dispersion des plantes par le cerf élaphe. Nous avons utilisé des données à l'échelle de l'individu pour comparer le nombre de diaspores, le nombre d'espèces et leurs traits associés pour chaque mode de dispersion étudié. Nous montrons que ni le nombre de diaspores, ni le nombre d'espèces transportées, à l'échelle de l'individu, ne diffèrent que l'on considère la dispersion endozoochore, la dispersion épizoochore dans le pelage ou la dispersion épizoochore sous les sabots. Par contre, la composition spécifique des plantes dispersées diffère entre modes de dispersion endozoochore et épizoochore avec peu de chevauchements, indiquant une complémentarité de ces modes de dispersion.

Note: Pour cette étude, nous avons utilisé un jeu de données publié et disponible en accès libre (Petersen and Bruun, 2019) pour 4 sites à travers le Danemark. Le jeu de données issu de notre échantillonnage à Chambord (60 échantillons complets de cerf et

58 de sanglier pour pelage, sabots et fèces) et d'un partenariat en Bavière (37 échantillons complets de cerf pour pelage, sabots et fèces) n'est pas encore exploitable du fait d'incertitudes d'identification des espèces de plante et sera exploité ultérieurement. Les données danoises ont été collectées à l'échelle de l'individu pour les différents modes de dispersion, sur des animaux prélevés durant la saison de chasse, selon un protocole similaire à celui que nous avons utilisé. Ceci nous a permis de tester nos hypothèses sur la complémentarité des modes de dispersion, à l'échelle de l'individu en utilisant leurs données.

Chapitre 6: Ce chapitre de livre (sous presse) sur le rôle des interactions biotiques dans l'invasion des plantes, est basé sur une revue de littérature évaluant le rôle des ongulés dans la propagation des plantes exotiques. Nous avons répertorié les données existantes pour 4 familles d'ongulés - Cervidae, Suidae, Bovidae et Equidae. Nous avons comparé ces informations par zone biogéographique et mode de dispersion (endozoochorie, régurgitation, et épizoochorie dans le pelage) et évalué leur rôle dans la dispersion des plantes exotiques. Les herbivores pousseurs tendent à disperser des plantes herbacées et des graminées, alors que les espèces omnivores comme les Suidae dispersent une plus grande diversité de types de plantes, incluant lianes, arbustes et arbres. Globalement, nous montrons une pénurie de données disponibles qui ne couvrent que la partie visible de l'iceberg. En effet, nous n'avons récolté des informations que pour 32 des 257 espèces d'ongulés existantes.

Dans le contexte de changement global de climat et d'habitat, ces interactions plantes-ongulés peuvent avoir des conséquences d'une portée considérable et leur rôle dans la propagation des plantes exotiques reste sous étudiée.

Je résume l'ensemble des conclusions de cette thèse dans le chapitre de synthèse
(**Chapitre 7**).

Introduction

(English version)

Dispersal is the movement from the place of birth to the place of reproduction (Matthysen, 2012). For sessile organisms such as plants, other abiotic (such as wind and water) and biotic vectors (such as vertebrates and invertebrates) are crucial to enable this movement. Seed dispersal connects genetically isolated populations; helps seeds escape predation and density dependent mortality by competition from other conspecifics, as well as colonize new, suitable habitats (Howe and Smallwood, 1982). At local scales, seed availability, i.e. seed limitation, affects the population size and growth rate. At regional scales, dispersal limitation affects the distribution of species (Münzbergová and Herben, 2005). Seed dispersal is, thus, a crucial ecological process governing spatial structure of plant populations (Nathan and Muller-Landau, 2000). While most seeds from a plant fall close to the parent-plant itself, a few travel to large distances, making most seed dispersal kernels leptokurtic in nature. Long distance dispersal (LDD) is important for the spread and migration of plant species, especially in the light of globally changing landscapes (McConkey et al., 2012).

Seed dispersal by animals

The process of primary seed dispersal (Fig.1.1) starts with the fruit production and seed availability on adult plants, the subsequent seed uptake by the dispersal vector and the deposition of seeds in suitable habitats for germination (Wang and Smith, 2002). For animal aided dispersal, this mutualistic interaction is beneficial to both plants who benefit from successful dispersal in space via seeds, as well as animals who benefit via acquiring nutritional resources and rewards. However, for seeds attached externally to animal bodies, the process is largely passive in nature (Sorensen, 1986). The success of dispersal or the effectiveness of a disperser depends on both the quality as well as quantity of dispersal (Schupp et al., 2010). While quality of dispersal relates to the handling of seed once picked up by the animal and the subsequent site of deposition; the quantity of dispersal relates to number of visits to the plant by the disperser as well as the number of seeds picked in each visit and carried away from the parent plant (Schupp et al., 2010).

Zoochory, i.e., animal-aided seed dispersal is an important LDD process. It mainly comprises of two primary modes- epizoochory or dispersal by external attachment on animal bodies; and endozoochory or dispersal of seeds ingested and passed intact via guts of the animal vector. We briefly discuss both here.

Epizoochory

Epizoochory, as stated before, is the attachment and transportation of seeds by adhesion to an animal's body. Seeds can be transported either via attachment to fur, via hooves, feather or legs of animals. Seeds with certain dispersal enabling seed and whole plant

traits such as modification of appendages for attachment to animal bodies, higher release height, affiliation to open habitats, etc. are said to benefit by seed uptake via epizoochory (Albert et al., 2015a). Studies on epizoochory are less common compared to endozoochory, largely due to methodological constraints of observing and enumerating seeds directly on the animal vectors. Studies have mostly employed attaching seeds onto tame animals, brushing of dead animals, mechanically shaking seeds attached animal coats in labs and data-driven simulation models. Epizoochory has been studied mainly in mammals, in mice (Agnew and Flux, 1970; Sorensen, 1986), in domestic ungulates such as sheep, goat, horse and donkey (Ansong and Pickering, 2013; Bläß et al., 2010; Couvreur et al., 2004; Fischer et al., 1996; Kaligarič et al., 2016; Mouissie et al., 2005; Shmida and Ellner, 1983); in native, wild ungulates such as wild boar, roe deer and red deer (Dovrat et al., 2012; Heinken and Raudnitschka, 2002a; Picard and Baltzinger, 2012; Schmidt et al., 2004), in dogs (Graae, 2002; Heinken, 2000; Hernández and Zaldívar, 2013), and in snub-nosed monkeys (Chen et al., 2018). However, there are also a few studies looking at epizoochorous dispersal in birds, for e.g. waterbirds (Brochet et al., 2010) and passerines (Costa et al., 2014).

Endozoochory

Endozoochory is the ingestion of seeds and their deposition at a later time. Studies on endozoochory, in particular frugivory, dominate the seed dispersal literature, mainly due to the possibility of measuring diaspore retention times on tame birds and animals by feeding them diaspores and recording time of defecation. Studies on endozoochory are disproportionately biased towards studying birds and primates in the tropics (Corlett, 1998). However, several other taxa are involved in ingestion and dispersal of diaspores

away from parent plant. For e.g. Corlett (1998) reviewed frugivory by different vertebrates in Asian rainforests and recorded two reptile, 17 bird and 12 mammal families as highly frugivorous. Large bodied frugivores for e.g. civets, bears and deer, consume large seeded fruits and disperse them over long distances (Spiegel and Nathan, 2007; Sridhara et al., 2016). The ability to be dispersed by endozoochory is enhanced by the presence of round seeds (Albert et al., 2015a), small seed size (Pakeman et al., 2002), ability to form persistent seed banks (Grime, 2007; Pakeman et al., 2002) and tough seed coats capable of surviving gut passage through the animal vectors (Traveset, 1998).

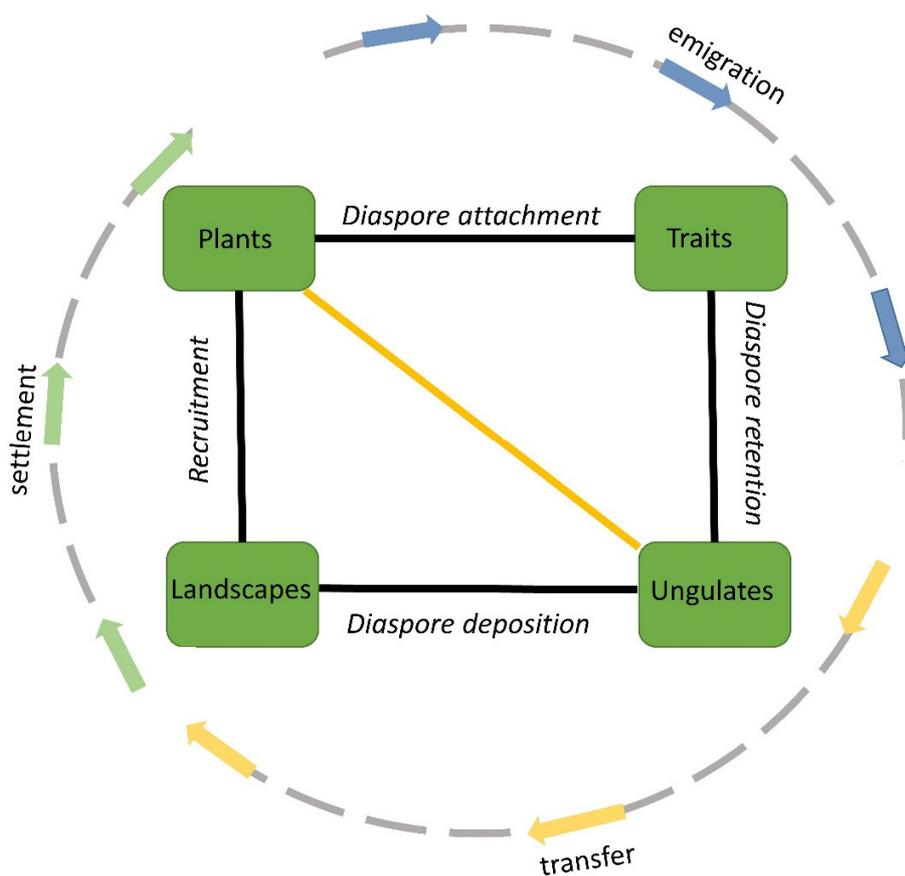


Figure 1.1: Ungulate-aided seed dispersal cycle (Modified from Wang and Smith, 2002). Stages of dispersal (Baguette and Van Dyck, 2007) shown in outer circle, with each stage marked in a different coloured arrow.

Seed dispersal by ungulates

In temperate ecosystems, large herbivores, especially ungulates, have maintained open area, grass-dominated landscapes via grazing for more than 1.8 million years (Pärtel et al., 2005). Ungulates with their large body sizes, several square kilometres of home range and daily movement and high population numbers can provide important ‘mobile links’ between habitats (Couvreur et al., 2004) as LDD vectors. Additionally, deer species in France are known to showcase high site fidelity (Richard et al., 2014). Ungulates are known ecosystem engineers changing soil conditions, selective herbivory and subsequent plant dispersal, local microhabitats via nutrient addition, wallowing, trampling, and bark removal. Additionally, seed uptake is sensitive to both plant and animal traits. Traits such as shoulder height of animal, gape size (for endozoochory) and fur type (for epizoochory), diaspore release height of plants, morphological adaptations of diaspore appendages, etc., all maximize the chances of contact between animals and plants and thereby enhance seed uptake probability. Seed dispersal has been studied in both wild (such as roe deer, red deer and wild boar, (Dovrat et al., 2012; Heinken et al., 2002; Heinken and Raudnitschka, 2002a; Pellerin et al., 2016; Picard et al., 2015; Picard and Baltzinger, 2012; Schmidt et al., 2004) and domestic ungulates (such as sheep and goat, (Benthien et al., 2016) in temperate regions. We further discuss the specific role of ungulates in seed dispersal in the literature review in Chapter 2.

Seed dispersal kernels

The most common way to characterize seed dispersal is by estimating the seed dispersal kernel, i.e. the probability density functions of distance of dispersed seed from the parent plant (Nathan and Muller-Landau, 2000). While seed shadow refers to the distances of

dispersed seeds from a single plant (Nathan and Muller-Landau 2000), these terms are used interchangeably in literature (Cousens et al., 2010). Estimation of dispersal kernel requires inclusion of a probability function, the most common of which are- Gaussian, lognormal, and 2Dt (Bullock et al., 2017). To estimate a seed dispersal kernel in its simplest form, the two basic variables to estimate are the time-specific distance covered by the animal vector and the diaspore retention time, either via gut passage (for endozoochory) or on the body of the animal (for epizoochory). Therefore, the movement trajectory of the animal is sensitive to its behavioural preferences (Russo et al., 2006; Westcott et al., 2005). When, why, where and how to move is governed by the intrinsic needs and external environment of the animal (Nathan et al., 2008) and each of these potentially influences the shape and magnitude of the consequent seed dispersal kernel. While it is more common to describe seed dispersal kernel including one or a few dispersers, each plant is dispersed by multiple dispersal vectors via one or more pathways/dispersal modes (called the 'total dispersal kernel' (TDK), Rogers et al. (2019)).

Seed dispersal in changing landscapes

In fast changing habitats, it is but obvious that the influence on fundamental ecosystem processes such as pollination or seed dispersal is profound. In shrinking favorable habitat sizes, animals cover shorter distances (Tucker et al., 2018) thereby reducing potential seed dispersal distances. Additionally, the changing composition of surrounding landscape matrix increases the chances of seeds landing in hostile conditions and fail to get recruited and established in the new sites. Additionally, dispersal limitation is identified as a major constraint for the ability of plants to reach new habitats, which will be a crucial requirement for them to keep up with climate change. One of the major challenges of

European forest ecosystems is the increase in the wild ungulate populations to unprecedented levels. This poses a multi-pronged problem of overabundance induced biotic homogenization, spread of non-native (exotic) species, which ultimately results in loss of dispersers for native plants.

With this background in mind, this thesis aims at assessing the role of wild ungulates, specifically red deer, in the process of epizoochorous seed dispersal in temperate forest ecosystems. I am primarily interested in understanding the role of ungulates and the dispersal services they provide in structuring local plant communities esp. with respect to dispersal-related plant traits. Additionally, I looked at the effect of landscape structure and composition on movement decisions made by animals and their effect on subsequent seed dispersal kernels. (See Fig.1.2 for details on the structure of the thesis).

Structure and overview of the thesis

Chapter 2: This is a literature review on the multiple mechanisms by which ungulates disperse diaspores in a landscape. We reviewed a total of 27 datasets across 23 studies for endozoochory; seven datasets across six studies for fur-epizoochory and 17 datasets across 11 studies looking at fur epizoochory and endozoochory at the same site. We assess and discuss all dispersal mechanisms – three primary and three secondary enabled by ungulates. We discuss the complementarity of dispersal vectors (two or more ungulates dispersing the same plant) and dispersal modes (single vector dispersing seeds by more than one dispersal mode). We then discuss these findings under the framework of the ‘seed dispersal effectiveness’ framework of Schupp et al. (2010) and finally assess the functional diversity of ungulates in an ecosystem by looking at dispersal-enabling traits. We found that ungulates offer a wider range of functional diversity and

dispersal services than indicated by single studies. However, lack of standardized length and protocol for germination experiments make it difficult to compare results from different studies. For management (like rewilding for instance) purposes, we suggest using ungulate species from different diet regimes to maximize efficiency of dispersal services.

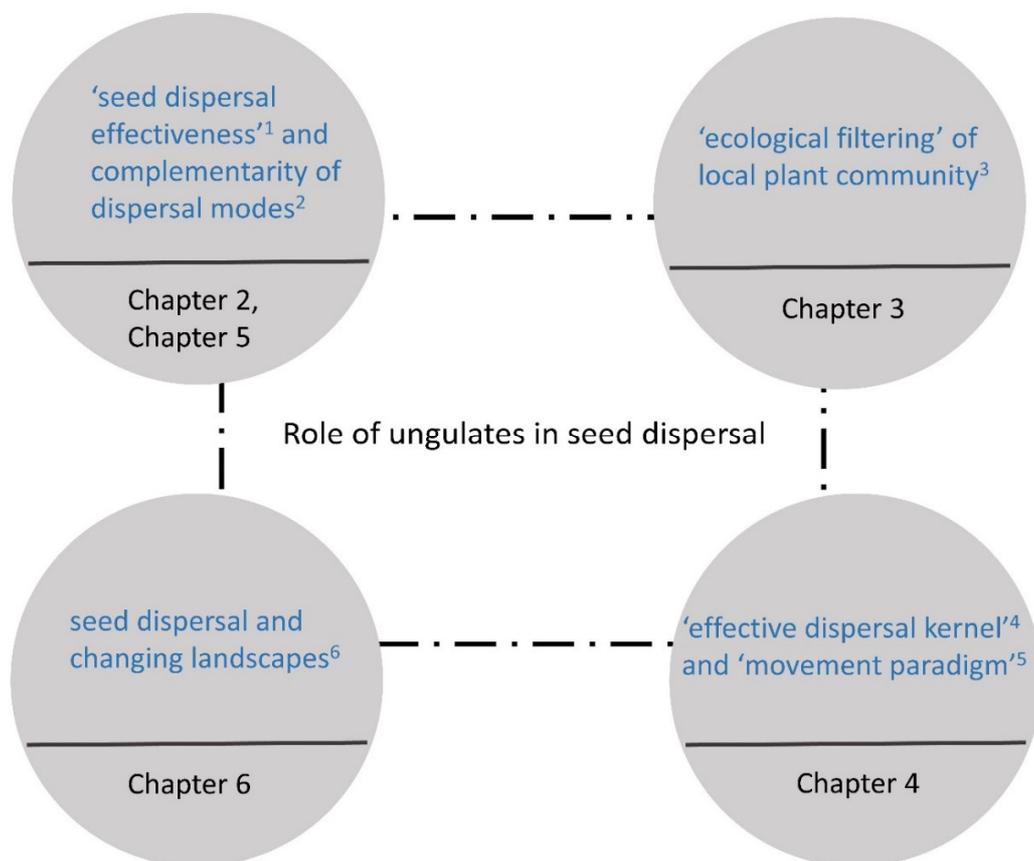


Figure 1.2: Thesis structure with main concepts of seed dispersal theory highlighted in blue font for each chapter. Sources: 1. Schupp et al. (2010), 2. Couvreur et al. (2005), 3. review by Albert et al. (2015), 4. Nathan and Muller-Landau (2000), 5. Nathan et al. (2008) and 6. review by McConkey et al. (2012).

Chapter 3: In this data chapter, we were interested in understanding the role of dispersal-related traits in plant species responses to ungulate presence. We use data for 105 (out of the 403 recorded plant species from 156 vegetation plots sampled in Domaine National de Chambord in north-Central France) and a hierarchical joint species distribution model to assess plant species response to ungulate presence in addition to other environment and habitat variables- distance to nearest road, canopy height and Normalized Difference Water Index (NDWI). We additionally used plant species level trait information to model plant species response to ungulate presence. Overall, ungulate presence was not a significant contributor in predicting plant species distribution. However, this could be a caveat associated with the extremely high abundance of ungulates at our study site, the over-simplified index measure of ungulate presence we used as well as small sample sizes.

Chapter 4: In this chapter, we take a data-driven simulation approach to try to assess how fine scale movement behavior of red deer affects seed dispersal kernel of an epizoochorous plant species, *Xanthium strumarium*, over a short term (five days) period. This was assuming that the individual animal crosses the home range at least once during that time. We used our retention time estimates from Liehrmann et al. (2018) of *Xanthium strumarium*, and GPS collar data of red deer from Domaine National de Chambord, France and Bavarian Forest National Park, Germany. We specifically test the effect of home ranging behavior, habitat preference within the home range and the habitat-specific step lengths and turning angles on the dispersal distance and habitat specificity of deposited seeds. Overall, our results highlight the importance of accounting for home ranging behaviour of animal in estimating seed dispersal kernels. Also, seeds from rare

habitats in the landscape matrix (such as open areas in our study) seem to benefit from animal-aided dispersal.

Chapter 5: In this chapter, we assess the functional and taxonomic complementarity of seed dispersal modes by red deer. We use information on individual red deer to assess the complementarity of number of transported diaspores, number of dispersed plant species and traits of dispersed plant species for each of the dispersal modes. We found no differences in the number of transported diaspores as well as the number of plant species dispersed by individual red deer between transported diaspores via fur, gut or hoof. However, the species composition of dispersed plants for each dispersal mode was different from each other with few overlaps, indicating complementarity of dispersal modes.

Note: For this study, we used an open-access published dataset from Petersen and Bruun (2019) on four sites across Denmark. The individual-based data from our own sampling in Chambord (60 individuals of red deer and 58 of wild boar from fur, hoof and gut) and Bavaria (37 individuals of red deer with data from gut, fur and hoof) lack species level identification at this stage and will be assessed at a later date. The data from Denmark was collected at the level of individual deer for all modes- gut, fur and hooves, on shot animals during hunting seasons; which is the same approach we took for collecting our data. This provided us with the opportunity to test our hypothesis on complementarity of dispersal modes for individual red deer using their data.

Chapter 6: This is a book chapter based on literature review on the role of biotic interactions in plant invasion, for assessing the role of ungulates in the spread of non-native plant species. We compiled existing data for four different families of ungulates-

Cervidae, Suidae, Bovidae and Equidae. We then compared them across biogeographic zones and dispersal modes (endo, regurgitation, fur-epizoochory) and assessed their role in dispersing non-native species. While grazers tend to disperse forbs and graminoids, omnivores disperse from a wider diversity of growth forms. Overall, there is a severe paucity of data available for non-native species dispersed by ungulates as we recorded data from only 32 of the total 257 existing ungulate species globally. In the view of global climate and habitat change, these plant-ungulate interactions can have far-reaching consequences and their role in spread of invasives remains understudied.

I summarise the findings from this thesis in the synthesis section (**Chapter 7**).

CHAPTER 2

Plants on the move: Hitch-Hiking with ungulates distributes diaspores across landscapes

Résumé (version français)

Nous décrivons ici les multiples mécanismes par lesquels les ongulés distribuent les diaspores à travers les paysages. Nous répertorions trois mécanismes de dispersion primaire et trois de dispersion secondaire, impliquant les ongulés avec ou sans l'intervention d'autres vecteurs biotiques ou abiotiques. Ces mécanismes peuvent être combinés en étapes interdépendantes.

Les ongulés sauvages, introduits et domestiques coexistent dans plusieurs écosystèmes et interagissent fréquemment avec de nombreuses plantes, ce qui facilite la dispersion à longue distance de plantes natives et exotiques. Cependant, la diversité taxonomique des ongulés cache une plus grande diversité de traits fonctionnels impliqués dans la dispersion des plantes (e.g., régime alimentaire, caractéristiques du pelage). Ces traits peuvent affecter profondément les phases d'émigration, de transfert et d'immigration pour la dispersion zoochore et en conséquence, ils peuvent aussi affecter l'efficacité globale de la dispersion des graines, à la fois quantitativement et qualitativement. Dans cette synthèse, nous comparons la dispersion interne, quand les graines doivent supporter la digestion (endozoochorie, régurgitation), avec la dispersion externe, quand les diaspores

sont véhiculées sur le corps (épizoochorie). Nous incluons à la fois la dispersion épizoochore primaire (adhésion directe au pelage) et secondaire (diaspores sous les sabots ou transfert par contact entre conspécifiques). Nous étudions le chevauchement et la complémentarité des ongulés pour les plantes qu'ils dispersent par une revue systématique de littérature. Quand deux espèces d'ongulés coexistent, il y a toujours une part de chevauchement dans les plantes dispersées par voie endo- ou par épizoochorie. Ensuite, quand on considère la proportion des plantes dispersées par voie interne et externe par un ongulé en particulier, le chevauchement pour les plantes dispersées est plus élevé pour les herbivores pisseurs que pour les autres régimes alimentaires. Nous identifions deux challenges pour le champ de l'écologie de la dispersion des plantes: évaluer la proportion de toutes les diaspores produites qui sont transportées par les ongulés et l'importance relative des ongulés au global comme vecteur principal de dispersion des plantes. De plus, le fait que de nombreuses plantes dispersées dans le pelage ne présentent aucune adaptation morphologique porte question sur les syndromes de dispersion. Nous discutons des challenges méthodologiques non résolus et soulignons des perspectives de recherche dans le domaine, par exemple le fait de considérer le comportement de l'animal et ses capacités cognitives, et le rôle des ongulés dans la propagation des plantes exotiques et la dispersion altitudinale des plantes.

Keywords: epizoochory, endozoochory, long distance dispersal (LDD), functional diversity index, plant-animal interactions.

Abstract

We here describe the multiple mechanisms by which ungulates distribute diaspores across landscapes. There are three primary and three secondary seed dispersal mechanisms by which ungulate dispersal agents contribute to the spread of plant diaspores, both with and without the intervention of other biotic and abiotic agents. These dispersal mechanisms may be combined in successive inter-dependent steps. Native, introduced and domestic ungulates co-occur in many ecosystems and frequently interact with numerous plant species, which facilitates long-distance dispersal of both native and exotic plants. However, ungulate taxonomic diversity conceals a much higher diversity in terms of the functional traits involved in ungulate-mediated dispersal (e.g., feeding regime, fur morphology). These traits may strongly affect emigration, transfer and immigration in the animal-mediated plant dispersal, and consequently; they may also impact overall seed dispersal effectiveness, both quantitatively and qualitatively. In this review, we compare internal mechanisms, where seeds must survive digestive treatments (endozoochory, regurgitation), with external mechanisms, where diaspores are carried on the outside of the vectors (epizoochory). We include both primary epizoochory (direct adhesion to fur essentially) and secondary epizoochory (diaspore-laden mud adhering to hooves or the body and, transfer through contact with a conspecific). We addressed the overlap/complementarity of ungulates for the plant species they disperse through a systematic literature review. When two ungulate species co-occur, there is always an overlap in the plant species dispersed by endozoochory or by fur-epizoochory. Further,

when we consider the proportion of plant species dispersed both internally and externally by an ungulate, the overlap is higher for grazing than browsing ungulates. We identify two challenges for the field of dispersal ecology: the proportion of all diaspores produced that are carried over long distances by ungulates, and the relative importance of ungulates on the whole as the main dispersal agent for plants. Furthermore, the fact that numerous plants dispersed by fur-epizoochory do not feature any specific adaptations is intriguing. We discuss unsolved methodological challenges and stress research perspectives related to ungulate-mediated dispersal: for example, taking animal behavior and cognition into account and studying how ungulates contribute to the spread of invasive exotic plants and altitudinal plant dispersal.

Introduction

Contrasting with the defaunation process currently impacting large mammals in tropical forest ecosystems (Galetti and Dirzo, 2013), ungulate populations in temperate forests are rapidly increasing, sometimes locally reaching higher populations than their historic records. This phenomenon concerns overabundant native deer populations (Côté et al., 2004) and introduced species thriving in different parts of the world (e.g., Canada, Japan, Australia, New Zealand).

They are mostly large mammals, their body mass ranges from kilograms to hundreds of kilograms, that inhabit open, semi-open and closed habitats (Loison et al., 1999). These animals explore large home ranges and cover long daily distances across composite landscapes, along more or less sinuous paths (e.g., see the gradient in path tortuosity from roe deer - *Capreolus capreolus*, to red deer - *Cervus elaphus*, to wild pig - *Sus*

scrofa, in Pellerin et al., 2016). Since they are mainly herbivores, they process and transport plant materials when roaming their home ranges, and are thus involved in ecosystem engineering by chemical transport (Wilby et al., 2001) through nutrient fluxes and contribute to soil chemical content heterogeneity (e.g., by feeding in nutrient-rich areas and randomly releasing faeces in forest-poor areas, Abbas et al., 2012; Murray et al., 2013). Albert et al. (2015a) demonstrated that temperate ungulates dispersed 44% of the regional pool of plants. Ungulate-mediated plant dispersal mainly occurs in the summer-fall seasons when most diaspores shed (Malo and Suárez, 1995). Dispersal also depends on ungulate feeding regime and other specific traits (Albert et al., 2015b).

Endozoochory, including frugivory, is the most widely studied ungulate-mediated plant dispersal mechanism (e.g., hoof- and fur-epizoochory concerns less than 12% of the samples, see table 3 in Albert et al., 2015a). However, Albert et al. (2015a) also stressed that, even though they are comparatively understudied, hoof- and fur-epizoochory were more selective processes than endozoochory and ungulates are involved in many different dispersal processes, both internal and external. Ungulate regurgitation, for instance, has been studied even less than hoof- and fur-epizoochory. This research gap seems logical since seed dispersal for fleshy-fruited plants occurs mainly in the tropics where birds, bats, primates and rodents are the main dispersal vectors (Jordano, 2000). Recently, however, more emphasis has been placed on other taxa, for instance reptiles (Sobral-Souza et al., 2017). Ungulates are important in plant dispersal for different reasons. First, they may play a role in long-distance plant dispersal (with maximal endozoochorous dispersal distances varying from 2.0 km for roe deer to 3.5 km for red deer, Pellerin et al., 2016). Second, they are present worldwide (except for Antarctica),

either as native or introduced species and they have great taxonomic diversity (240 and 17 species within the Artiodactyla and Perissodactyla orders, respectively, Wilson and Reeder, 2005). Their communities are diverse (e.g., 5 species in remnant old-growth forests in Poland - Jaroszewicz et al., 2013; 10 species in Renosterveld, South Africa - Shiponeni and Milton, 2006; see table 2.3), and they occur in a variety of ecosystems (e.g., forests, tree savannahs, grasslands). Finally, they have high functional diversity in plant-dispersal related traits (Albert et al., 2015b), e.g., various feeding regimes (Hofmann, 1989) and a wide range of body sizes (Clauss et al., 2007).

McAlpine et al. (2016) called for the integration of plant- and animal- based approaches for biodiversity conservation actions and restoration efforts. Emphasis should be on key biotic interactions, for example how both plants and animals are involved in pollination and plant dispersal. Recent studies in various ecosystems suggest that many ungulates - native (e.g., white-tailed deer - *Odocoileus virginianus*, Connecticut, Williams and Ward, 2006), domestic (e.g., cattle - *Bos taurus*, California, Chuong et al., 2016) and introduced (e.g., Philippine deer - *Rusa marianna* and wild pig, Mariana Islands, Gawel et al., 2018) are involved in the spread of exotic plants, questioning their potential to help restore degraded habitat. Human-modified ecosystems and plant communities can also be affected by the presence of these large ungulates.

In this review, we aim to shed new light on the specific role of ungulates in long-distance plant dispersal, and to better understand how they have contributed to past plant distribution patterns, how they shape present plant communities and how they might help future plant communities cope with rapid and drastic human-induced changes (e.g., land

use modifications, biological invasions, global warming, habitat loss and fragmentation, McConkey et al., 2012).

We have specifically addressed the following four objectives. In the first part, we sum-up the primary and secondary dispersal mechanisms through which ungulates distribute diaspores across landscapes and describe how each of these processes influences the fate of the diaspores carried by the vectors. We highlight diplochorous sequences where ungulates are involved in at least one of the dispersal steps. In the second part, we propose to adapt the seminal conceptual framework of seed dispersal effectiveness for frugivory and endozoochory proposed by Schupp (1993) and revisited by Schupp et al. (2010) to the two other ungulate-mediated primary processes: regurgitation and fur-pizoochory. In the third part, we discuss the functional diversity of ungulates, how it might affect the fate of the seeds dispersed, and how this should be used to build further research. In the fourth part, we performed a systematic literature review to assess the overlap and complementarity of sympatric ungulates in plant dispersal first and then of different ungulate-mediated plant dispersal mechanisms. Finally, we discuss unsolved methodological challenges, potential ungulate-mediated habitat restoration options and suggest research perspectives.

Diversity of ungulate-mediated dispersal mechanisms

No review to date has systematically addressed all the dispersal mechanisms through which ungulates convey diaspores across the landscapes. These mechanisms comprise both internal and external dispersal, primary and secondary dispersal events (i.e., diplochory, Vander Wall and Longland, 2004). They involve either biotic vectors alone

(ungulates, ungulates and coprophagous beetles - D'hondt et al., 2008), or more complex systems involving primates or birds, ungulates and coprophagous beetles (Newton, 1989) or both abiotic vectors (wind, water, gravity) and ungulates. These different mechanisms move diaspores from the parent plant to different releasing locations. Some primates or birds feeding on fruits in the tree canopy can make them fall to the ground where they become accessible to forest-dwelling ungulates. These interactions were reviewed by Newton (1989) and have more recently been assessed for the langur-chital association in India (Ramesh et al., 2012).

Internal mechanisms (left side of fig. 2.1) concern consumed diaspores, which must withstand digestion (mechanical, thermal and chemical treatments). They include two specific processes: regurgitation, or partial endozoochory (where diaspores are ingested and regurgitated, Prasad et al., 2006), and full endozoochory (where diaspores are ingested and defecated). External mechanisms (right shaded side of fig. 2.1), where diaspores are carried on the outside of the vectors on various body parts, include primary fur-epizoochory (direct adhesion to fur essentially) and secondary epizoochorous processes: transfer through contact with a conspecific (Liehrmann et al., 2018) and diaspore-laden mud adhering to hooves (Schulze et al., 2014) or the body (Heinken and Raudnitschka, 2002). We have used a model ungulate to depict primary and secondary dispersal mechanisms of diaspores from a parent plant present in its home range (fig. 2.1).

Regurgitation or partial endozoochory

First, let us look at one of the most understudied primary internal processes, regurgitation or partial endozoochory (described by scenario In1a in fig. 2.1). Here, fruit is ingested,

then the endocarp is regurgitated after a lapse of time in the rumen. Regurgitation has been documented all around the world: e.g., in India for the different fruits consumed by the chital (*Axis axis*, Prasad et al., 2006), in Mexico for the white-tailed deer (Mandujano et al., 1994), in western Africa for the duikers (*Cephalophus sp.*, Feer, 1995), in southern Morocco for goats (*Capra aegagrus hircus*, Delibes et al., 2017), and more recently, in Spain for red deer (Castañeda et al., 2017). Some fleshy-fruited plants known to be consumed by European roe deer (Cornelis et al., 1999; Cransac et al., 2001) for example, dogwood (*Cornus sanguinea*) and ivy (*Hedera helix*) share similar characteristics (fruit, endocarp and seed size) with the plants mentioned in these studies. Dogwood and ivy do not germinate from roe deer dung samples (Heinken et al., 2001; Picard et al., 2016); we therefore suppose that the endocarps are regurgitated and not defecated. Clean regurgitated endocarps were found at specific and predictable resting/ruminating sites (i.e., directed dispersal, Wenny, 2001) whereas defecated seeds were more or less randomly deposited within the home range.

Endozoochory and secondary dispersal by dung beetles

Now let us look at the most studied primary internal process: endozoochory (Picard et al., 2016, described by scenario In1b in fig. 2.1). Here diaspores are consumed, undergo complete gut passage and are defecated. Releasing sites are much less predictable than for regurgitation as ungulates can defecate away from their resting/ruminating site, while walking or feeding.

Faeces and their diaspore content can then be mobilized by other biotic vectors in a secondary step as depicted with coprophagous beetles (scenario Bi2, fig. 2.1). Depending on their functional group (Milotić et al., 2018, 2019), dung beetles move diaspores

horizontally (small and large rollers), bury them more or less deeply (small and large tunnellers and rollers, D'hondt et al., 2008) or leave them roughly in the same place (dwellers). This case is known as diplochory, or secondary dispersal.

Fur-epizoochory including transfer-epizoochory

The right side of fig. 2.1 represents external processes, which have been much less studied than endozoochory (Albert et al., 2015a). One primary external process is fur-epizoochory (described by scenario Ex1, fig. 2.1). Here diaspores become attached to the fur of passing ungulates. Diaspores carried in the fur of ungulates generally present a high turn-over - most of them will fall off during the first few hours (Bullock et al., 2011) - though attachment time does depend on the characteristics of the fur (e.g., hair curliness, hair length, Liehrmann et al., 2018). Diaspores can drop accidentally or the animals can detach them during specific grooming sessions with teeth, by scratching or by rubbing against tree trunks (Heinken et al., 2006). Allo-grooming events or games between conspecifics in social ungulates can also lead to secondary external dispersal (described by scenario Ex2a, fig. 2.1). Liehrmann et al. (2018) have recently documented this mechanism, called transfer-epizoochory for dwarf goats, Poitou donkeys and red deer hinds.

Diaspore transfers might occur more frequently during the reproduction period and while rearing young. We also suppose that transferred diaspores move from the home range of the first vector to the neighboring home range of its conspecific (fig. 2.1).

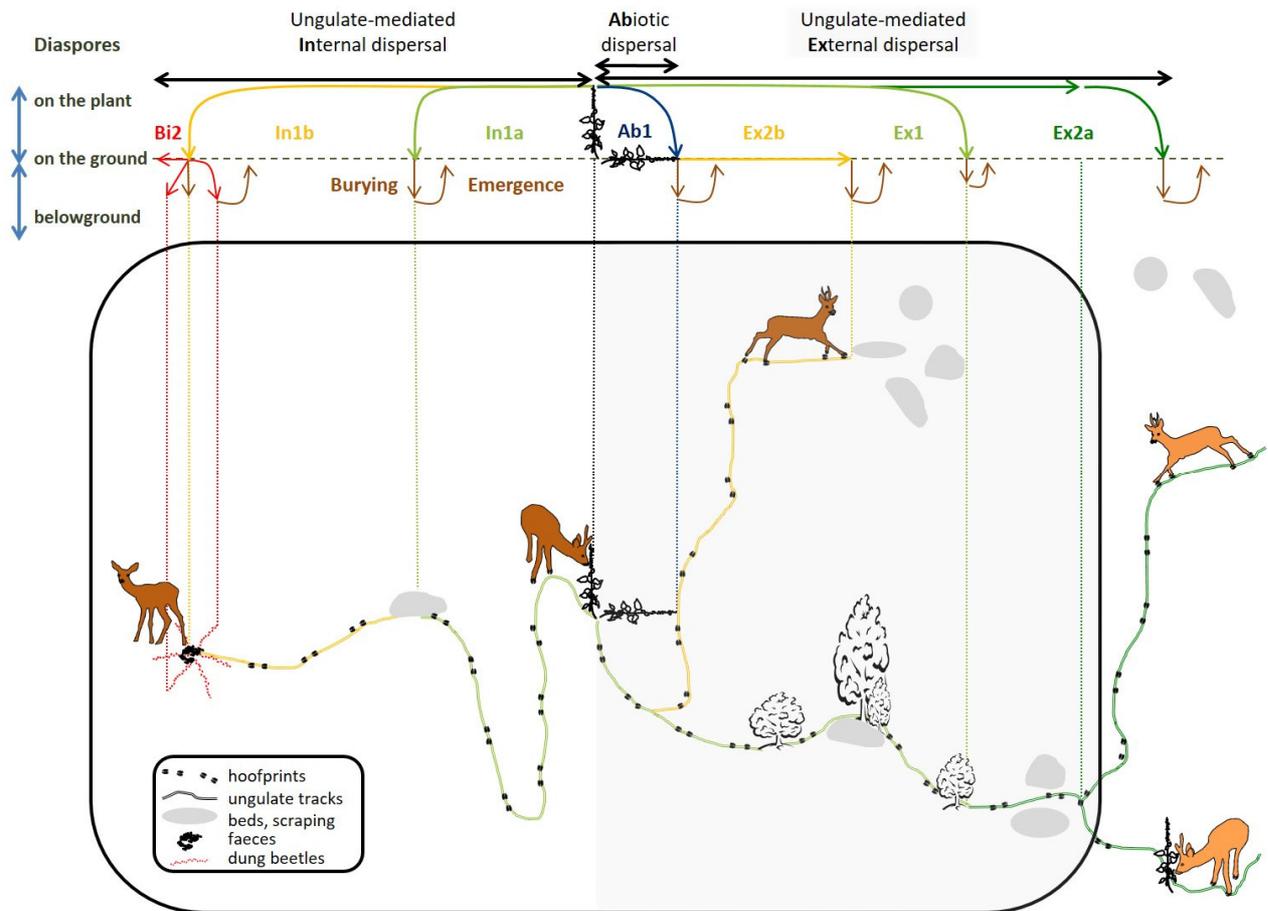


Figure 2.1: General spatial representation of primary internal ungulate-mediated plant dispersal mechanisms (indicated by 1: **In1a regurgitation**, **In1b endozoochory**) and primary (**Ex1 fur-epizoochory**) and secondary external ungulate-mediated plant dispersal mechanisms (indicated by 2: **Ex2a transfer-epizoochory**, **Ex2b hoof-epizoochory**) and the associated horizontal and vertical trajectories of the carried diaspores. To the left side of the parent plant, the diagram describes internal mechanisms; the shaded part to the right represents external mechanisms. **Abiotic dispersal by gravity (Ab1 barochory)** can be considered as a first step of dispersal. And secondary dispersal by other **biotic** vectors like coprophagous beetles (**Bi2**) is considered as a second step following endozoochory (**In1b**). The top part of the diagram shows the fate of a diaspore for each dispersal mechanism from the parent plant to its final destination (moving from the diaspore regional pool to the transferred pool, the soil surface pool and finally, the soil seed bank, box 1). The large black rectangular shape delimits the home range of the vector.

Hoof-epizoochory

When diaspores are not dispersed by ungulates and other biotic or abiotic vectors, they simply fall to the ground when the parent plant withers, this is called barochory (described by scenario Ab1, fig. 2.1). These diaspores therefore have a maximal distance equivalent to the diaspore releasing height. All the diaspores released on the ground within the ungulate's home range, whatever the dispersal process, constitute the soil surface pool (box 1). These diaspores may either germinate and take root, enter the soil seed bank or be dispersed again by ungulates through hoof-epizoochory (described by scenario Ex2b, fig. 2.1), as often occurs on loose soils when diaspore-laden mud sticks to the hooves (roe deer, red deer and wild pig in Picard and Baltzinger, 2012; European bison - *Bison bonasus* in Schulze et al., 2014) or to other body parts. Secondary epizoochory may also happen when ungulates like wild pig wallow for thermal comfort or to get rid of ectoparasites (Heinken and Raudnitschka, 2002). These diaspores can drop off further along trails (e.g., white-tailed deer in Lefcort and Pettoello, 2012; and horse, *Equus caballus* in Wells and Lauenroth, 2007) where germinating conditions may be more favorable, for example in microhabitats like hoof prints of ungulates (fig. 2.1) where rainwater can stand longer. Diaspores can also drop off nearby rubbing trees (Welanders, 2000).

Spatial trajectory of conveyed diaspores

The top part of fig. 2.1 shows the fate, spatial trajectory and associated successive movements (from release by the parent plant to deposition on the ground) of the conveyed diaspores for each dispersal mechanism considered (the color code corresponds to the associated internal or external mechanism). Some of the diaspores will contribute to the

build-up of the soil seed bank (Jaroszewicz, 2013) through gradual burying (Burying, fig. 2.1) or thanks to the tunneling activities of paracoprid and telecoprid dung-beetles and can further reemerge (Emergence, fig. 2.1) on the soil surface through physical changes in the soil, with or without mediation by ungulates (Jones et al., 1994) to find propitious germination conditions (e.g., light and humidity).

Seed dispersal effectiveness revisited for ungulate-mediated processes including regurgitation and fur-epizoochory

Schupp (1993) defined a conceptual framework to study seed dispersal effectiveness (SDE), defined as the result of a quantitative component, the emigration phase, and a qualitative component, the transfer and immigration phases (table 2.1). The plant dispersal process is therefore composed of three distinct phases, namely emigration, transfer and immigration (table 2.1). The emigration phase for ungulate-mediated dispersal relies on the spatial and temporal availability of diaspores in the vegetation physically accessible within the home range of a given dispersal agent. This diaspore load depends on the interaction between the traits of the plant and of its diaspores and the traits of the dispersal agent (Albert et al., 2015b). The transfer phase determines the trajectory covered by the diaspores transported by the dispersal agent during gut retention and regurgitation time or the time elapsed between the attachment of the diaspore to the dispersal agent and its detachment. The immigration phase concerns the germination of the released diaspores, their establishment as seedlings, their growth to adult plants able to reproduce. Thus ungulate-mediated seed dispersal is potentially important for plant demography from one generation to the next (Wang and Smith, 2002; Vellend et al., 2006) and plays a role in metapopulation dynamics (e.g., see fig.6 in Jabot

et al., 2008, and the link between migration and the proportion of mammal-dispersed trees).

Box 1. Spatial and temporal diaspore availability within ungulate home ranges and populations

The **regional plant pool** corresponds to all the plants in their adult reproductive stage accessible to the ungulate, within its home range or within the geographic area occupied by the population of ungulates. The **local plant pool** corresponds to the plants members of the plant community at the local scale.

At the diaspore stage (e.g., seed, fruit) and within an ungulate's home range, four pools of diaspores differ in their spatial and temporal availability: the **regional diaspore pool**, the **transferred diaspore pool**, the **soil surface diaspore pool** and the **soil seed bank**.

- the **regional diaspore pool** defines all the diaspores available on the parent plants at diaspore releasing height during the seed shedding period. Some plants maintain a dead erect stem and therefore lengthen temporal availability for potential dispersal agents.

- the **transferred diaspore pool** defines diaspores when they have left the mother plant via biotic or abiotic dispersal. The duration and associated distance of the ungulate-mediated transfer phase depend on internal or external retention time (fig. 2.2).

- the **soil surface diaspore pool** combines diaspores released on the ground by biotic or abiotic vectors with diaspores falling on the ground when the plant withers. In that case, maximal dispersal distance equals diaspore releasing height. Released diaspores can germinate, be moved by dung beetles or between the hooves of ungulates during secondary dispersal, or build-up the **soil seed bank**.

- the **soil seed bank** includes diaspores with varying longevity, from transient (< 1 year), short-term (< 5 years) to longer term (over 5 years, as for soft rush, *Juncus effusus*). These diaspores can encounter favorable germination conditions following soil disturbance and/or improved light conditions at different time scales.

In an updated version of this conceptual framework, Schupp et al. (2010) suggested that their framework should not be restricted to the sole study of frugivory and endozoochory, but that it could be adapted to other dispersal processes like fur-epizoochory. In table 2.1, we follow this suggestion by comparing the three primary ungulate-mediated dispersal processes: endozoochory and regurgitation (internal) and fur-epizoochory (external). We will sequentially treat the different components and sub-components involved in SDE and

highlight the ungulate characteristics that affect each dispersal phase. The quantitative component (emigration phase) corresponds to the product of the number of visits to the plant and the number of diaspores loaded per visit (table 2.1).

Number of visits

Whatever the dispersal process considered, the number of visits to the parent plant will depend on three parameters: the local ungulate abundance, a degree of selectivity and the frequency and length of contacts with the parent plant. For internal dispersal processes (endozoochory and regurgitation), feeding selectivity will determine where, when and which plant will be consumed (Boulanger et al., 2009) and will depend on the feeding regime of the ungulate considered. For instance, Intermediate Mixed Feeders like the red deer (Gebert and Verheyden-Tixier, 2001; Latham et al., 1999) are less selective and consume a higher diversity of plants than sympatric Concentrate Selectors like roe deer (Cornelis et al., 1999; Cransac et al., 2001). The frequency and the length of the feeding bouts will also determine the occurrence of contacts with the selected feeding items. The number of active bouts (including feeding bouts) varies across the year and is generally higher during summer (e.g., 12 for red deer - Pépin et al., 2006; 16 for moose, *Alces alces* and 26 for roe deer in Cederlund, 1989).

Table 2.1: Components of ungulate-mediated seed dispersal effectiveness comparing three primary processes: endozoochory, regurgitation and fur-epizoochory (modified from table 1 in Schupp, 1993, and fig. 2 in Schupp et al., 2010).

Plant dispersal	Component	Sub-component	Endozoochory	Regurgitation	Fur-epizoochory
Emigration phase	Quantitative How many diaspores are loaded by the vector?	number of visits	- local ungulate abundance - selective feeding (feeding regime) - frequency and length of feeding bouts		- local ungulate abundance - within home range fidelity (used trails, core areas) - frequency and length of active, including feeding, bouts
		number of diaspores loaded per visit	- number of diaspores consumed per visit - loss before and during ingestion - physical accessibility - body mass		- number of diaspores hung per contact - loss by grooming - height of contact - body surface, body part and fur characteristics
Transfer phase	Qualitative What is the chance for a loaded diaspore to become an adult plant?	treatment quality by vector	- mechanical (mastication), thermal and chemical (rumination, digestive strategy) - gut passage time (fig. 2.2)	- mechanical (mastication), thermal and chemical (rumination) - regurgitation time	- mechanical (rubbing), thermal (body temperature buffer) and climatic (humidity) - external retention time (fig. 2.2)
Immigration phase		deposit quality of the released diaspores	- random or directed defecation - fecal matrix - diverse and numerous diaspores	- regurgitation at ruminating/resting site - no matrix - assumed few diaspores at a time	- random or directed to rubbing structures (trees, rocks or the ground) - no matrix - weakly diverse and isolated diaspores
		quality of the deposition site for germination and growth	- environmental filter (abiotic conditions) - strong biotic interactions with predators, decomposers, herbivores or among plants	- environmental filter (abiotic conditions) - weak biotic interactions with predators, herbivores or among plants	- environmental filter (abiotic conditions) - weak biotic interactions with predators, herbivores or among plants

By comparison with external processes (fur-epizoochory), daily home range fidelity (Richard et al., 2014), how regularly ungulates use the same paths (Lefcort and Pettoello, 2012; Torn et al., 2010; Wells and Lauenroth, 2008) or how frequently they use specific parts (e.g., core areas in Le Corre et al., 2009) of their home range should determine the number of visits. The frequency of the active bouts and their length during each visit will lead to the passive attachment of some diaspores to different body parts of the ungulate (Fischer et al., 1996), more specifically to the head and/or the breast of the animal while feeding on specific plants (“foliage is the fruit” hypothesis extended to fur-epizoochory - Janzen, 1984; Couvreur et al., 2005).

Number of diaspores loaded per visit

The number of diaspores consumed during each visit will depend on the feeding regime. More diaspores are consumed by generalist herbivores like Grass and Roughage Eaters (e.g., European bison, cattle) or Intermediate Mixed Feeders (e.g., red deer, chamois - *Rupicapra rupicapra*) than by more selective herbivores like Concentrate Selectors (e.g., roe deer, moose in Hofmann, 1989). It will also depend on the body mass, as heavier species and heavier individuals will eat more plant material than lighter ones to meet energy requirements (e.g., see the difference between two concentrate selectors: roe deer, < 30kg vs. moose, >300kg, Loison et al., 1999). Finally, diaspore availability on the plant and its accessibility to the ungulates also have an influence (box 1). Albert et al. (2015b) showed that Concentrate Selectors consumed diaspores at a specific diaspore releasing height. Some of the diaspores detached from the parent plant might be lost before ingestion, especially when the fruits and diaspores are not the main focus of the feeding bouts and are accidentally consumed (Janzen, 1984). For fur-epizoochory, the

number of diaspores loaded during each visit will depend on the number of diaspores attached per contact, resulting from the interaction between diaspore releasing height and ungulate body height (Fischer et al., 1996; Albert et al., 2015b). The number of diaspores attached to the ungulate body also depends on fur characteristics like hair length and curliness (Albert et al., 2015b) and on which body surface area is exposed (Bohême, 2012). Wild pig dispersed more diaspores of more plants than did red deer, and red deer more than did roe deer (see fig. 2 in Picard and Baltzinger, 2012). Bohême (2012) assessed the body surface exposed per individual for wild pig, red deer and roe deer and no longer found any significant difference in seed load per surface unit between red and roe deer. Liehrmann et al. (2018) confirmed the interspecific effects of fur characteristics (by comparing red deer, dwarf goat and Poitou donkey, *Equus asinus*) and extended that pattern to different body parts (head, flanks or rump) of a given individual. They also showed that some diaspores may be lost during auto-grooming events.

The qualitative component (transfer and immigration phases) combines the quality of the treatment exerted by the vector, the deposit quality of the released diaspores and finally the quality of the deposition site, i.e. both abiotic conditions and biotic interactions encountered at the release site (table 2.1).

Treatment quality by the vector

Diaspores consumed by an ungulate undergo different treatments of variable duration: physical (mastication and rumination), and thermal and chemical (digestive process). Mastication, i.e. the chewing process, may lead to the destruction of the diaspores consumed; especially concerning large seeds (e.g., acorns).

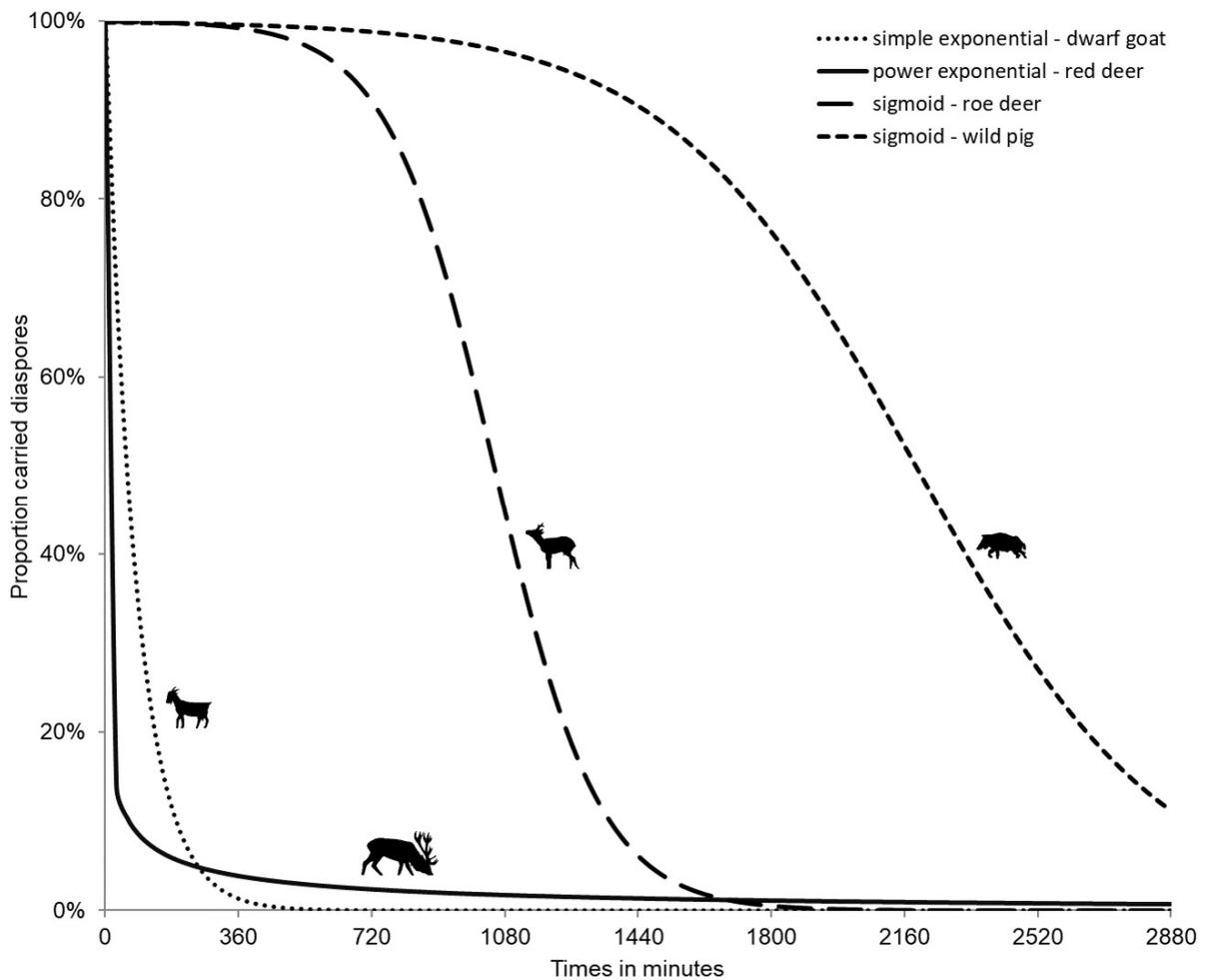


Figure 2.2: Internal (endozoochory, right curves for roe deer, *Capreolus capreolus* and wild pig, *Sus scrofa*) and external (fur-epizoochory, left curves for dwarf goat, *Capra aegagrus hircus* and red deer, *Cervus elaphus*) diaspore retention time (adapted from Picard et al., 2015; Liehrmann et al., 2018).

Indeed, most of the studies on ungulate endozoochory highlight preferential dispersal of small-sized (Janzen, 1984; Heinken et al., 2002; Pakeman et al., 2002; Picard et al., 2016) and rounded seeds (Mouissie et al., 2005a), which germinate in higher proportions in ungulate dung, though Bruun and Poschlod (2006) showed that this pattern might be

linked to the greater overall availability of small seeds (i.e, reproductive trade-off). The digestive process itself adds thermal and chemical treatments in the gut (Milotić and Hoffmann, 2016b), which differentially affect the seed coat, its permeability and subsequent ability to germinate once released in the fecal matrix.

Picard et al. (2015) showed, for instance that bramble (*Rubus fruticosus*) seeds germinated when consumed by wild pig whereas unconsumed control seeds and those consumed by ruminant deer species did not. Gut passage time is a function of ungulate body mass (Illius and Gordon, 1992) for both ruminants and non-ruminants: the heavier the animals the longer the transit (Clauss et al., 2007; and e.g., see the shift between the roe deer and wild pig in fig. 2.2, Picard et al., 2015). Digestive systems opposing ruminants to non-ruminants will also have differing effects on the fate of the seeds. For ruminants, larger seeds will be processed longer and smaller ones will pass the gut more rapidly (Picard et al., 2015). Above a given size, endocarps from fleshy fruits will be regurgitated (Sridhara et al., 2016). Empirical experimental data on gut passage time vary from one to three days for ungulates (e.g., see table 2 in Pakeman, 2001) for temperate forest ungulates ranging in body mass between less than 30 kg (roe deer) and more than 300 kg (moose, Loison et al., 1999), though Illius and Gordon's equations have been questioned (Clauss et al., 2007). Internal retention time requires a minimal time for the first diaspores to be released, and non-ruminant species release different-sized diaspores simultaneously (Picard et al., 2015). Data on regurgitation times are scarce: in India for chital, they range from seven to 27 hours (Prasad et al., 2006) and for red deer in Spain from 1 to 4 days after ingestion (Castañeda et al., 2017).

The treatment effect for externally attached diaspores is much weaker. This effect could be linked to rubbing (against trees or through grooming) or to weather (body versus air temperature and humidity - effect of precipitation). Whereas in internal processes, all diaspores are released after a specific gut passage time, in external processes like fur-epizoochory, most of the diaspores drop off very quickly, though but a few can be retained much longer (fig. 2.2, for red deer), thus contributing to very long-distance dispersal (Bullock et al., 2011; Liehrmann et al., 2018).

Deposit quality of the released diaspores

As ungulates defecate either after leaving resting or ruminating sites, during walking, or feeding events, we can consider defecation sites to be randomly distributed in comparison to regurgitation sites, where endocarps are released only at ruminating sites (Prasad et al., 2006). However, Picard et al. (2016) suggest that internally-dispersed plants are typically selected in open feeding habitats and are then released when ungulates rest under forest cover (Abbas et al., 2012); this could be considered a non-random directional movement. Diaspores can detach accidentally and randomly from the fur, however it could also be considered as a non-random process of dispersal as evidenced by soil seed bank of diaspores near rubbing trees, where more viable diaspores are found than nearby non-rubbed trees (Heinken et al., 2006; Welander, 2000). The deposit quality of the released diaspores is linked to the presence of a fecal matrix. In experiments done with 15 grassland plants, Milotić and Hoffmann (2016c) showed that sowing seeds in ungulate dung reduced germination rate and lengthened germination time; this pattern was even stronger for cattle compared to horse dung. These findings highlight the significance of dung material characteristics (ruminant vs. non-ruminant) in deposit quality. The diversity

of the feeding regime will determine the diversity of the seeds present in the dung (higher for Intermediate Mixed Feeder than for Concentrate Selector, e.g., see Picard et al., 2016) and the body mass will determine the abundance of seeds, as heavier ungulates or individuals will ingest more plant material (red deer vs. roe deer, Picard et al., 2016). We assume that regurgitated endocarps might be less diverse as they generally concern one specific nutrient-rich resource at a time (Prasad et al., 2006). As externally conveyed diaspores are not released in a fecal matrix, their chances to be released as isolated and undetectable diaspores in the field are high (e.g, through experimental assessment in Liehrmann et al., 2018).

Quality of the deposition site for germination and growth

The quality of the deposition site will, of course, depend on the local abiotic conditions (i.e., environmental filter, Kraft et al., 2015) including light, temperature and humidity. Ungulates leave hoofprints while walking on loose soils, and they also create specific microhabitats while scraping (e.g., roe deer in Johansson, 2000) or digging (e.g., wild pig in Welander, 2000) the ground. Acting as ecosystem engineers (Jones et al., 1994), they modulate the resources available to other taxa, including diaspores. The quality of the deposition site will also depend on biotic factors. The presence of the fecal matrix, which differentiates full endozoochory from both regurgitation and fur-epizoochory, will favor biotic interactions with different functional and taxonomic groups. Decomposers (e.g., soil macroinvertebrates, different types of dung beetles, Milotić et al., 2018, 2019) will move diaspores towards specific microhabitats. D'hondt et al. (2008) showed that dung beetles had a negative effect on short-term seedling establishment, probably due to the deep burial of diaspores by large tunnellers. Fungi frequently develop on faeces and may affect

the tegument of the dispersed seeds. Small rodents, attracted by the clumped seeds in the faeces, may also predate on the seeds dispersed. Other plants may benefit from the nutrients released and compete for resources with establishing seedlings. Milotić and Hoffmann (2016a) showed that the effect of the fecal matrix was beneficial for post-germination stages of the plant development. Large herbivores that feed selectively on nitrophilous plants (Janzen, 1984; Albert et al., 2015a) may be attracted by nutrient-rich vegetation patches, and also interact at the deposition site with establishing seedlings.

The functional diversity of ungulates and associated effects on the fate of diaspores

The ungulates are numerous and taxonomically and functionally diverse (Groves and Grubb, 2011). This diversity may intervene at different steps in ungulate-mediated diaspore dispersal processes, from the scale of the individual vector to groups of individuals, populations and communities (table 2.2). At the scale of the individual, mostly physiological and morphological traits will be concerned, and are depicted in the two following sub-sections. The third sub-section reports to higher scales of organization (i.e., from pairs to groups of individuals).

Body mass, feeding regime and digestive strategy

Concerning endozoochory, large body mass increases the amount of diaspores consumed (Picard et al., 2016), and once consumed, body mass will affect gut retention time (Picard et al., 2015 but see Steuer et al., 2011 for a comprehensive review). Furthermore, gut retention time varies with diaspore size (Clauss et al., 2009; Picard et al., 2015). Digestive strategy will also affect endozoochory, with ruminants sorting food items according to their size (Schwarm et al., 2008).

Table 2.2: Effects of ungulate functional diversity gradients on the different phases of internal (endo: endozoochory and regurgitation) and external (epi: fur-epizoochory) plant dispersal (CS : Concentrate Selector, IMF : Intermediate Mixed Feeder, GRE : Grass and Roughage Eater and OM : Omnivore). Upper letters refer to citations listed below the table.

Socio-spatial scale	Ungulate characteristics	Emigration	Transfer	Immigration
Individual level (physiology and morphology)	Body mass	endo ^{a,b}	endo ^c	
	Feeding regime (CS, IMF, GRE and OM)	endo ^b /epi ^d		
	Digestive strategy (ruminant or not)		endo ^{c,e}	
	Body size (shoulder height)	endo ^f /epi ^{f,g}		
	Body surface area	epi ^h	epi ^h	
	Fur characteristics (hair length and curliness, fur thickness)	epi ^{i,j}	epi ^{i,j}	
	Auto-grooming (wallowing, rubbing against structures)	epi ^j	epi ^{j,k,l}	epi ^{k,l}
Population level	Sociality/hierarchy (from pairs to herds)	epi ^m /endo ^m	epi ^j	
	Allo-grooming	epi ^j	epi ^j	
Landscape level	Habitat use (home range fidelity, activity rhythm)	endo ^{n,o,p} /epi ^{n,o,p}	endo ^{n,o,p} /epi ^{n,o,p}	endo ^{n,o,p} /epi ^{n,o,p}
	Movement (home range size, daily distance, tortuosity)		endo ^{q,r} /epi ^{q,r}	

^aIllius and Gordon, 1992; ^bPicard et al., 2016; ^cPicard et al., 2015; ^dCouvreur et al., 2005; ^eSchwarm et al., 2008; ^fAlbert et al., 2015b; ^gFischer et al., 1996; ^hBohême, 2012; ⁱPicard and Baltzinger, 2012; ^jLiehrmann et al., 2018; ^kHeinken et al., 2006; ^lWelander, 2000; ^mSarasa et al., 2009; ⁿRichard et al., 2014; ^oKeuling et al., 2008; ^pLe Corre et al., 2009; ^qPakeman, 2001; ^rPellerin et al., 2016

Picard et al. (2015) showed that smaller rounded diaspores were retained for shorter times in the gut of red and roe deer than were larger diaspores, whereas in wild pig all types of diaspores were generally released at the same time (see also differences between banteng, *Bos javanicus* and pygmy hippopotamus, *Hexaprotodon liberiensis* in Schwarm et al., 2008). Feeding regime will determine the growth form, diversity and

amount of the plants consumed (European bison, a Grass and Roughage Eater, Kowalczyk et al., 2011; red deer, an Intermediate Mixed Feeder, Gebert and Verheyden-Tixier, 2001; roe deer, a Concentrate Selector, Cornelis et al., 1999 and wild pig, an Omnivore, Schley and Roper, 2003), but also which part of the plant is consumed, with browsers being much more selective than grazers. Feeding regime will affect the emigration phase for both endo- and fur-epizoochory, because by feeding and spending time in open areas, herbivores will enhance chances for diaspores to attach to different parts of their body (e.g., head, belly, flanks).

Body size, body surface, fur characteristics and grooming

Body size, with respect to plant-animal interactions, relates to the height at which vegetation is encountered in the area explored by the ungulates. This affects both endo- and fur-epizoochory as it determines which plants are accessible, or reachable, for feeding (Fischer et al., 1996; Albert et al. 2015b). Albert et al. (2015b) showed that body size approximated by shoulder height interacted with plant diaspore releasing height for both endozoochory (i.e., which vegetation layers are consumed) and fur-epizoochory (i.e., which vegetation can touch the animal's body). Eventhough, ungulates may stand on their hind legs or take advantage of snow cover to access vegetation above their head height, shoulder height remain a good predictor that can be used for comparative approaches. Body surface area is another important characteristic with regard to external dispersal. Bohême (2012) revealed that the abundance of diaspores on different individuals with similar fur characteristics (red deer and roe deer) was directly related to the total surface area made accessible to the plants to attach. Liehrmann et al. (2018) further showed that hair length and curliness were also factors of diaspore attachment and detachment.

Ungulates such as the Poitou donkey (undercoat and long hairs) or the wild pig stock the diaspores in their fur, while others like the dwarf goat (short and wavy hairs) or the red and roe deer showed a rapid turnover of diaspores. Fur thickness can affect diaspore attachment and detachment and thus directly determine the time the diaspores stay attached to the different parts of the animal's body. Finally, single individuals will groom themselves with their teeth or legs (Liehrmann et al., 2018), rub against trees or wallow to get rid of parasites (Welandar, 2000; Heinken et al., 2006). These grooming events will affect the loss, the gain and also the transfer phase of different diaspores.

Sociality, habitat use and movement patterns

At the population scale, or at least for individuals living in pairs, interactions among individuals (e.g., playing games, mother-young relationships, resting in groups, allo-grooming) can lead to both diaspore detachments and transfers from one individual to another (Liehrmann et al., 2018). These interactions will mainly affect external seed dispersal. Sarasa et al. (2009) showed that the access by Iberian ibex to feeding stations was dependent on the sex and age of the individuals, which conditioned the access to the vegetation but also the infestation by pseudoectoparasites, and potentially the attachment of diaspores adapted to fur-epizoochory. At larger scales, the way ungulates use the different habitats that compose their home range will affect the fate of seed dispersal (e.g., Keuling et al., 2008 for the wild pig; Le Corre et al., 2009 for the roe deer). Picard et al. (2016) suggested that feeding habitat preferences filtered out some of the potential diaspores which could be conveyed by ungulates. Directed dispersal might occur if animals regularly return to the same sites and use the same trails between feeding and resting/ruminating sites. Home range fidelity at different temporal scales (e.g., day,

season, year, Richard et al., 2014) also means that ungulates might move diaspores to very predictable places associated to routine movements (Riotte-Lambert et al., 2017). The alternation of active and passive bouts of interaction with vegetation also determines when diaspores are attached and when they can be released. The extent (see definition in Pakeman, 2001) of the home range, which is closely related to animal body mass and energy requirements, constrains daily movements and determines how animals explore the space available. For instance, roe deer describe more tortuous trajectories than do red deer or even wild pig (Pellerin et al., 2016), leading to shorter dispersal distances for a given walked distance.

Overlap and complementarity of ungulate-mediated dispersal

In plant dispersal networks, diaspores produced by the parent plant can be dispersed through endozoochory by different co-occurring vectors. These networks have been established principally for frugivory and endozoochory (Dugger et al., 2018; Miguel et al., 2018). Fedriani and Delibes (2009) studied the role of different mammals (e.g., wild pig; red deer; badger, *Meles meles* and red fox, *Vulpes vulpes*) dispersing the Iberian pear (*Pyrus bourgaeana*). Jaroszewicz et al. (2013) showed that numerous plant species were dispersed by a guild of dispersal agents (table 2.3). On the other hand, situations also occur where one specific ungulate vector disperses the same plant through different mechanisms, i.e. endozoochory, fur- and hoof-epizoochory. Birch (*Betula pendula*) was dispersed between the hooves and on the fur of wild pig, red deer and roe deer (Picard and Baltzinger, 2012). Both the characteristics of the dispersal vector and the considered mechanism will ultimately affect seed dispersal effectiveness (table 2.1) and may generate complex and unpredictable dispersal kernels.

In this section, we look at plant species that can potentially germinate after long-distance ungulate-mediated dispersal; however, without considering how the transfer phase occurred. We emphasize the overlap and complementarity resulting from co-occurring ungulates, which disperse plants through either endozoochory or fur-epizoochory, and from a single ungulate on a specific site dispersing the same plants through both endo- and fur-epizoochory. Here, overlap and complementarity are understood in terms of plant species diversity dispersed between ungulates and between dispersal mechanisms, though other components of the SDE (table 2.1) such as seed load and distances travelled are also relevant. We carried out a systematic literature review on internal and external ungulate-mediated dispersal processes across worldwide with the following search string in ISI Web of Science (July 9th, 2018)

TS=(Ungulate OR Artiodactyl* OR Perissodactyl* OR Ruminant* OR Antilocapridae OR Bovidae OR Camelidae OR Cervidae OR Equidae OR Giraffidae OR Hippopotamidae OR Moschidae OR Rhinocerotidae OR Suidae OR Tapiridae OR Tayassuidae OR Tragulidae OR [Genus of all different ungulate species]) AND TS=(Seed* OR endo*zoochor* OR ecto*zoochor* OR epi*zoochor* OR exo*zoochor* OR regurgitation OR frugivor* OR zoochor*) AND TS=(Plant* OR invasive* OR exotic* or introduced or non-native*)*

The list of all different ungulate genera was retrieved from www.ultimateungulate.com.

We then used basic functional traits (feeding regime and fur characteristics, Albert et al., 2015a,b) to check if we can predict how sympatric ungulates provide overlapping or complementary endozoochorous or epizoochorous dispersal services. We proceeded

similarly to predict the overlap and complementarity between endozoochory and fur-epizoochory.

This search provided 22 studies (corresponding to 27 datasets) for endozoochory where at least two ungulate vectors were considered on the same site (i.e., some studies referred to multiple sites and different ungulate communities and were handled as distinct datasets, table 2.3). For fur-epizoochory, we retrieved only six studies (corresponding to 7 datasets, table 2.4), mainly in Europe. For both endo- and fur-epizoochory combined, we retrieved 17 datasets from 12 studies (i.e., studies including endo- and fur-epizoochory for two ungulate vectors were considered as distinct datasets, table 2.5). All the retrieved studies and extracted data are included in tables 2.3, 2.4 and 2.5.

Most of the studies on ungulate-mediated dispersal retrieved from this search by ungulate community mentioned two or three co-occurring ungulates - studies with 2 ungulates: 11 and 5 for endozoochory and fur-epizoochory, respectively; with 3 ungulates: 12 and 2, respectively (table 2.3 and table 2.4). Studies on ungulate endozoochory (table 2.3) involving more than three ungulates were rare (e.g., see Sigwela, 2004; Young, 2012 and Jaroszewicz et al., 2013), though one study mentioned up to 13 ungulates in South Africa (Milton and Dean, 2001). Second, most of the studies involved wild ungulates; and domestic ungulates were mentioned more rarely (Mitlacher et al., 2002; Cosyns et al., 2005; Mouissie et al., 2005b; Benthien et al., 2016 and Treitler et al., 2017, table 2.3).

Table 2.3 Studies on ungulate endozoochory included in the overlap and complementarity of ungulate-mediated plant dispersal: ungulate sample size (given as weight in grams or as number of fecal samples), publication, location (site, country), total number of plant species dispersed, % of plant species dispersed by 2 vectors or more, and germination period (* indicates studies where diaspores were identified under a magnifying glass and not after seedling emergence). Na: unavailable information.

Ungulate vectors (sample size)	Publication	Site, country	Total number of plant species dispersed	% of plant species dispersed by 2 vectors (number of plant species)	% of plant species dispersed by > 2 vectors (number of plant species)	Germination period (in months)
European bison (46), elk (35), red deer (80), roe deer (33), wild pig (90)	Jaroszewicz et al., 2013	Białowieża Forest, Poland	191	28.80% (55)	25.13% (48)	36
fallow deer (104), red deer (103), cattle (104)	Malo and Suárez, 1995	Castillo de Vinuelas estate, Spain	102	30.39% (31)	38.24% (39)	10
red/fallow deer (235), muntjac (296), roe deer (225)	Eycott et al., 2007	Thetfort Forest, England, UK	100	25.00% (25)	21% (21)	10
red deer (105), roe deer (48), wild pig (77)	Karimi et al., 2018	Hyrcanian forest, Golestan NP, Iran	86	19.77% (17)	13.95% (12)	15
red deer (77), wild pig (72), wild goat (70)	Karimi et al., 2018	Scrub & woodland, Golestan NP, Iran	81	29.63% (24)	7.41% (6)	15
cattle (20), elk (20), mule/white-tailed deer (10)	Bartuszevige and Endress, 2008	Oregon, USA	52	40.38% (21)	7.69% (4)	3
cattle (10), horse (10), sheep (10)	Mouissie et al., 2005b	Oosterwalde, Netherlands	49	30.61% (15)	36.73% (18)	9
camel (6), cattle (1143), goat (19), sheep (49), donkey (1), eland (200g), gemsbok (100g), giraffe (400g), duiker (159), rhebuck (100g), kudu (225), springbok (1), wildebeest (100g)	Milton and Dean, 2001	North & West provinces, South Africa	48	27.08% (13)	14.58% (7)	na

red deer (60), roe deer (60), wild pig (60)	Picard et al., 2016	Lorris, France	46	21.74% (10)	8.70% (4)	12
zebra (na), eland (na), wildebeest (na)	Shiponeni and Milton, 2006	EPNR, South Africa	43	25.58% (11)	20.93% (9)	12
muntjac (173), roe deer (126), red/fallow deer (54)	Panter and Dolman, 2012	England, UK	41	12.20% (5)	29.27% (12)	> 2
chamois (61), red deer (106), wild pig (45), sheep (12966)	Young, 2012	Arthurs Pass NP, New Zealand	34	11.76% (4)	8.82% (3)	36
nilgai (100), cattle (100), wild pig (100)	Middleton and Mason, 1992	Keoladeo NP, Rajasthan, India	25	16.00% (4)	36.00% (9)	12
rhinoceros (na), eland (na), kudu (na), bushbuck (na), goat (na), duiker (na), grysbok (na)	Sigwela, 2004	Eastern Cape, South Africa	23	26.09% (6)	21.74% (5)	0*
gazelle (100), oryx (194), wild ass (84)	Polak et al., 2014	Negev desert, Israel	22	22.73% (5)	4.55% (1)	13
bushpig (119), bushbuck (103), grysbok (19)	Castley et al., 2001	ACD, South Africa	16	12.50% (2)	6.25% (1)	0*
donkey (87), goat (88)	Treitler et al., 2017	Sardinia, Italy	113	43.36% (49)	-	6
sheep (10), goat (6)	Benthien et al., 2016	Luebeck, Germany	97	17.53% (17)	-	0*
red deer (190), wild pig (87)	Lepkova et al., 2018	Bohemia, Czech Republic	80	35.00% (28)	-	12
cattle (4), konik horse (7)	Cosyns et al., 2005	Westhoek North, Belgium	67	79.10% (53)	-	6
cattle (4), Shetland horse (19)	Cosyns et al., 2005	Westhoek South, Belgium	63	87.30% (55)	-	6
fallow deer (3728g), wild pig (3942g)	Heinken et al., 2001	Kraemer, Germany	50	36.00% (18)	-	6
cattle (14), sheep (15)	Mitlacher et al., 2002	Öland, Sweden	45	46.67% (21)	-	4
urial (70), gazelle (70)	Karimi et al., 2018	Steppe, Golestan NP, Iran	32	31.25% (10)	-	15
roe deer (152g), wild pig (2448g)	Heinken et al., 2001	Breiselang, Germany	25	12.00% (3)	-	6
roe deer (60), wild pig (60)	Picard et al., 2016	Montargis, France	15	20.00% (3)	-	12
Philippine deer (20), feral pig (31)	Gawel et al., 2018	Guam, Mariana Islands, USA	10	30% (3)	-	15

Endozoochory by at least two ungulates

In its “foliage is the fruit hypothesis”, Janzen (1984) proposed different predictions. The first one states that [...] *herbaceous plant vegetation is edible to several large herbivores* [...]. The review we made confirms this first prediction as we showed that co-occurring ungulates dispersed at least two similar plant species in each considered study. Indeed, we revealed a systematic overlap when two ungulates are present at a site, with both ungulate species dispersing between 11.76% (Young, 2012) and 87.30% (Cosyns et al., 2005) of the total number of plant species dispersed (table 2.3). These proportions correspond to two (Castley et al., 2001) to a maximum of 55 plant species (Cosyns et al., 2005; Jaroszewicz et al., 2013). This pattern is reinforced when we consider studies where at least three ungulates are present. In these cases, again a significant proportion of all the plant species dispersed are dispersed by three ungulates or more. This proportion ranges from 4.55% (Polak et al., 2014) to 38.24% (Malo and Suárez, 1995) of the total number of plants dispersed (table 2.3) and corresponds to one (Castley et al., 2001; Polak et al., 2014) to a maximum of 48 plant species (Jaroszewicz et al., 2013). These results demonstrate that some plant species can rely on different co-occurring ungulates. At the same time, other plant species are solely dispersed by a single vector species. In this case, ungulates provide complementary dispersal services at the scale of the plant community.

Further, we assessed all combinations of two ungulates (n=98 cases, table 2.6) from the datasets retrieved (ungulate endozoochory, table 2.3) and we summarized the proportion of plant species dispersed, taking into account the feeding regime of each ungulate (Hofmann, 1989; Hempson et al., 2015).

Table 2.4: Studies on ungulate fur-epizoochory included in the overlap and complementarity of ungulate-mediated plant dispersal: ungulate sample size (given as number of brushed individuals), publication, location (site, country), total number of plant species dispersed, % of plant species dispersed by 2 vectors or more.

Ungulate vectors (sample size)	Publication	Site, country	Total number of plant species dispersed	% of plant species dispersed by 2 vectors (number of plant species)	% of plant species dispersed by > 2 vectors (number of plant species)
cattle (125), donkey (46), horse (30)	Couvreur et al., 2004	Flanders, Belgium	75	25.33% (19)	14.67% (11)
red deer (5), roe deer(16), wild pig (6)	Picard and Baltzinger, 2012	Lorris, France	18	5.56% (1)	5.56% (1)
goat (17), sheep (3)	Shmida and Ellner, 1983	Har Gilo, Israel	57	38.60% (22)	-
roe deer (25), wild pig (9)	Heinken and Raudnitschka, 2002	Breiselang, Germany	55	40.00% (22)	-
roe deer (41), wild pig (25)	Schmidt et al., 2004	Herzogtum Lauenburg and Luechow- Dannenberg, Germany	42	30.95% (13)	-
sheep (10), goat (6)	Benthien et al., 2016	Luebeck, Germany	38	28.95% (11)	-
roe deer (7), wild pig (11)	Picard and Baltzinger, 2012	Montargis, France	29	6.90% (2)	-

The sample size of each combination varies between four (a Grass and Roughage Eater with an Omnivore) and eighteen (a Grass and Roughage Eater with an Intermediate Mixed Feeder, table 2.6). Combinations of two Grass and Roughage Eaters (n=9) shared the highest number of plant species dispersed, nearly 50%, whereas for all other combinations of different feeding regimes, this proportion ranged from 10% (two Concentrate Selectors) to 25% (a Grass and Roughage Eater with an Omnivore) and showed high variability (table 2.6).

Fur-epizoochory by at least two ungulates

We used the same approach to evaluate the six studies retrieved on fur-epizoochory (table 2.4). Couvreur et al. (2004) mentioned a maximum of 75 plant species dispersed by three domestic ungulates (cattle, donkey and horse) whereas Picard and Baltzinger (2012) found 18 plant species dispersed by three wild ungulates: red deer, roe deer and wild pig. Here again, we revealed a systematic overlap when two ungulates are present at a site, with both ungulate species dispersing between 5.56% (one plant species, Picard and Baltzinger, 2012) and 40 % (22 plant species, Heinken and Raudnitschka, 2002) of the total number of plant species dispersed (table 2.4). When we consider studies where at least three ungulates are present, again a significant proportion of all the plant species dispersed are dispersed by three ungulates. This proportion ranges from 5.56% (one plant species, Picard and Baltzinger, 2012) to 14.67% (11 plant species, Couvreur et al., 2004) of the total number of plants dispersed (table 2.4)

Further, we assessed all combinations of two ungulates from the datasets retrieved (ungulate fur-epizoochory, table 2.4) and we summarized the proportion of plant species dispersed, taking into account two fur characteristics (hair length and curliness, as described by Albert et al., 2015b). Fur-epizoochory provided many fewer comparisons (n=11 cases for each characteristic, table 2.6); therefore, our results must be carefully interpreted and considered to be mere trends. The highest shared number of plant species dispersed systematically involved a curled-haired ungulate (between 26 and 34% of shared plant species dispersed) or the presence of one long-haired ungulate (between 21 and 30% of shared plant species dispersed, table 2.6).

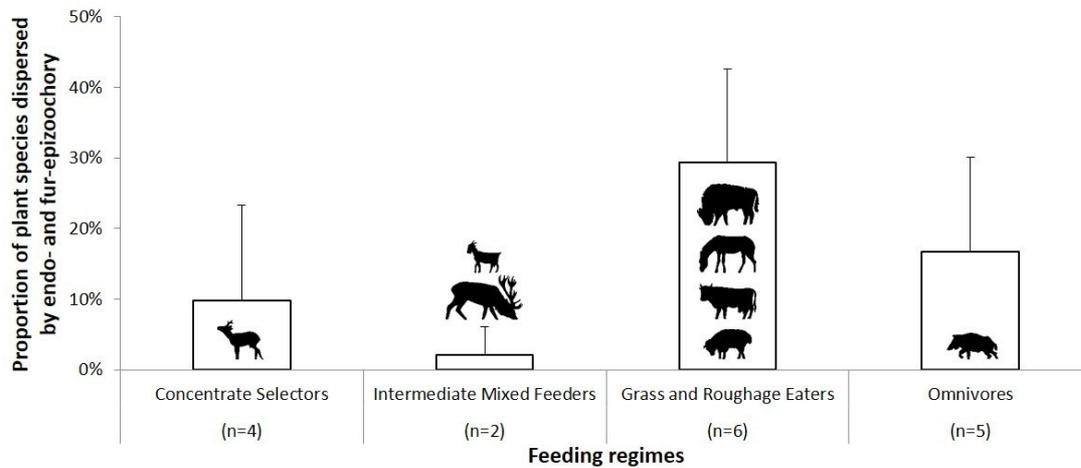


Figure 2.3: Proportion of plant species dispersed through endozoochory and fur-epizoochory by ungulates according to their feeding regime (table 2.5). Concentrate Selectors are represented by roe deer (*Capreolus capreolus*); Intermediate Mixed Feeders by goat (*Capra aegagrus hircus*) and red deer (*Cervus elaphus*); Grass and Roughage Eaters by American bison (*Bison bison*), donkey (*Equus asinus*), cattle (*Bos taurus*) and sheep (*Ovis aries*) and Omnivores by wild pig (*Sus scrofa*).

Complementarity of fur-epizoochory and endozoochory

The last part of this section is dedicated to the complementarity of the two main ungulate-mediated dispersal mechanisms, fur-epizoochory and endozoochory. We retrieved 17 cases where both mechanisms were studied for at least one ungulate on a specific site, 12 cases involving different wild ungulates (roe deer, red deer, American bison, *Bison bison* and wild pig) and 5 cases involving domestic ungulates (goat, sheep, *Ovis aries*, donkey and cattle) (table 2.5, fig. 2.3). We have seen that the temporal dynamics of the seed release varies with the ungulate species and the dispersal mechanisms (fig. 2.2) with implications for plant dispersal distances. The extreme number of plants dispersed by a domestic ungulate vary between 37 (cattle, Chuong et al., 2016) and 132 (sheep, Benthien et al., 2016) different plant species dispersed through endozoochory and/or fur-

epizoochory (table 2.5). If we consider wild ungulates, the total number of plant species dispersed ranges between 8 (roe deer, Picard and Baltzinger, 2012; Picard et al., 2016) and 71 (wild pig, Schmidt et al., 2004, table 2.5). No plant species was dispersed through both mechanisms by roe deer or red deer in France (Picard and Baltzinger, 2012; Picard et al., 2016), whereas American bison displayed the highest number of plant species dispersed through both endo- and fur-epizoochory with 36 different plant species, representing more than 55% of the total number of plant species dispersed (Eyheralde, 2015). Roe deer (n=4), the single Concentrate Selector and wild pig (n=5), the single Omnivore, are the most frequently studied ungulates. They disperse variable numbers of plant species, ranging between 8 and 41 for roe deer, and between 33 and 71 for wild pig (Picard and Baltzinger, 2012; Picard et al., 2016; Schmidt et al., 2004). We can take a similar picture if we consider the proportion of plant species dispersed by endo- and fur-epizoochory, ranging between 0% and nearly 30% for Concentrate Selectors (here, roe deer), and between 2.5 to 38% for Omnivores (here, wild pig, table 2.5). Concerning Grass and Roughage Eaters (n=6, including American bison, cattle, donkey and sheep), and especially American bison, a significant proportion (nearly 30%) of the dispersed plant species are dispersed both externally and internally. Intermediate Mixed Feeders (n=2, red deer and goat) dispersed both externally and internally the lowest proportion plant species (fig. 2.3). Finally, among the 17 study cases reviewed and whatever the ungulate species concerned, 12 study cases report higher number of plant species strictly dispersed by endozoochory in comparison with 5 study cases by fur-epizoochory.

Table 2.5: Studies with both fur-epizoochory and endozoochory on the same site included in the overlap and complementarity of ungulate-mediated plant dispersal: ungulate sample size (given as number of brushed individuals for fur-epizoochory and weight in grams or number of fecal samples for endozoochory); feeding regime (CS: Concentrate Selector; IMF: Intermediate Mixed Feeder; GRE: Grass and Roughage Eater; OM: Omnivore), publication, location (site, country), total number of plant species dispersed, % of plant species strictly dispersed by fur-epizoochory and % of plant species strictly dispersed by endozoochory. **Bold** figures in one of the last two columns indicate the highest value per study case

Ungulate vectors (sample size for fur-epizoochory/ for endozoochory; ; feeding regime)	Publication	Site, country	Total number of plant species dispersed	% of plant species dispersed by both mechanisms (number of plant species)	% of plant species strictly dispersed by fur-epizoochory (number of plant species)	% of plant species strictly dispersed by endozoochory (number of plant species)
bison (557/1131; GRE)	Eyheralde, 2015	Iowa, USA	65	55.38% (36)	29.23% (19)	15.38% (10)
bison (111/144; GRE)	Rosas et al., 2008	Oklahoma, USA	53	43.40% (23)	30.19% (16)	26.42% (14)
sheep (6/10; GRE)	Benthien et al., 2016	Luebeck, Germany	132	11.36% (15)	35.61% (47)	53.03% (70)
sheep (60/8; GRE)	Schoenbaum et al., 2009	Migda, Israel	45	20.00% (9)	22.22% (10)	57.78% (26)
donkey (41/28; GRE)	Couvreur et al., 2005	Flanders, Belgium	66	24.24% (16)	19.70% (13)	56.06% (37)
cattle (40/45; GRE)	Chuong et al., 2016	California, USA	37	21.62% (8)	27.03% (10)	51.35% (19)
red deer (5/60; IMF)	Picard and Baltzinger, 2012; Picard et al., 2016	Lorris, France	40	0% (0)	7.50% (3)	92.50% (37)
goat (6/6; IMF)	Benthien et al., 2016	Luebeck, Germany	49	4.08% (2)	40.82% (20)	55.10% (27)
roe deer (25/152g; CS)	Heinken et al., 2001; Heinken and Raudnitschka, 2002	Breiselang, Germany	41	9.76% (4)	82.93% (34)	7.32% (3)
roe deer (41/805.9g; CS)	Schmidt et al., 2004	Herzogtum Lauenburg and Luechow-Dannenberg, Germany	41	29.27% (12)	12.20% (5)	58.54% (24)
roe deer (16/60; CS)	Picard and Baltzinger, 2012; Picard et al., 2016	Lorris, France	11	0% (0)	27.27% (3)	72.73% (8)
roe deer (11/60; CS)	Picard and Baltzinger, 2012; Picard et al., 2016	Montargis, France	8	0% (0)	37.50% (3)	62.50% (5)
wild pig (25/2513g; OM)	Schmidt et al., 2004	Herzogtum Lauenburg and Luechow-Dannenberg, Germany	71	25.35% (18)	28.17% (20)	46.48% (33)

Table 2.6: Proportion of shared dispersed plant species for different combinations of feeding regimes (GRE: Grass and Roughage Eater; IMF: Intermediate Mixed Feeder; CS: Concentrate Selector; OM: Omnivore) for endozoochory (left columns) and hair characteristics (hair curliness: curly, wavy and straight; hair length: short, medium and long as described in Albert et al., 2015b) for fur-epizoochory (right columns). Bold figures show highest values

Endozoochory		Fur- epizoochory	
Feeding regimes (sample size)	% of shared dispersed plant species (mean \pm 95% CI)	Hair characteristics (sample size)	% of shared dispersed plant species (mean \pm 95% CI)
GRE - GRE (n=9)	47.44 \pm 10%	curly - wavy (n=2)	33.77 \pm 10%
GRE - IMF (n=18)	17.43 \pm 6%	curly - straight (n=2)	26.67 \pm 10%
GRE - CS (n=16)	12.89 \pm 6%	wavy - wavy (n=1)	5.56%
GRE - OM (n=4)	25.34 \pm 19%	wavy - straight (n=5)	18.9 \pm 13%
IMF - IMF (n=6)	12.93 \pm 14%	straight - straight (n=1)	16.00%
IMF - CS (n=17)	16.05 \pm 7%	long - medium (n=6)	21.09 \pm 12%
IMF - OM (n=10)	16.15 \pm 11%	long - short (n=3)	29.63 \pm 10%
CS - CS (n=9)	10.26 \pm 9%	medium - medium (n=1)	5.56%
CS - OM (n=9)	19.64 \pm 12%	medium - short (n=1)	16.00%

Perspectives

Methodological challenges

First, we would like to again underline the limitations involved in comparing the available studies on ungulate-mediated endozoochory in the literature. There are still no standardized criteria applied to the samples for either germination conditions (e.g., closed versus open greenhouses; greenhouse versus natural conditions) or abiotic conditions (e.g., controlled versus fluctuating temperatures; with or without irrigation). Even the length of the germination experiments differed greatly amongst the studies (see table 2.3). Generally, at least one full year is advised to assess germination success and identify the plant species, but Young (2012) and Jaroszewicz et al. (2013) prolonged that period for

up to three years. Notably, Jaroszewicz et al. (2013) showed that Yellow Star of Bethlehem (*Gagea lutea*), an ancient forest species, only germinated in European bison dungs during the third year of the experiment. They further observed that some seedlings emerged up to seven years after the beginning of the experiment. Time for germination of ungulate-dispersed seeds is rarely reported (but see Milotić et al., 2016c). The application of average germination conditions might not fit the germination requirements of each of the diaspores present in the faeces. One solution might be to check each seed for viability (tetrazolium test). However, this method only indicates the intrinsic ability of a seed to germinate while the abiotic conditions at the release site might not fit its germination requirements; such a viability test could easily lead to an over-estimation of germination success. Pakeman and Small (2009) showed that the germination success under natural conditions was lower than in greenhouses. In three of the retrieved studies on endozoochory (table 2.3), dispersed seeds were morphologically identified and submitted neither to seedling emergence nor to viability test (Castley et al., 2001; Sigwela, 2004 and Benthien et al., 2016).

Fur-epizoochory and regurgitation need to be studied in much greater depth, and in association with endozoochory on the same sites and within communities of ungulates (table 2.3). Future research should also focus on plant dispersal networks involving ungulates and other taxa of dispersal agents to help addressing the relative importance of ungulates as plant dispersal agents (e.g., see Fedriani and Delibes, 2009).

Overlap and complementarity ungulate-mediated dispersal services for habitat restoration

The results from our systematic literature review enable us to provide preliminary recommendations concerning ungulates as potential tools for habitat restoration, thanks to their dispersal services. At the landscape scale, dispersal agents with the highest overlap in dispersed plant species between them might replace one another to some extent, while those with the least overlap provide a complementary service. When choosing appropriate dispersal vectors to be included in the management or restoration of a landscape (i.e., rewilding concept), the total amount of plant species and diaspores dispersed by a given ungulate should be a selection criterion for consideration (e.g., sheep, Rico et al., 2014). Grass and Roughage Eaters, thanks to their diversified feeding regime, disperse a large amount of different plant species. They are also the most similar vectors when more than one ungulate species of this same feeding regime co-occur; this is even true when we compare different dispersal processes, like endozoochory and fur-epizoochory. Consequently, if the aim is to restore degraded habitats, managers of natural areas should consider introducing or re-introducing complementary ungulates and at least one of the following species: sheep, cattle or bison. Associating a Grass and Roughage Eater, efficient for quantitative dispersal, with an ungulate from a different feeding regime (Concentrate Selector or Omnivore) for qualitative dispersal would create a beneficial complementarity in the restoration program.

Fur-epizoochory highlights the overlapping plant dispersal services of long- and curly-haired ungulates with other ungulates. Sheep would again offer effective dispersal services. Rico et al. (2014) demonstrated that rotational shepherding might be useful in

restoring plant communities. Wild pigs are likely to offer contradictory services, being an effective epizoochorous dispersal agent but also a potential consumer of the seeds.

Research perspectives

In a recent paper, John et al. (2016) have called for researchers to include the role of animal cognition on plant-animal interactions such as seed dispersal, herbivory and pollination. Animal memory can lead to directed dispersal: animals may select specific plants at specific places and release them at predictable safe resting places. Richard et al. (2014) provided quantitative proof of temporal home range fidelity for ungulates like red and roe deer and, Riotte-Lambert et al. (2017) developed a framework for the study of routine movement behavior. Similarly, taking animal behavior (Russo et al., 2006) and animal sociality (Sarasa et al., 2009; Liehrmann et al., 2018) into account will open new research opportunities for the further investigation of ungulate-mediated plant dispersal. Though this may be challenging in closed forest environments, one could start by matching behavioral observations of ungulates mainly dwelling in open areas, for instance reindeer in mountainous areas (Mårell et al., 2002) or mountain ibex in alpine grasslands, with the study of plant dispersal. The use of acceleration sensors (Nams, 2014; Kröschel et al., 2017) and its calibration with control animals will help determine activity (active vs. resting) and specific behaviors (e.g., lying, feeding, walking, trotting) of the equipped animals together with its location in open or closed habitats. This could render more realistic the study of the transfer phase of ungulate-mediated dispersal that generally combines retention times and associated distances travelled (Westcott et al., 2005; Pellerin et al., 2016). Wang and Smith (2002) proposed new techniques to the study of seed dispersal among which stable isotope ratios and molecular genetic markers to link

dispersed seeds to parent plants. More recent applications of genetic tools to seed dispersal allow the identification of the disperser (DNA barcoding) and relate dispersed seeds to parent plants (DNA microsatellites, González-Varo et al., 2017). They could be used for guild of ungulate dispersers.

We found very few studies on mountain ungulate communities (but see Young, 2012 for New Zealand alpine ecosystems and Karimi et al., 2018, for North-Eastern Iran), whereas ungulate contribution to altitudinal plant dispersal should be investigated. Bertrand et al. (2011) showed that mountain plant communities coped with climatic changes better than did lowland communities. Rumpf et al. (2018) also used vegetation resampling to assess temporal changes of lower and upper range limits of a set of plants of the European Alps, but dispersal-related traits failed to explain the upward movement of the plants. However, these traits were computed from data obtained on lowland ungulates (Römermann et al., 2005; Mouissie et al., 2005a) probably inappropriate in mountainous areas. Following this, further studies are required to ascertain and quantify the role of mountain ungulates like chamois, mouflon or mountain ibex, especially in relation to plant response to climate change in alpine ecosystems.

Recent studies have stressed the implication of native, domestic and introduced ungulates in the dispersal of exotic plants. Some researchers have found that native ungulates aid the spread of exotic invasive plants (Myers et al., 2004; Eschtruth and Battles, 2009; Vavra et al. 2007) as Schiffman (1997) suggested. But, how do the traits of these exotic invasives compared to those of native plants in terms of ungulate-mediated dispersal? Preliminary observations tend to show that some exotic plants occupy a complementary feeding niche (i.e., phenological shift) for large herbivores by

offering green edible material when the rest of the vegetation is dry. This is the case for instance for the leaves and fruits of tickberry (*Lantana camara*) consumed by giraffes (*Giraffa camelopardalis*), nyalas (*Tragelaphus angasii*) and zebras (*Equus burchelli*) in South Africa during austral winter.

In addition to being dispersal agents, these large herbivores mediate plant-plant interactions and modify the local abiotic conditions where diaspores are released, through nutrient fluxes (white-tailed deer; Seagle, 2003) and physical disturbance (repeated rooting or scraping). They thus create windows of opportunity for plants to establish (Myster, 1993). Ungulates also interact with other taxa, both animal (earthworms, Dávalos et al., 2015) and plant (shrubs, Boulanger et al., 2018), for the recruitment of forest plants. Finally, few studies have formally demonstrated the role ungulates in long distance plant dispersal (Vickery et al., 1986); most studies use indirect approaches (Boulanger et al., 2011; Milotić et al., 2017). To conclude, large strides have been made despite methodological constraints in the direct measurement of dispersal by large ungulates. However, one fundamental question still remains, i.e., what is the proportion of diaspores produced by a given plant that are carried over long distances by large ungulates? Addressing this question will help us to gain a deeper understanding of the full range of effects ungulates have in an ecosystem.

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CHAPTER 3

Ecological filtering of local plant community: combined effects of habitat, long-term ungulate presence and dispersal related plant-traits

Résumé (version française)

Questions: Les ongulés, ingénieurs de l'écosystème, sont connus pour structurer les communautés de plantes par l'herbivorie, la zoochorie, la redistribution des nutriments, l'altération physique de la surface du sol et la modification des microhabitats. Nous nous sommes intéressés ici à comprendre le rôle des traits des plantes liés à la dispersion dans leur réponse à la présence des ongulés.

Localisation: L'étude a été menée dans le Domaine National de Chambord, centre Nord de la France.

Méthodes: Nous avons analysé la distribution des plantes en fonction de la hauteur de la canopée, de la distance à la route la plus proche, d'un indice d'humidité et d'un indice de présence des ongulés. Nous avons utilisé un modèle hiérarchique de distribution conjointe des espèces tenant compte de la structuration spatiale et incluant les traits des plantes impliqués dans la dispersion, afin de quantifier comment ces traits affectent la réponse des espèces de plantes à la présence des ongulés et aux autres variables environnementales.

Résultats: Nous avons identifié 403 espèces de plantes vasculaires dans 156 relevés échantillonnés, et des signes de présence des ongulés dans 112 de ces relevés. Notre indice de présence des ongulés ne s'avère pas significatif pour expliquer la distribution des plantes. Nous attribuons cela aux très fortes et anciennes populations d'ongulés sur notre site d'étude, clos de mur. Concernant l'influence des traits des plantes liés à la dispersion sur la réponse des plantes à la présence des ongulés, nous relevons une association avec les plantes de masse de graine faible.

Conclusions: Les modèles hiérarchiques de distribution conjointe des espèces constituent un outil prometteur pour explorer comment les traits des plantes modulent le lien entre les ongulés sauvages et la distribution spatiale des plantes.

Keywords: ecological filter, plant-ungulate interactions, functional traits, seed dispersal, overabundance, plant communities, species distribution, spatial model, red deer, wild boar, *Cervus elaphus*, *Sus scrofa*

Abstract

Questions: Ungulates, as ecosystem engineers, are known to structure plant communities via herbivory, plant seed dispersal, nutrient redistribution, and physical alteration of soil surface and other microhabitat conditions. Here, we were interested in understanding the role of dispersal-related traits in plant species responses to ungulate presence.

Location: The present study was carried out in Domaine National de Chambord, in north-central France.

Methods: We analyzed plant species occupancy in dependence of canopy height, distance to nearest road, and mean Normalized Difference Water Index (NDWI) in addition to an index of ungulate presence-absence. We used a hierarchical joint species distribution model accounting for spatial structure, and included dispersal-related functional plant traits in the model, to quantify how these traits affect the response of plant species to ungulate presence and other environmental predictors.

Results: We identified 403 vascular plant species in 156 sampled plots, and recorded signs of ungulate presence in 112 of the plots. Our index of ungulate presence was not statistically significant in predicting plant species' distributions. We attribute this to chronic very high ungulate densities in our closed study area that limited the ability to detect effects of ungulate presence on plant species distributions. Regarding the influence of

dispersal-related traits on plant species responses to ungulate presence, there was some indication that plant species with lower seed mass were associated with ungulate presence.

Conclusions: Hierarchical joint species distribution models are a promising tool to investigate how plant traits mediate the linkage between ungulates and plant species spatial distribution.

Introduction

Plant communities are known to be structured at the local scale as a result of dispersal, environmental filtering, and biotic interactions (Keddy, 1992; Kraft et al., 2015; Lortie et al., 2004). Local plant species composition is a result of deterministic processes that affect species niches through abiotic and biotic factors, as well as of stochastic processes like rare events such as long distance dispersal (Chase and Myers, 2011). Biotic interactions are important in structuring species assemblages at local scales. While the analysis of plant-plant species interactions has received much recent attention, other important interaction pathways such as plant-ungulate interactions remain less explored.

Ungulates have maintained grass-dominated open areas of temperate European regions for centuries (Pärtel et al., 2005) and are recognized 'ecological filters' transporting plant species with certain dispersal-enabling traits more than others (Albert et al., 2015a; Baltzinger et al., 2019). On one hand, they can affect the different processes underlying plant community structure, e.g. via effects on nutrient cycling in soil (Olf and Ritchie, 1998), grazing and/or trampling (Hester et al., 2000), or as seed dispersal agents (Baltzinger et al., 2019). On the other hand, when present in higher densities, ungulates

are known to reduce functional diversity of plant communities and increase biotic homogenization (Martin et al., 2010; Rooney, 2009).

Plant functional traits have been instrumental in advancing our understanding of how different community structuring processes affect individual species (Cavender-Bares et al., 2004). Local habitat conditions act as a filter by operating on traits and removing those that are unsuitable for a particular environment (Keddy, 1992; Kraft et al., 2015). Dispersal-enabling traits are important in establishing the ability of different plant species to (disperse over long distances and) reach new habitats or environments over more or less long distances with the support of different biotic and abiotic vectors such as wind, water, mammals and birds (Ozinga et al., 2004). Functional plant traits such as diaspore releasing height (Albert et al., 2015a, 2015b; Thomson et al., 2018); seed mass (Thomson et al., 2011); diaspore shape (Albert et al., 2015a) or other morphological adaptations of diaspores (Bullock et al., 2001; Tackenberg et al., 2006) have been recognized as important in shaping local plant communities in previous studies.

In sum, seed dispersal is a crucial ecological process shaping plant communities and ungulates can play a pivotal role as 'ecological filters' (Albert et al., 2015a). Plants, especially those that depend on animal-aided dispersal and develop certain traits, are likely to benefit more than other species. For endozoochory, the ability of a diaspore to survive passage through the gut of an animal is one of the crucial adaptations to being dispersed successfully (Traveset, 1998). On the other hand, epizoochory is more likely improved by the ability of the diaspore to remain attached on the body of the animals (Sorensen, 1986). However, plants without any specific adaptation for attachment to

bodies of animals are also likely to be dispersed via 'hitchhiking' on animals (Albert et al., 2015a; Picard and Baltzinger, 2012).

While the role of ungulates as ecological filters and the influence of functional plant traits in structuring plant communities have been previously investigated, few studies have tested them together with empirical data. (Nishizawa et al., 2016) tested the role of herbivory by ungulates in plant assembly on forest floors using traits as filter. The overall contribution of ungulate presence in a landscape to plant species niches' and the role of traits at the species-level response of plants to ungulate presence remains mostly untested.

In this study, we were interested in assessing the role of wild ungulate presence in structuring local plant communities, and whether individual plant species response to animal presence is related to their (plant) traits, focusing on dispersal-related traits. We hypothesized that plant species with animal-aided dispersal related traits (e.g. diaspores with appendages, high diaspore releasing height) would be more likely to be found at sites where ungulates occur than plant species lacking such traits. In sum, our objectives were to assess 1) whether ungulate presence affects plant species occurrences within a landscape, and 2) whether dispersal-related traits could explain plant species responses to ungulate presence.

Methods

Study area

The study was carried out in the Domaine National de Chambord (DNC) in north- central France. The area is mainly an intensively managed hunting reserve for wild game like red

deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) since 1947, the hunting bags/100 ha in the 2016-18 period totaled 3.77 for red deer, 0.04 for roe deer, 17.24 for wild boar and 0.55 for mouflon (Cocquelet et al., 2019). However, there is an increased emphasis on biodiversity conservation alongside game management as evidenced by DNC's designation as a Natura 2000 site.

Covering a total area of about 5400 ha, the DNC is a mosaic of several, spatially-structured forest parcels (Fig.3.1). The park mainly consists of forested area of about 4860 ha, agricultural farms (200 ha), managed grasslands for game species (150 ha) and built-up areas (the castle and nearby village – 150 ha). The forest is mostly dominated by native oaks i.e., *Quercus* sp., but also includes stands of introduced conifers (esp. *Pinus* sp.) and very few mixed stands that include *Betula pendula*, *Carpinus betulus*, *Sorbus* sp. and other mid-storey canopy trees. The entire park is enclosed within a 2 m-high boundary stone wall of 32 km. The elevation ranges from 75-125 m a.s.l.

Vegetation data

The main sampling period was between 29th May and 20th July 2017. This period coincides with peak flowering/fruitletting period in our study area and thus enabled us to identify most individuals to species level. This period also coincides with the period of maximum dispersal especially for herb and shrub level species (Malo and Suárez 1995; Picard et al. 2016). We conducted field observations to record plant species in 156 plots of 5 m radius (Total area = ca 78.5 m² each) along 20 transect lines (Fig.1). Each transect line had between 7 to 9 plots with a minimum distance of 70 m between consecutive plots covering different habitats (forest/open/ecotone/humid/road-edge/grassland). We searched and recorded all plant species under 2 m height within each plot (i.e., vegetation

accessible to red deer), limiting the search to a maximum of 40 minutes per plot (i.e. search effort). Voucher samples were collected from plant species that could not be identified in field directly and identified later in the lab.

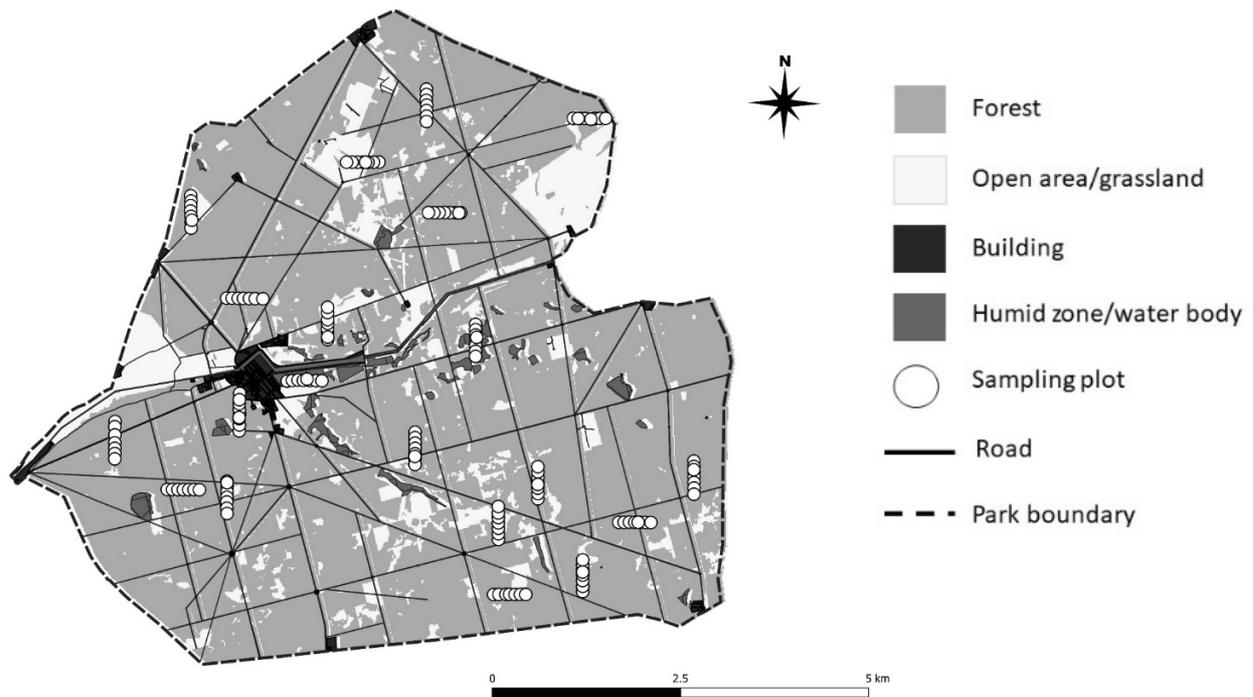


Figure 3.1: Map of study area. Domaine National de Chambord, north-central France with locations of the sampling plots.

The starting points and the orientation (North-South/East-West) of the transects were randomly chosen and pre-fixed using the ‘Random points in layer’ and ‘Advanced Digitizing toolbox’ in QGIS v2.18 “Las Palmas” (QGIS Development Team, 2017).

We recorded the local frequency of each plant species following the Braun-Blanquet system (Braun-Blanquet, 1964) of plant abundance classification, assigning a percentage class by visual estimation (i = single individuals, + = few individuals, 1 = up to 5%, 2 = 5-

25%, 3 = 25-50%, 4 = 50-75% and 5 = 75-100%). We also collected information at each plot on the percentage of bare ground, overall percentage of vegetation cover at ground level and above 2 m from ground, and signs of ungulate presence (animal paths, bedding site, hoof marks, faecal pellets and/or disturbed ground). Since it was often difficult to distinguish between wild boar and deer hoof-prints or between fresh and old signs, especially in areas with tall grass or dried ground, we resolved to consider any signs as ungulate presence rather than distinguish to species level or age.

In total, we recorded and identified 403 plant species in 156 sampled plots during our study. We recorded signs of ungulate presence in 112 out of 156 plots. In the statistical analyses, we considered only those plant species that occurred in more than eight plots i.e. more than 5% frequency occurrence in 156 plots (total = 105 species). A full list of all recorded species (along with the species codes we used) is included in the supplementary material (Appendix S1).

Spatial data: GIS layers

The roads within the DNC are constructed of a different material (i.e. limestone) than the surrounding acidic soil present in the forest, thereby changing the substrate and influencing the plant species that are present on the road edges (Bergès et al., 2013). Roads were extracted from the digitized maps provided by the Hunting and Forest Office of the DNC. We then overlaid these vector layers with the spatial location of our sampling and calculated the distance to nearest roads for each of the plots (Fig.3.1).

Spatial data: Sentinel Data

We used Sentinel-II data for our study area coinciding with the sampling period (Image acquisition dates: 26 May, 18 June and 18 July 2017). We calculated the Normalized Difference Water Index (NDWI) and the Normalized Difference Vegetation Index (NDVI) for each of our plots and considered the mean values calculated from the three images for further analyses. NDVI and NDWI values were highly correlated within our study area and since NDWI is sensitive to water levels within the vegetation layer (Gao, 1996), we retained NDWI as an index of the green cover and surface soil moisture during the study period.

Spatial data: LiDAR data

We used previously acquired LiDAR imagery for our study area (Crozet et al., 2017) to extract information on the vertical structure of the forest. In particular, we used the 90 percentile of canopy height, calculated over pixels of 10 m size, using R package lidR (Roussel and Auty, 2017).

Plant traits data

The names of all recorded plant species were standardized using TAXREF v11.0 (Gargominy et al., 2017). We used trait values considered (and previously shown to be) important in transport of diaspores by animals: diaspore shape (Vs), seed mass, diaspore releasing height, Ellenberg values for light (EIV-L) and nitrophily (EIV-N), and diaspore appendage type for our analyses. We extracted plant trait information from the LEDA traitbase (Kleyer et al., 2008). We supplemented missing data from additional databases such as Baseflor (Julve, 1998), Biolflor (Kühn et al., 2004), Digital Seed Atlas of

Netherlands (Cappers et al., 2012), JUICE (Tichý, 2002) and D3 database (Hintze et al., 2013).

We used the three dimensions of seeds (length, width and height) to calculate the variance in dimensions (Vs) for diaspores), following the formula described in Albert et al. (2015b). In some cases, not all dimensional measures were available. Hence, we used the 'aregImpute' function in the package Hmisc v.4.0 of R (Harrell et al., 2017) to calculate the missing dimension based on the other two. We used the average of five imputations/estimates for the missing value. Vs was measured on a scale of 0 to 0.2 (i.e. from round(ed) to elongated shape of the diaspore).

Release height and seed mass variables were log transformed. Ellenberg values (Ellenberg et al., 1991) were not available for all species, and where necessary, we used data from other datasets (e.g. Tichý (2002), to complete the information. Diaspore appendage type were extracted from the D3 database (Hintze et al., 2013). We included information on presence of nutrients, elongated, hooked and mucilage type of appendages on diaspores as animal-aided dispersal-enabling traits, i.e. a value of 1 and categorized the absence of such appendages as 0.

Data analyses

We used R for all statistical analyses (R Core Team, 2017). We analyzed the data using the Hierarchical Modeling of Species Communities (Hmsc-R package, v0.4.3.0) by (Ovaskainen et al., 2017)). The HMSC implements a joint species distribution modeling (JSDM) approach, which allows for analyzing of community data by using spatial latent variables along with environment and traits data to determine species niches. The latent variables allow accounting for species-to-species correlations, which can be due to inter-

species biotic interactions or due to unmeasured variables (Warton et al., 2015). HMSC presents a community-level perspective of co-occurrence of multiple species and allows including species-level traits alongside the other key parameters. Since we are interested in how plant species respond to animal presence as well as how traits influence the species response to animal presence, this was a promising approach for analyzing our dataset.

We simplified the plant species abundance data collected from field into presence–absence of species, and modelled it with a probit model. We used animal presence (categories from collected data collapsed into presence/absence of animal signs), canopy height (at 90 percentile), mean NDWI, and distance to nearest road as environmental covariates, and also included search effort (in minutes). These variables were scaled to zero mean and unit variance using the inbuilt functions of the HMSC package. While we acknowledge that recording only the presence and absence of ungulate signs in our plots is far from ideal, we think this measure is an easy way to distinguish areas where ungulates move regularly versus not at all. Red deer are after all known to use same areas repeatedly over long periods (Richard et al., 2014).

We ran two models, with and without spatial structure, in our dataset. In the spatial model, we considered transect line id ('LineID') as the community-level random effect variable, and included the coordinates for each plot to account for the spatial dependency of our data (Ovaskainen et al., 2016). We used the default HMSC priors, and we ran each of the models for 500,000 iterations, thinned at every 50th value, thus giving 10,000 posterior sample estimates for a single chain. The first half of the samples were discarded as burn-in values (bringing the total number of iterations to 750,000 for each chain). We used a

total of four parallel chains, bringing the total posterior samples to 40,000 for each of the models. We evaluated convergence with Gelman and Rubin's diagnostics.

We quantified the variance contribution of each of the environmental covariates to the plant species responses using inbuilt functions of the HMSC package. We used a two-fold cross validation approach using in-built functions of the HMSC package to test the predictive power of our models. We compared the discriminatory performance of the two models for the explanatory and predictive power of both the models with the AUC (Area under the receiver-operator characteristic curve).

Results

Model performance

Both models showed convergence, with overall potential scale reduction factors (psrf) ranging from 0.99-1.00 across all parameters in both the spatial and non-spatial model. The median of the effective sizes of beta estimates approached 40000 (equivalent to the sample size) in both cases (Appendix S2: Fig S2.1). The model with the spatial structure performed better compared to the non-spatial model with respect to both its explanatory and predictive power (Fig.3.2). We therefore focus the result presentation and interpretation on the spatial model.

Environmental covariates and plant species response

The environmental covariates accounted for a large part of the explained variation (43.1%), with the remainder explained variation accounted for by the spatial latent variable ('LineID') (mean of 30.7%) and plot-level search effort (mean of 26.2%) (Table1a). Contrary to our expectation, the mean contribution of ungulate presence was

less than 6% to the overall variance in each of the models (mean = 3.8% in the spatial model, and 5.8% in the non-spatial model). Availability of water and surface moisture (NDWI) was the most important environmental covariate, the mean NDWI accounted for 16.5% of the overall variance contribution in the model, followed by distance to nearest road (mean percentage of explained variance 13.4%), and canopy height (9.4%) (Table 3.1a). Species with statistically significant responses (mean posterior beta \pm 95% CI) to canopy height, mean NDWI and distance to road were 11, 36 and 36 respectively (Appendix S2: Fig S2.2a-c).

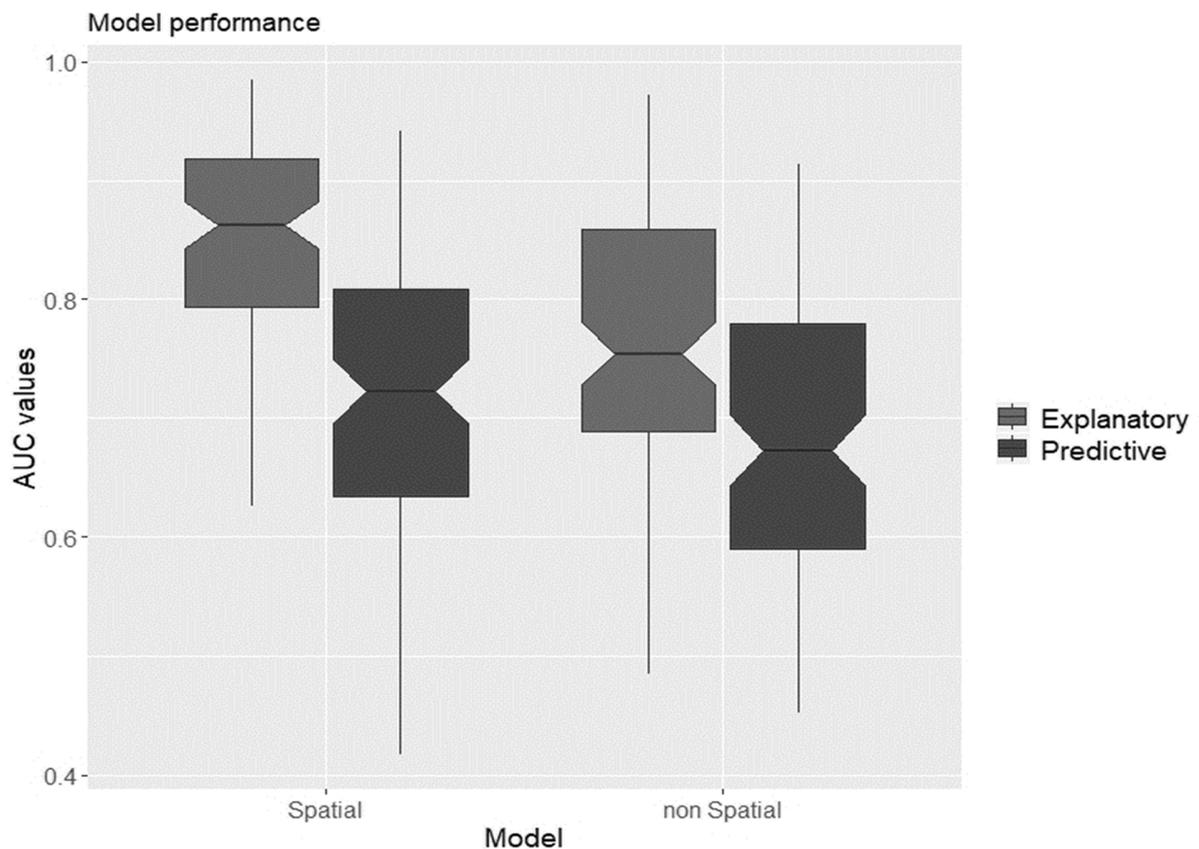


Figure 3.2: Explanatory and predictive power of the spatial and non-spatial models in terms of distributions of species-specific Area under the receiver-operator characteristic curve (AUC) values

Despite the overall low contribution of ungulate presence with respect to plant species niches, there were some species that showed trends we wish to highlight. Only two species, *Bellis perennis* (Bell.pere.) and *Digitalis purpurea* (Digi.purp), showed a statistically significant but opposite response to animal presence (mean \pm 95% CI, non-overlapping with zero): *Bellis perennis* showed a negative and *Digitalis purpurea* a positive response. At the 90% support level (i.e. with 90% CI), we found an additional 10 species responding to animal presence (Fig. 3.3). Of these *Taraxacum sec ruderale* (Tara.sec.rud), *Medicago lupulina* (Medi.lupu), *Verbena officinalis* (Verb.offi), *Lolium perenne* (Loli.pere), *Solanum dulcamara* (Sola.dulc), *Erica scoparia* (Eric.scop), *Carex pilulifera* (Care.pilu.pilu) and *Scutellaria minor* (Scut.mino) showed a trend towards negative association, whereas *Agrostis capillaris*, and *Anthoxanthum odoratum* showed a trend towards a positive association with ungulate presence.

Contribution of traits to species response to environmental covariates

The overall variation explained by traits (Tjuur's R^2) in the model with spatial structure was 0.37, and 0.32 for the non-spatial model (Table 3.1b). This value indicates the contribution of trait values to the species niches in response to the environmental covariates. The R^2 value of traits explaining variation within species in response to each covariate ranges from 0.08-0.41 in the spatial model and 0.17-0.35 in the non-spatial model (Table 3.1b). For canopy height, traits explained 33% (canopy height in Table 3.1b) mean variation out of the overall 9.4% (canopy height in Table 1a) explained variance in the spatial model.

Table 3.1a: mean explained variance (Tjuur's R² values) for each environmental covariate (variance partitioning) for spatial and non-spatial models.

Covariate	mean explained variance (spatial model)	mean explained variance (non-spatial model)
search effort	26.2	39.7
ungulate presence	3.8	5.8
canopy height (90 percentile)	9.4	17.8
mean NDWI	16.5	23.0
distance to road	13.4	13.7
Random: lineID	30.7	NA

Table 3.1b: Mean variation (Tjuur's R² values) explained by traits for each covariate.

	Covariate	variation explained by traits (spatial model)	variation explained by traits (non-spatial model)
Covariate-wise contribution of traits (across all species)	Intercept	0.36	0.28
	search effort	0.41	0.33
	ungulate presence	0.20	0.18
	canopy height (90 percentile)	0.33	0.26
	mean NDWI	0.37	0.35
	distance to road	0.08	0.20
Overall for the model	Variation explained by traits in species occurrences	0.37	0.33

None of the traits showed a statistically significant relationship with plant species responses to ungulate presence (Fig. 3.4). Still, the interquartile ranges for (presence of) diaspore appendage and log diaspore releasing height were positive. Similarly, the log seed mass, Ellenberg indicator for light (EIV-L) and seed shape (Vs), while not statistically

significant, showed a trend towards a negative association with the response to ungulate presence.

Overall, our results indicate that there is positive association between presence of appendage on diaspores, lower seed mass, rounded diaspore shape, higher releasing heights and lower Ellenberg indicator for light values (Fig. 3.4).

Discussion

In this study, we were interested in assessing the role of ungulates in structuring local plant communities in tandem with other habitat factors and the influence of plant traits in species responses to ungulate presence. The role of ungulates in structuring plant communities has already been well-established in grasslands and forests (Bakker et al., 2006; Cosyns et al., 2005; Olf and Ritchie, 1998; Putman, 1996; Ramirez et al., 2019), but the present approach using a joint species distribution model allowed us to also include the effect that dispersal-related traits have on plant species responses to ungulate presence while accounting for spatial structure of the study area.

One of the caveats of our study is probably the small sample sizes that made it difficult to find strong generalizable results. While ungulate presence did not have a statistically significant contribution to plant community structure in our case, we would like to discuss some of the identified trends.

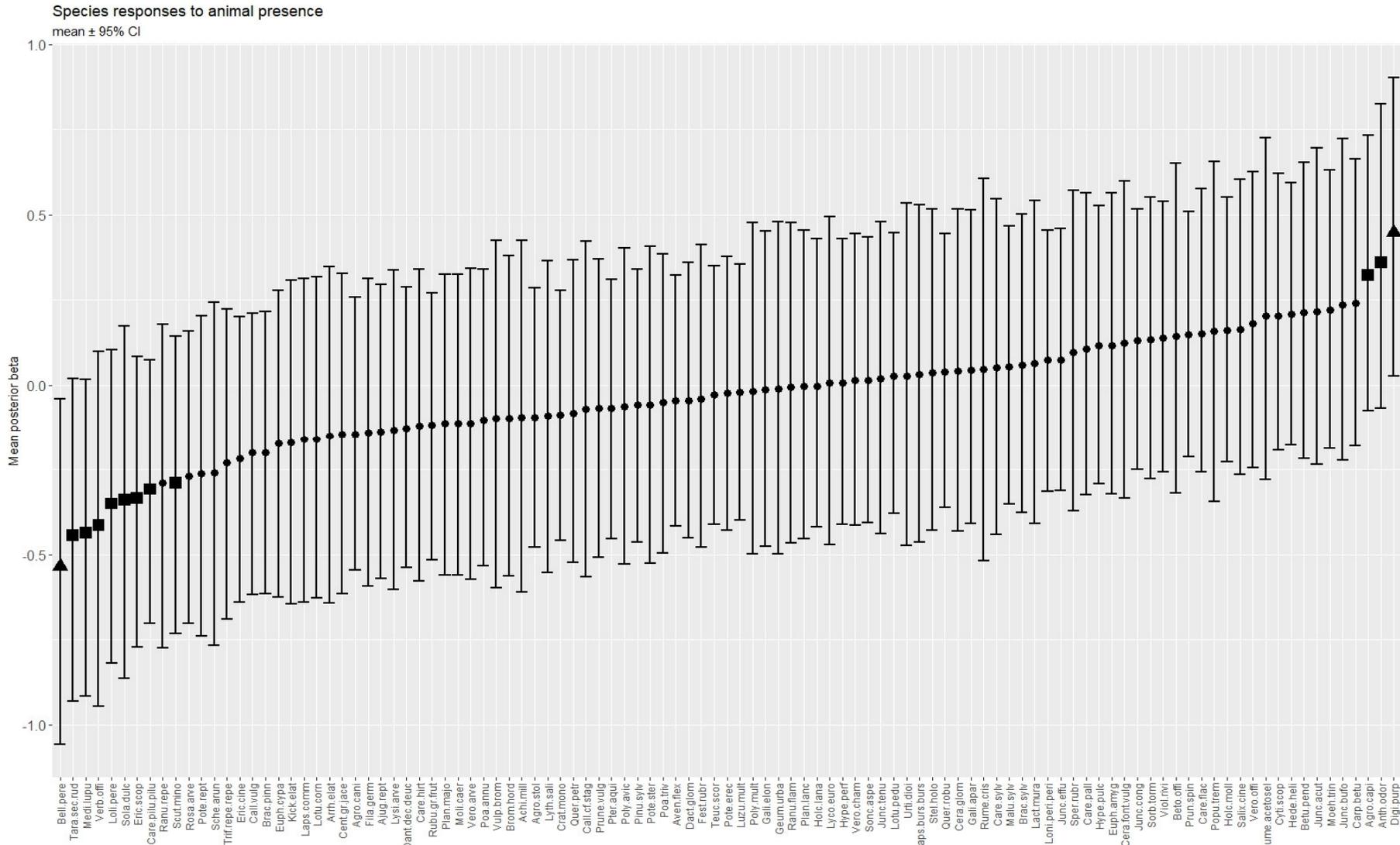


Figure 3.3: Species-wise mean (\pm 95% CI) responses to ungulate presence. Posterior beta coefficients for the model with spatial structure. (Triangular arrowheads = species with 0.95 statistical support, i.e., non-overlapping with zero at 95% CI; square arrowheads = species with 0.9 statistical support i.e., non-overlapping with zero at 90% CI).

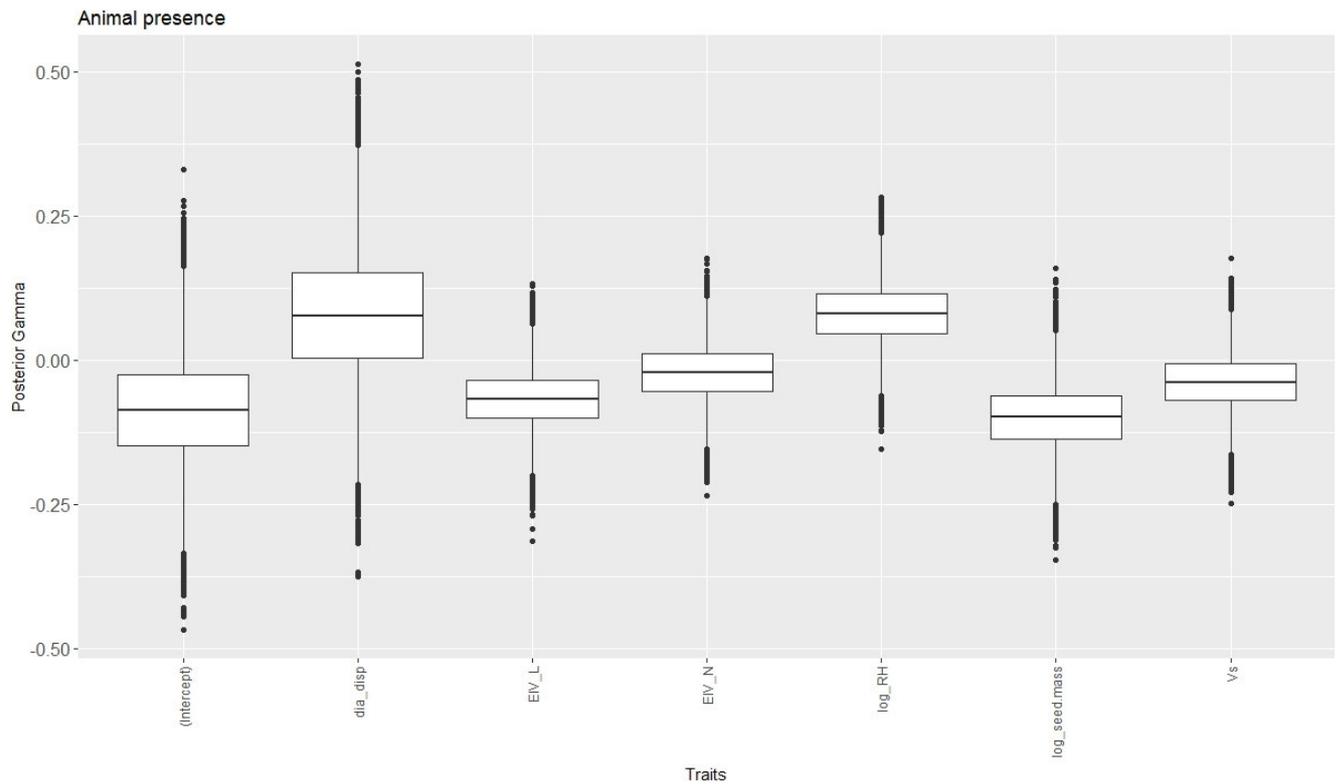


Figure 3.4: Trait- wise posterior gamma coefficients for ungulate presence for the model with spatial structure. (dia_disp= diaspores with dispersal enabling modifications-elongated/hooked appendages or nutrients; EIV-L = Ellenberg indicator values for light; EIV-N = Ellenberg indicator values for nitrophily; log_RH= diaspore releasing height (log); log_seed.mass = seed mass (log))

Environmental covariates and plant species response

The available species pool is filtered by the prevailing habitat conditions. Several species show strongly negative or positive association with each of the habitat covariates, i.e. there are signs of environmental filtering. Overall, the two forest related variables, NDWI (which we used as an index of green cover as well as surface moisture within the vegetation layer) and canopy height, together explained most of the variation in species response (Table 3.1a). Most species showing negative association with both

variables are species that grow in open areas with overall low canopy height as well as low NDWI values.

Distance to roads acts as a major environmental filter at our study site. This is perhaps not at all surprising given that roads verges differ strongly in their vegetation composition compared to other adjoining habitats (Bergès et al., 2013; Cousins, 2006). Road verges are long, linear, disturbed habitats with strong edge effects. Additionally, the limestone substrate used to construct roads is basic, different from the acidic adjoining soil, influencing the plant community growing on it. Roads are also subject to higher disturbance from the vehicular and, in some designated parts of the park, tourist traffic, and therefore support more disturbance tolerant species. All the species showing a strong response to distance from road show a negative association, confirming that the plant species composition along roads in our study site are strongly different from other plots. On the other hand, no species shows a strongly positive association to distance from road.

Overall, ungulate presence contributed less than 4% to the explained variance of the spatial model. Previous studies have shown that the contribution of ungulates to overall structuring of plant communities depends on the plant species consumed by the ungulates (Boulanger et al., 2018; Côté et al., 2004). However, the lower contribution of ungulate presence in the model could possibly be due to a methodological constraint we adopted while carrying out the plot surveys. The different ungulate presence signs were considered as a single category and simplified into presence-absence data. This could have reduced the explanatory capacity of the covariate, i.e., we have used an overly simplified measure of animal presence. Another contribution of this reduced explanatory capacity could be the very high density of game population in the DNC, and it was perhaps not sufficient to simply record presence-absence of ungulates,

which is an instantaneous measure. However, keeping our particular hypothesis in mind, we were interested in differentiating areas within the park where animals move more regularly than in areas with lesser or no use. Moreover, for this, a measure of presence-absence can be suitable assuming ungulates tend to reuse similar habitats over time.

In addition, since the game population within the park is intensively managed for hunting, the animal population (and consequently the habitat use) stays more or less constant over time. Previous studies have shown the effects of long term grazing and herbivory pressure can already filter out species sensitive to grazing, making the local plant community resistant to changes both in open and forested areas as well as resulting in biotic homogenization (Holmes and Webster, 2011; Kirby, 2001; Milchunas and Lauenroth, 1993; Rooney et al., 2004). Given that ungulates are maintained chronically high densities within our study area, the local plant community might not include the presence of species that have been already filtered out by long-term impacts of high ungulate densities.

Plant species with significant response to ungulate presence

In this study, we were mainly interested in assessing the role of ungulates as ecological filters in plant community assemblage at local scales. Despite the fact that ungulate presence did not have an overall significant contribution, we would like to discuss the specific species that did show strong associations.

In our study, the species with significant response to ungulate presence are light-demanding species with Ellenberg-Light values between 7 and 9 (Ellenberg et al., 1991). A previous study comparing plant species richness in presence of ungulates across 82 sites within France (Boulanger et al., 2018) has reported a higher species

richness in the herbaceous layer with more light-demanding species in areas outside enclosures where ungulates could move freely.

One of the ways we can interpret these associations is by taking a closer look at the palatability and tolerance to grazing of these plant species. The species forming the diet composition of ungulates depend on three factors- the plant species pool present in the local area, the likelihood of encounter between plant and animals, and the diet preference of the animal (Borowski and Kossak, 1975). Highly preferred forage species by ungulates are known to decrease drastically in their biomass in the presence of high grazing pressure by ungulates. Our study site has very high densities of game species especially red deer and wild boar, which are likely to influence local abundance and occurrence of some plant species. In agreement with previous studies (Rooney, 2009), our results indicate that forbs/herbs and graminoids show the most significant responses to ungulate presence. Of the twelve species that show significant response to ungulate presence in our study, four species are graminoids (i.e., grass/sedge: *Agrostis capillaris*, *Anthoxanthum odoratum*, *Lolium perenne* and *Carex pilulifera*), seven species are forbs/herbs (*Bellis perennis*, *Taraxacum ruderalis*, *Medicago lupulina*, *Verbena officinalis*, *Solanum dulcamara*, *Scutellaria minor*, *Digitalis purpurea*), and a single species of shrub (*Erica scoparia*).

Grazing/browsing by ungulates and plant species that might benefit from zoochorous dispersal pose a somewhat paradoxical problem. For example, *Erica scoparia*, though known to be resistant to browsing pressure (Paula and Ojeda, 2011), is still a highly preferred species for consumption especially by deer species (Fernández-Olalla et al., 2006) but shows a negative response to ungulate presence in our study. Similarly, Williams et al. (2008) have reported a single germinating seedling of *Solanum dulcamara* from the faecal pellet of white-tailed deer, indicating a low preference for

this species. But Boulanger et al. (2018) have reported *Solanum dulcamara* as an “ungulate benefitting species” based on their 10-year enclosure experiment, while in our study it shows a negative association with ungulate presence. Likewise, *Bellis perennis* which is known to be highly resistant to grazing pressure (Kühn et al., 2004) but also, highly preferred by deer for consumption i.e., germinate in high proportions from faecal pellets of deer (von Oheimb et al., 2005), shows a negative response to ungulate presence in our study. These results indicate that a more complex interaction of ungulate diet preference, local plant species pool, soil disturbance, species fecundity, and resistance to grazing and other factors affecting both plant species occurrence and ungulate presence together might be affecting the direction of the interaction between plants and ungulates. Additionally, such interactions are likely to be context dependent.

In our opinion, different types of interactions between ungulates and plant species are relevant. For species that are low in forage value but highly tolerant of disturbance or benefiting from soil disturbance created by ungulate activity (for e.g. - *Digitalis purpurea* in our study), they are likely to show positive correlation with ungulate presence. On the other hand, species that are high in their forage value but also show a high tolerance to grazing (such as the graminoids *Anthoxanthum odoratum* and *Agrostis capillaris* in our study) show a more positive response to ungulate presence. Being highly fecund graminoid species, these plants are unlikely to show negative impacts from high grazing pressure. However, a species with low to moderate tolerance to grazing and/or moderate to high forage value is likely to show a negative response to ungulate presence (for e.g. the forb *Medicago lupulina* in our study).

However, since ungulate presence is not a significant environment variable in our model results, we would suggest erring on the side of caution while interpreting our results.

Contribution of traits to species response to environmental covariates

Even though none of the traits were statistically significant when considering animal presence, we found some interesting trends. The seed mass of species has a more negative association with ungulate presence. This is in agreement with the findings of previous studies that indicate that diaspores with lower seed mass are likely to be dispersed by large ungulates (Albert et al., 2015a; Cosyns and Hoffmann, 2005). Similarly, the release height of diaspores shows a positive association with animal presence. This can be expected as plants would have to be of a particular height to benefit from interactions with animals, taking into account animal traits such as e.g. body size (height), fur characteristics. However (Albert et al., 2015b) found opposite trends for diaspores dispersed by different dispersal modes, with higher release height associated with epizoochory and lower release height with endozoochory.

A previous study by Ozinga et al. (2005) compared different dispersal vectors along major environment gradient and found that long distance dispersal by mammals (both epi- and endozoochory) is significantly associated along the gradient of light availability. Large herbivores preferentially feed in open areas (Jaroszewicz et al., 2009; von Oheimb et al., 2005) and have a higher impact on light-demanding species. In addition, seeds that depend on animal-aided dispersal via endo or epizoochory are likely to benefit from this preferential feeding in open areas. However, surprisingly, our results show a negative trend for Ellenberg indicator values for light, meaning species with lower requirements of light have a somewhat higher tendency to be predicted by ungulate presence.

We also found a positive trend of diaspore appendage type, which was an all-encompassing presence/absence trait type that included all morphological adaptations that are known to be important for successful seed dispersal. Our results indicate that morphological adaptations in diaspores are likely to influence plant species niches', especially for those that depend on animal-aided dispersal. The diaspore shape (Vs) shows a negative trend for species response to ungulate presence. This indicates that plant species with more rounded diaspores respond to ungulate presence. Rounded diaspores are known to be important for endozoochorous dispersal as these are likely to pass the gut without much damage (Janzen, 1984). Also, ungulates are known to carry larger number of species away from parent plants via endozoochory (Albert et al., 2015b). Additionally, a previous study by Vild et al. (2017) found that biotic homogenization by long-term ungulate impacts in an area results in an increase in endozoochorous species, and a reduction in epizoochorous and anemochorous species. The trend in our results towards more rounded seeds could be a reflection of a similar effect by high densities of ungulates over long-term homogenous use of the study area.

Conclusions

Contrary to our expectation, our results indicate that when considering environmental or habitat filtering, ecological filtering by ungulates had a rather weak signal in species niches. Overall, light-demanding, open area-associated species appeared to show higher occurrence probabilities where ungulates were present. However, this was mainly true for specific species that have a significant response to ungulate presence. At the community level, this trend was reversed, with high release height and lighter diaspores with rounded shape with adaptations for dispersal (e.g. presence of elongated or hooked appendages) showing a significant response to the presence of

animals. Given the constraints of our study system, we suggest that future studies that wish to test the contribution of traits in determining plant species responses to ungulate presence consider testing: a) across a gradient of different ungulate densities or of length (history) of presence (such as experiments carried out in Haida Gwaii for e.g.: Stockton et.al. 2004; Martin et.al. 2010), and b) across a gradient of habitat types, possibly at different scales. Most studies in plant ecology that use functional traits to account for biotic interactions tend to focus on plant-plant interactions. However, ungulate-plant interactions are essential ecosystem-level processes that play a crucial role in structuring plant communities at different scales. Our study might be a useful step in illustrating the potential integration of biotic interactions and functional traits in plant ecology studies.

Acknowledgements

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Appendix S1: List of plant species (with species codes used) recorded in Domaine National de Chambord, France

- *Abies alba* (Abie.alba)
- *Acer campestre* (Acer.camp)
- *Acer pseudoplatanus* (Acer.pseu)
- *Achillea millefolium* (Achi.mill)
- *Achillea ptarmica* (Achi.ptar)
- *Agrimonia eupatoria* (Agri.eupa)
- *Agrostis canina* (Agro.cani)
- *Agrostis capillaris* (Agro.capi)
- *Agrostis stolonifera* (Agro.stol)
- *Aira caryophylla* (Aira.cary)
- *Aira praecox* (Aira.proe)
- *Ajuga genevensis* (Ajug.gene)
- *Ajuga reptans* (Ajug.rept)
- *Alisma lanceolatum* (Alis.lanc)
- *Alisma plantago-aquatica* (Alis.plan)
- *Alliaria petiolata* (Alli.peti)
- *Alopecurus aequalis* (Alop.aequ)
- *Alnus glutinosa* (Alnu.glut)
- *Alopecurus pratensis pratensis* (Alop.prat.prat)
- *Andryala integrifolia* (Andr.inte)
- *Anemone peucedanum gallicum* (Anem.peuc)
- *Anisantha sterilis* (Anis.ster)
- *Anthoxanthum odoratum* (Anth.odor)
- *Aphanes australis* (Apha.aust)
- *Arabidopsis thaliana* (Arab.thal)
- *Arenaria serpyllifolia* (Aren.serp)
- *Arrhenatherum elatius* (Arrh.elat)
- *Asparagus officinalis* (Aspa.offi.offi)
- *Asphodelus albus* (Asph.albu)
- *Athyrium filix-femina* (Athy.fili)
- *Atriplex patula* (Atri.patula)
- *Avenella flexuosa* (Aven.flex)
- *Barbarea intermedia* (Barb.inte)
- *Barbarea vulgaris* (Barb.vulg)
- *Bellis perennis* (Bell.pere)
- *Betonica officinalis* (Beto.offi)
- *Betula pendula* (Betu.pend)
- *Bidens frondosa* (Bide.fron)
- *Brachypodium pinnatum* (Brac.pinn)
- *Brachypodium sylvaticum* (Brac.sylv)
- *Briza media media* (Briz.medi.medi)
- *Bromus hordeaceus* (Brom.hord)
- *Bromopsis ramosa ramosa* (Brom.ramo)
- *Calamagrostis epigejos* (Calam.epig)
- *Callitriche hamulata* (Call.hamu)
- *Callitriche cf. stagnalis* (Call.cf.stag)
- *Callitriche* sp. (Callitriche.sp)
- *Calluna vulgaris* (Call.vulg)
- *Campanula rapunculus* (Camp.rapu)
- *Capsella bursa-pastoris* (Caps.burs.burs)
- *Cardamine hirsuta* (Card.hirs)
- *Cardamine pratensis* (Card.prat)
- *Carex acuta* (Care.acuta)
- *Carex acutiformis* (Care.acutif)
- *Carex caryophylla* (Care.cary)
- *Carex demissa* (Care.demi)
- *Carex disticha* (Care.dist)
- *Carex divulsa* (Care.divu)
- *Carex echinata* (Care.echi)
- *Carex elata* (Care.elat)
- *Carex elongata* (Care.elon)
- *Carex flacca* (Care.flac)
- *Carex hirta* (Care.hirt)
- *Carex leersii* (Care.leer)
- *Carex leporina* (Care.lepo)
- *Carex pallescens* (Care.pall)
- *Carex paniculata* (Care.pani)
- *Carex pilulifera pilulifera* (Care.pilu.pilu)
- *Carex praecox* (Care.prae)
- *Carex pseudocyperus* (Care.pseu)
- *Carex remota* (Care.remo)
- *Carex riparia* (Care.ripar)
- *Carex sylvatica* (Care.sylv)
- *Carex vesicaria* (Care.vesi)
- *Carpinus betulus* (Carp.betu)
- *Catapodium rigidum* (Cata.rigi)
- *Centaurea decipiens* (Cent.deci)
- *Centaureum erythraea erythraea* (Cent.eryt.eryt)
- *Centaurea gr. jacea* (Cent.gr.jace)
- *Centaureum pulchellum* (Cent.pulc)
- *Cerastium fontanum vulgare* (Cera.font.vulg)
- *Cerastium glomeratum* (Cera.glom)

- *Cerastium semidecandrum* (Cera.cera.semi)
- cf. Asteraceae (cf. Asteraceae)
- *Chaenorrhinum minus* (Chaen.minu.minu)
- *Chamaecyparis lawsoniana* (Cham.laws)
- *Chamaemelum nobile* (Cham.nobi)
- *Chenopodium album* (Chen.albu)
- *Circaea lutetiana* (Circ.lute)
- *Cirsium arvense* (Cirs.arve)
- *Cirsium vulgare* (Cirs.vulg)
- *Clematis vitalba* (Clem.vita)
- *Clinopodium vulgare* (Clin.vulg)
- *Convolvulus arvensis* (Conv.arve)
- *Convolvulus sepium* (Conv.sepi)
- *Cornus sanguinea* (Corn.sang)
- *Corrigiola littoralis* (Corr.litt)
- *Corylus avellana* (Cory.avel)
- *Crassula tillaea* (Cras.till)
- *Crataegus laevigata* (Crat.laev)
- *Crataegus monogyna* (Crat.mono)
- *Crepis capillaris* (Crep.capi)
- *Crepis setosa* (Crep.seto)
- *Cynodon dactylon* (Cyno.dact)
- *Cynoglossum officinale* (Cyno.offi)
- *Cytisus scoparius* (Cyti.scop)
- *Dactylis glomerata* (Dact.glom)
- *Danthonia decumbens* (Dant.dec.deuc)
- *Daucus carota* (Dauc.caro)
- *Datura stramonium* (Datu.stam)
- *Deschampsia cespitosa* (Desc.cesp)
- *Dianthus armeria* (Dian.arme.arme)
- *Digitalis purpurea* (Digi.purp)
- *Digitaria sanguinalis* (Digi.sang)
- *Dioscorea communis* (Dios.comm)
- *Dryopteris carthusiana* (Dryo.cart)
- *Elytrigia campestris* (Elyt.comp)
- *Elytrigia repens* (Elyt.repe.repe)
- *Epilobium parviflorum* (Epil.parv)
- *Epilobium tetragonum* (Epil.tetr)
- *Epipactis microphylla* (Epip.micr)
- *Equisetum arvense* (Equi.arve)
- *Equisetum palustre* (Equi.palu)
- *Erica cinerea* (Eric.cine)
- *Erica scoparia* (Eric.scop)
- *Erica tetralix* (Eric.tetr)
- *Erigeron canadensis* (Erig.cana)
- *Erodium cicutarium* (Erod.cicu)
- *Euonymus europaeus* (Euon.euro)
- *Eupatorium cannabinum* (Eupa.cann)
- *Euphorbia amygdaloides* (Euph.amyg)
- *Euphorbia cyparissias* (Euph.cypa)
- *Euphorbia dulcis* (Euph.dulc)
- *Euphorbia helioscopia* (Euph.heli)
- *Euphorbia stricta* (Euph.stri)
- *Fagopyrum esculentum* (Fago.escu)
- *Fagus sylvatica* (Fagu.sylv)
- *Fallopia convolvulus* (Fall.conv)
- *Fallopia dumetorum* (Fall.dume)
- *Festuca gigantea* (Fest.giga)
- *Festuca heterophylla* (Fest.hete)
- *Festuca gr. ovina* (Fest.gr.ovin)
- *Festuca pratensis* (Fest.prat)
- *Festuca rubra* (Fest.rubr)
- *Ficaria verna* (Fica.vern)
- *Filago germanica* (Fila.germ)
- *Filago lutescens* (Fila.lute)
- *Filipendula ulmaria* (Fili.ulma)
- *Fragaria vesca* (Frag.vesc)
- *Frangula dodonei* (Fran.dodo)
- *Fraxinus excelsior* (Frax.exce)
- *Fumaria officinalis* (Fuma.offi)
- *Galeopsis tetrahit* (Gale.tetr)
- *Galium aparine* (Gali.apar)
- *Galium elongatum* (Gali.elon)
- *Galium mollugo* (Gali.moll)
- *Galium sp.* (Gali.sp)
- *Galium uliginosum* (Gali.ulig)
- *Galium verum* (Gali.veru)
- *Geranium columbinum* (Gera.colu)
- *Geranium dissectum* (Gera.diss)
- *Geranium molle* (Gera.moll)
- *Geranium robertianum* (Gera.robe)
- *Geum urbanum* (Geum.urba)
- *Glechoma hederacea* (Glec.hede)
- *Glyceria fluitans* (Glyc.flui)
- *Gnaphalium uliginosum* (Gnap.ulig)
- *Hedera heli* (Hede.heli)
- *Helleborus sp.* (Hell.sp)
- *Hieracium argillaceum* (Hier.argi)
- *Hieracium murorum* (Hier.muro)
- *Hieracium umbellatum* (Hier.umbe)
- *Holcus lanatus* (Holc.lana)

- *Holcus mollis* (Holc.moll)
- *Hydrocotyle vulgaris* (Hydr.vulg)
- *Hypericum elodes* (Hype.elod)
- *Hypericum humifusum* (Hype.humi)
- *Hypericum perforatum* (Hype.perf)
- *Hypericum pulchrum* (Hype.pulc)
- *Hypericum tetrapterum* (Hype.tetr)
- *Hypochaeris radicata* (Hypo.radi)
- *Ilex aquifolium* (Ilex.aqui)
- *Illecebrum verticillatum* (Ille.vert)
- *Iris pseudacorus* (Iris.pseu)
- *Jacobaea vulgaris* (Jaco.vulg)
- *Juncus acutiflorus* (Junc.acut)
- *Juncus articulatus* (Junc.arti)
- *Juncus bufonius* (Junc.bufo)
- *Juncus bulbosus* (Junc.bulb)
- *Juncus conglomeratus* (Junc.cong)
- *Juncus capitatus* (Junc.capi)
- *Juncus effusus* (Junc.effu)
- *Juncus inflexus* (Junc.infl)
- *Juncus tenuis* (Junc.tenu)
- *Kickxia elatine* (Kick.elat)
- *Knautia arvensis* (Knau.arve)
- *Lactuca muralis* (Lact.mura)
- *Lactuca serriola* (Lact.serr)
- *Lamium amplexicaule* (Lami.ampl)
- *Lapsana communis* (Laps.comm)
- *Lathyrus linifolius* (Lath.lini)
- *Lemna minor* (Lemn.mino)
- *Leontodon saxatilis* (Leon.saxa)
- *Leucanthemum vulgare* gr. (Leuc.vulg.gr)
- *Ligustrum vulgare* (Ligu.vulg)
- *Linaria repens* (Lina.repe)
- *Linaria vulgaris* (Lina.vulg)
- *Linum catharticum* (Linu.cath)
- *Lipandra polysperma* (Lipa.poly)
- *Lithospermum officinale* (Lith.offi)
- *Lobelia urens* (Lobe.uren)
- *Logfia minima* (Logf.mini)
- *Lolium multiflorum* (Loli.mult)
- *Lolium perenne* (Loli.pere)
- *Lonicera periclymenum* (Loni.peri.peri)
- *Lotus corniculatus* (Lotu.corn)
- *Lotus pedunculatus* (Lotu.pedu)
- *Luzula campestris* (Luzu.camp)
- *Luzula forsteri* (Luzu.forste)
- *Luzula multiflora* (Luzu.mult)
- *Lychnis flos-cuculi* (Lych.flos-cu)
- *Lycopus europaeus* (Lycu.euro)
- *Lysimachia arvensis* (Lysi.arve)
- *Lysimachia minima* (Lysi.mini)
- *Lysimachia nummularia* (Lysi.numu)
- *Lysimachia vulgaris* (Lysi.vulg)
- *Lythrum salicaria* (Lyth.sali)
- *Malus sylvestris* (Malu.sylv)
- *Medicago lupulina* (Medi.lupu)
- *Medicago sativa* (Medi.sati.sati)
- *Melampyrum pratense* (Mela.prat)
- *Melica uniflora* (Meli.unif)
- *Mentha aquatica* (Ment.aqua)
- *Mentha arvensis* (Ment.arve)
- *Moehringia trinervia* (Moeh.trin)
- *Molinia caerulea* (Moli.caer)
- *Montia fontana* (Mont.font)
- *Myosotis arvensis* (Myos.arve.arve)
- *Myosotis discolor* gr. (Myos.disc.gr)
- *Myosotis laxa* (Myos.laxa)
- *Myosotis ramosissima* (Myos.ram.ram)
- *Myosotis scorpioides* (Myos.scor)
- *Myosoton aquaticum* (Myosot.aqu)
- *Nardus stricta* (Nard.stri)
- *Oenanthe aquatica* (Oena.aqua)
- *Ononis spinosa* (Ono.spin)
- *Orchis purpurea* (Orch.purp)
- *Ornithopus perpusillus* (Orni.perp)
- *Oxalis fontana* (Oxal.font)
- *Pedicularis sylvatica* (Pedi.sylv)
- *Persicaria hydropiper* (Pers.hydr)
- *Persicaria maculosa* (Pers.macu)
- *Persicaria minor* (Pers.mino)
- *Peucedanum gallicum* (Peuc.gall)
- *Phalaris arundinacea* (Phal.arun)
- *Phragmites australis* (Phra.aust)
- *Picris hieracioides* (Pacr.hier)
- *Pilosella officinarum* (Pilo.offi)
- *Pimpinella saxifraga* (Pimp.saxi)
- *Pinus pinaster* (Pinu.pina)
- *Pinus laricio* (Pinu.lari)
- *Pinus sylvestris* (Pinu.sylv)
- *Pisum sativum* (Pisum.sati)
- *Plantago lanceolata* (Plan.lanc)
- *Plantago major* (Plan.majo)

- *Poa annua* (Poa.annu)
- *Poa compressa* (Poa.comp)
- *Poa nemoralis* (Poa.nemo)
- *Poa pratensis* (Poa.prat)
- *Poa trivialis* (Poa.triv)
- *Polygonum aviculare* (Poly.avic)
- *Polygonatum multiflorum* (Poly.mult)
- *Polygala serpyllifolia* (Poly.serpy)
- *Polygala vulgaris* (Poly.vulg)
- *Populus canescens* (Popu.cane)
- *Populus tremula* (Popu.trem)
- *Potamogeton polygonifolius* (Pota.poly)
- *Potentilla erecta* (Pote.erec)
- *Potentilla neglecta* (Pote.negl)
- *Potentilla reptans* (Pote.rept)
- *Potentilla sterilis* (Pote.ster)
- *Poterium sanguisorba* (Poter.sang)
- *Primula veris* (Prim.veri)
- *Prunella vulgaris* (Prune.vulg)
- *Prunus spinosa* (Prun.spin)
- *Pseudotsuga menziesii* (Pseu.menz)
- *Pteridium aquilinum* (Pter.aqui)
- *Pulicaria dysenterica* (Puli.dyse)
- *Pulmonaria longifolia* (Pulm.long)
- *Quercus petraea* (Quer.petr)
- *Quercus robur* (Quer.rob)
- *Quercus rubra* (Quer.rubr)
- *Radiola linoides* (Radi.lino)
- *Ranunculus acris* (Ranu.acri)
- *Ranunculus bulbosus* (Ranu.bulb)
- *Ranunculus flammula* (Ranu.flam)
- *Ranunculus repens* (Ranu.repe)
- *Ranunculus sardous* (Ranu.sard)
- *Ranunculus sceleratus* (Ranu.scel)
- *Ranunculus cf. trichophyllus* (Ranu.tric)
- *Ranunculus tripartitus* (Ranu.trip)
- *Raphanus raphanistrum* (Raph.raph)
- *Ribes rubrum* (Ribe.rubr)
- *Robinia pseudoacacia* (Robi.pseu)
- *Rorippa sylvestris* (Rori.sylv)
- *Rosa arvensis* (Rosa.arve)
- *Rosa canina* (Rosa.cani)
- *Rosa rubiginosa* (Rosa.rubi)
- *Rubus caesius* (Rubu.caes)
- *Rubus gr.fruticosus* (Rubu.gr.frut)
- *Rubus ulmifolius* (Rubu.ulmi)
- *Rumex acetosa* (Rume.acetosa)
- *Rumex acetosella* (Rume.acetose)
- *Rumex conglomeratus* (Rume.cong)
- *Rumex crispus* (Rume.cris)
- *Rumex obtusifolius* (Rume.obtu)
- *Rumex sanguineus* (Rume.sang)
- *Ruscus aculeatus* (Rusc.acul)
- *Sagina apetala* (Sagi.apet)
- *Sagina procumbens* (Sagi.proc)
- *Salix atrocinerea* (Salix.atro)
- *Salix cinerea* (Salix.cine)
- *Sanicula europaea* (Sani.euro)
- *Schedonorus arundinaceus* (Sche.arun)
- *Schedonorus giganteus* (Sche.giga)
- *Scorzoneroideis autumnalis* (Scor.autu)
- *Scorzonera humilis* (Scor.humi)
- *Scrophularia nodosa* (Scro.nodo)
- *Scutellaria galericulata* (Scut.gale)
- *Scutellaria minor* (Scut.mino)
- *Sedum cepaea* (Sedu.cepa)
- *Senecio vulgaris* (Sene.vulg.vulg)
- *Senecio sylvaticus* (Sene.sylv)
- *Serratula tinctoria* (Serr.tinc.tinc)
- *Setaria italica* (Seta.ital)
- *Sherardia arvensis* (Sher.arve)
- *Silene baccifera* (Sile.bacc)
- *Silene latifolia alba* (Sile.lati.alba)
- *Sisymbrium officinale* (Sisy.offi)
- *Solanum dulcamara* (Sola.dulc)
- *Solanum nigrum* (Sola.nigr)
- *Solidago virgaurea* (Soli.virg.virg)
- *Sonchus asper* (Sonc.aspe)
- *Sorbus aucuparia* (Sorb.aucu)
- *Sorbus domestica* (Sorb.dome)
- *Sorbus* sp. (Sorb.sp)
- *Sorbus torminalis* (Sorb.torm)
- *Spergula arvensis* (Sper.arve)
- *Spergula rubra* (Sper.rubr)
- *Spirodela polyrhiza* (Spir.poly)
- *Stachys palustris* (Stac.palu)
- Caryophyllaceae cf. *Stellaria alsine* (Stel.alsi?)
- *Stellaria graminea* (Stel.gram)
- *Stellaria holostea* (Stel.holo)
- *Stellaria media* (Stel.medi)
- *Succisa pratensis* (Succ.prat)

- *Taraxacum sec. ruderalis* (Tara.sec.rud)
- *Taxus baccata* (Taxu.bacc)
- *Teucrium scorodonia* (Teuc.scor)
- *Thelypteris palustris* (Thel.palu)
- *Thymus pulegioides* (Thym.pule)
- *Thymus praecox* (Thym.prae)
- *Thysselinum palustre* (Thys.palu)
- *Tilia platyphyllos* (Tili.plat)
- *Torilis japonica* (Tori.japo.japo)
- *Trifolium arvense* (Trif.arve)
- *Trifolium dubium* (Trif.dubi)
- *Trifolium incarnatum* (Trif.inca)
- *Trifolium medium* (Trif.medi)
- *Trifolium pratense* (Trif.prat)
- *Trifolium repens* (Trif.repe.repe)
- *Triticum* sp. (Trit.sp)
- *Trocdaris verticillatum* (Troc.vert)
- *Tuberaria guttata* (Tube.gutt)
- *Ulex europaeus* (Ulex.euro)
- *Ulex minor* (Ulex.mino)
- *Ulmus mino* (Ulmu.mino)
- *Urtica dioica* (Urti.dioi)
- *Valerianella locusta* (Vale.locu.locu)
- *Valeriana officinalis* (Vale.offi)
- *Verbascum blattaria* (Verb.blatt)
- *Verbena officinalis* (Verb.offi)
- *Veronica arvensis* (Vero.arve)
- *Veronica chamaedrys* (Vero.cham)
- *Veronica officinalis* (Vero.offi)
- *Veronica persica* (Vero.pers)
- *Veronica serpyllifolia* (Vero.serp)
- *Viburnum opulus* (Vibu.opul)
- *Vicia angustifolia* (Vici.angu)
- *Vicia cracca* (Vici.crac)
- *Vicia hirsuta* (Vici.hirs)
- *Vicia sativa* (Vici.sati)
- *Vicia sepium* (Vici.sepi)
- *Vicia tetrasperma* (Vici.tetr)
- *Viola arvensis* (Viol.arve)
- *Viola canina* (Viol.cani)
- *Viola hirta* (Viol.hirt)
- *Viola odorata* (Viol.odor)
- *Viola riviniana* (Viol.rivi)
- *Vulpia bromoides* (Vulp.brom)
- *Vulpia myuros* (Vulp.myur)
- Unknown sp.1

Appendix S2 plots for effective sizes of beta coefficients; beta coefficient values for environmental predictors; and beta coefficients for ungulate presence vs species trait values.

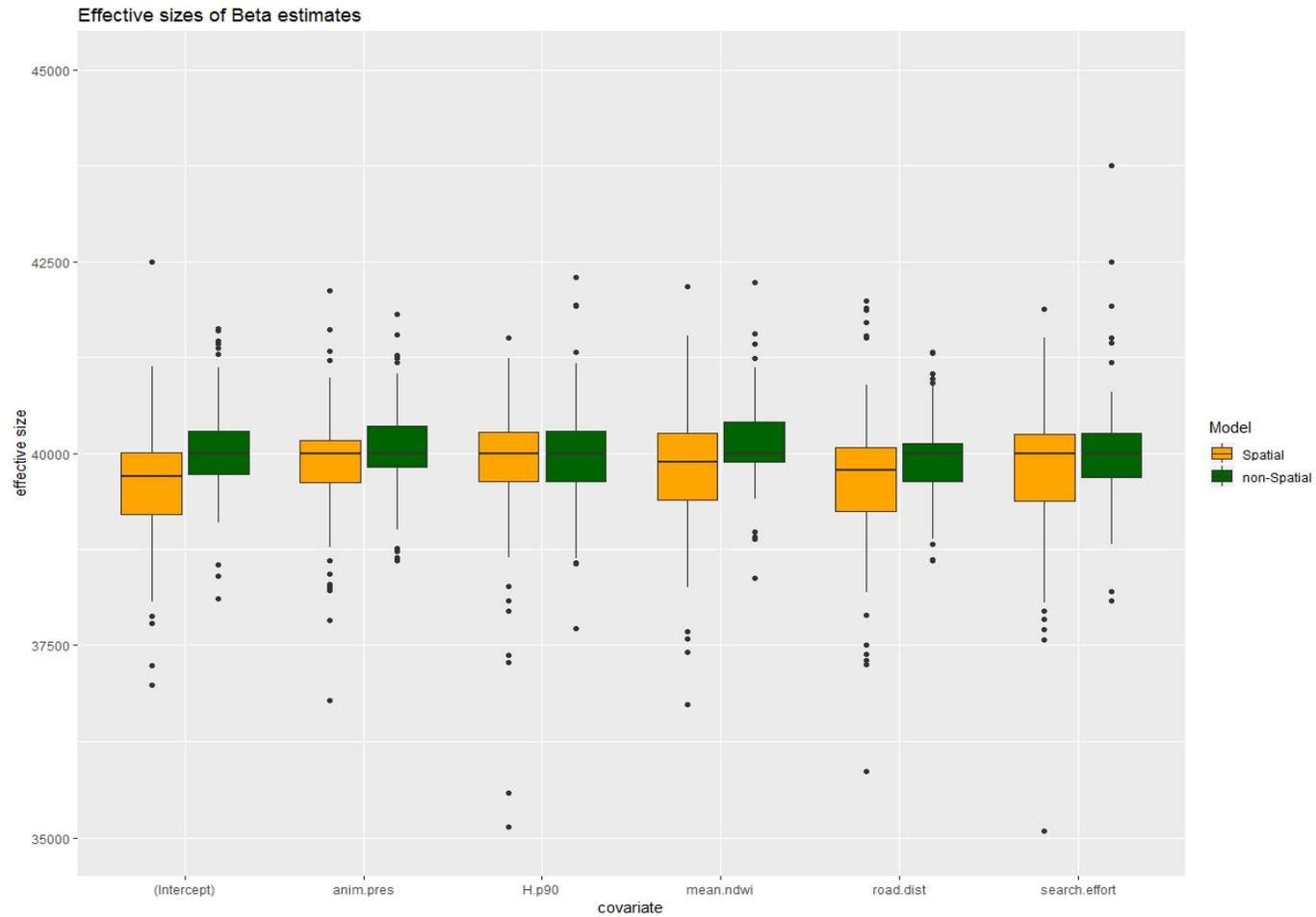


Fig S2.1: Effective sizes of beta coefficients for each of the environmental covariates

Species responses to mean NDWI

mean \pm 95% CI

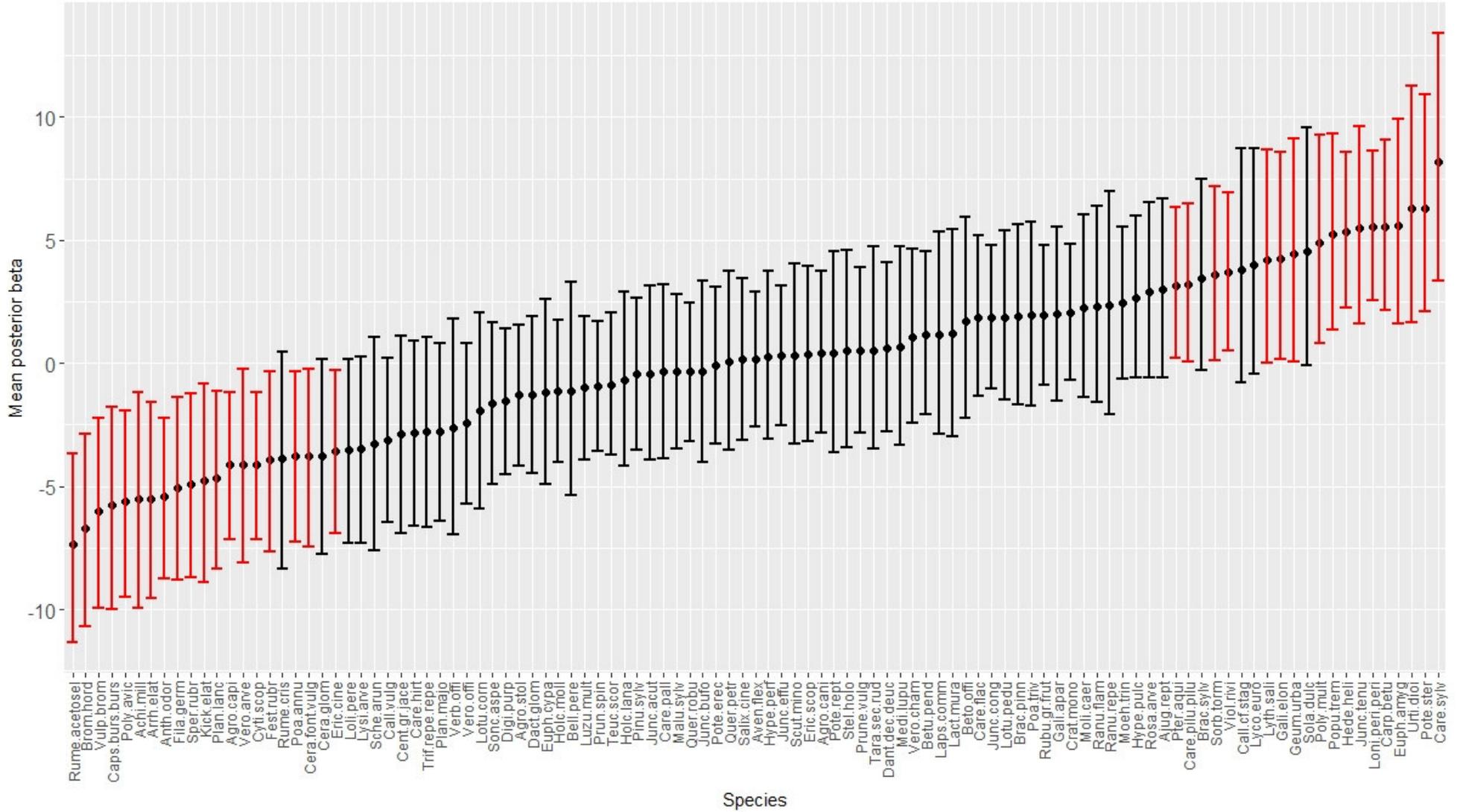


Fig S2.2a Mean posterior beta coefficients for species response to mean NDWI (mean \pm 95% CI).

Species responses to canopy height

mean \pm 95% CI

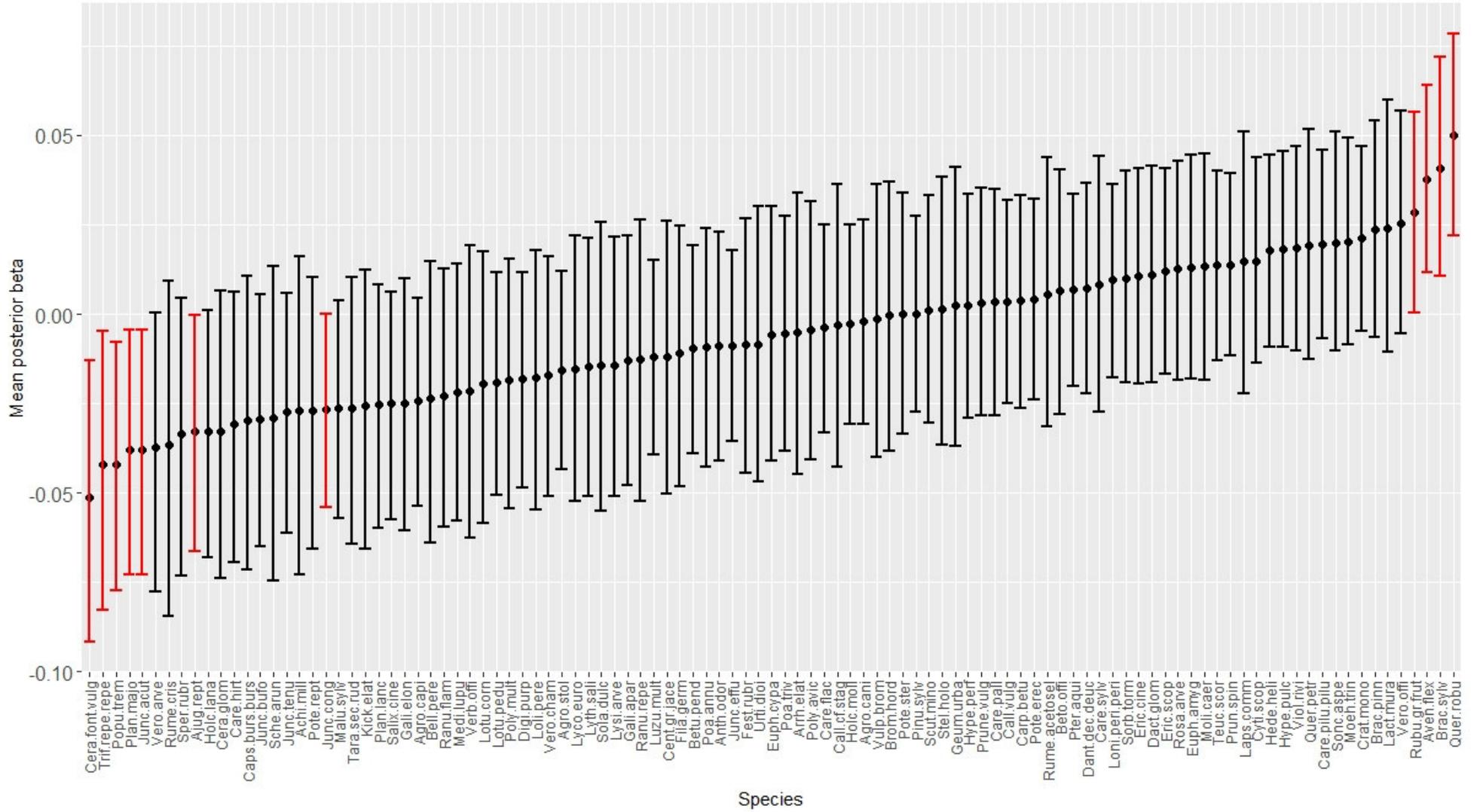


Fig S2.2b Mean posterior beta coefficients for species response to canopy height at 90 percentile (mean \pm 95% CI)

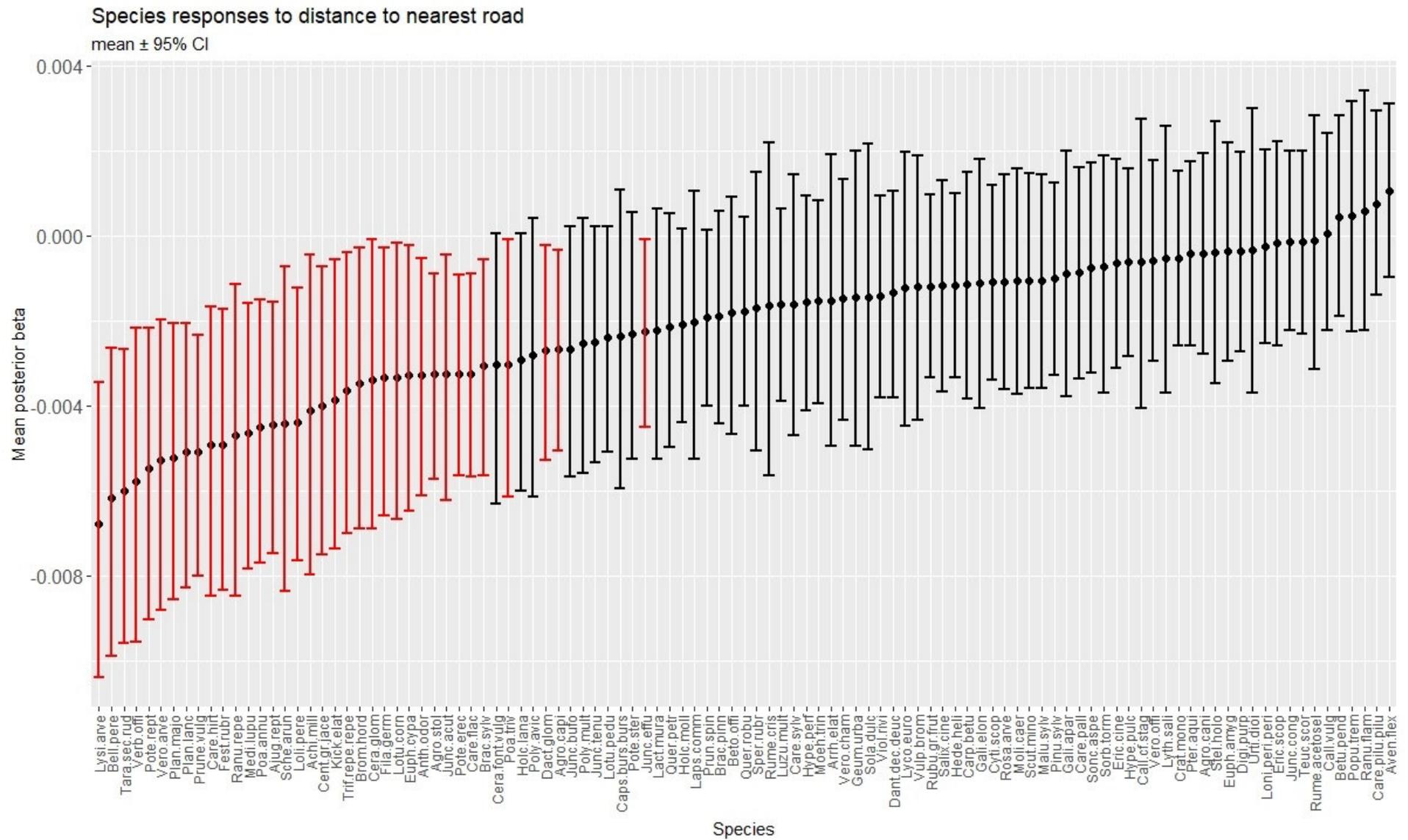


Fig S2.2c Mean posterior beta coefficients for species response to distance to nearest road (mean \pm 95% CI)

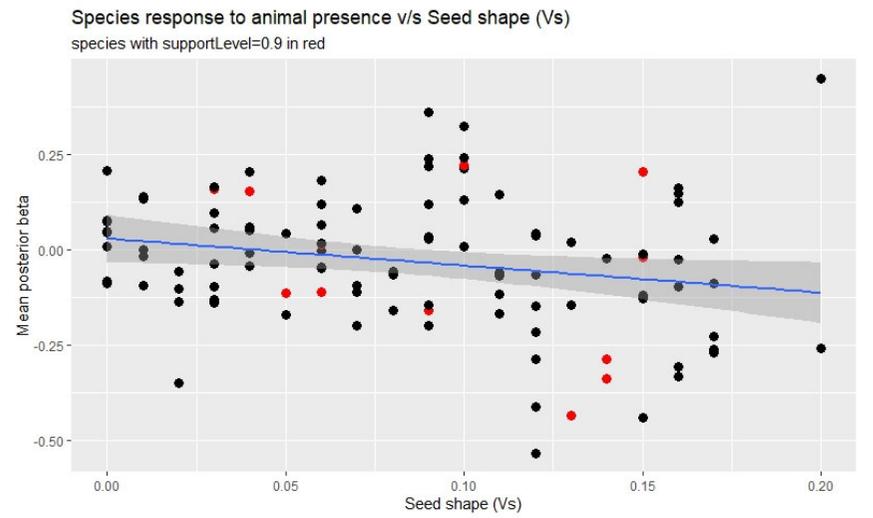
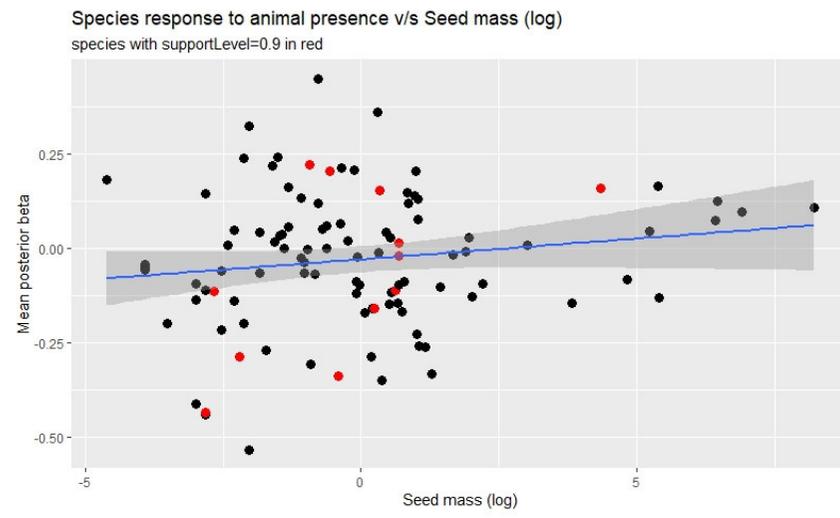
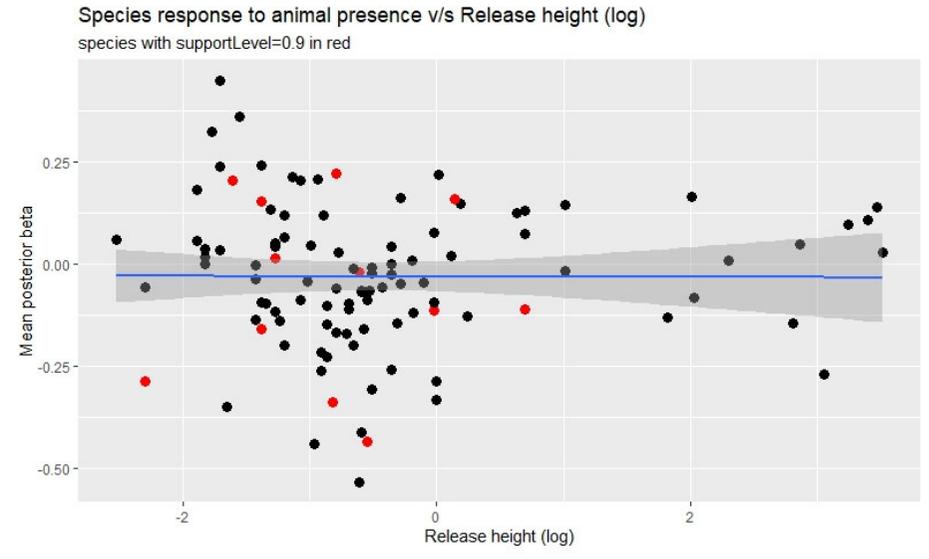
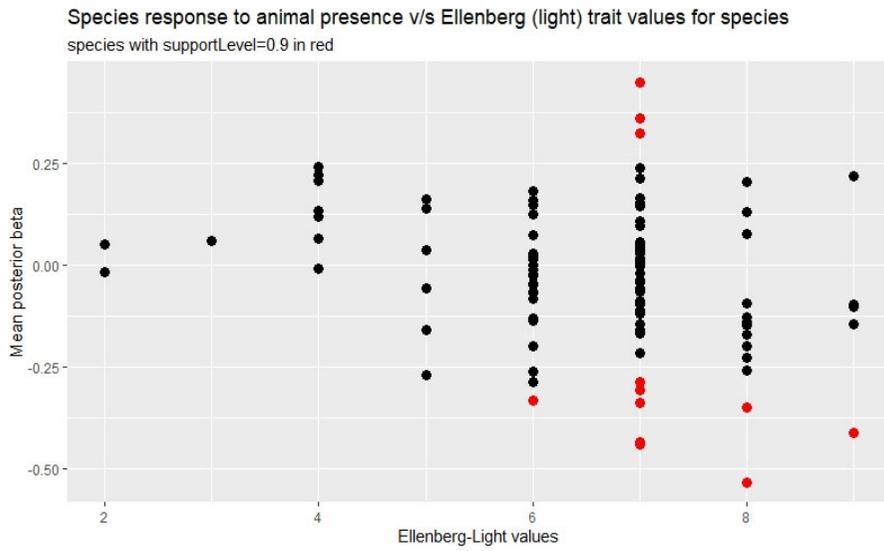


Fig S2.3: Mean posterior beta coefficients for species response to ungulate presence versus the species-wise trait values. a) Ellenberg-Light values b) diaspore releasing height c) seed mass and d) seed shape (Vs)

CHAPTER 4

How movement rules translate to epizoochorous seed dispersal kernels: A data-driven simulation approach

Résumé (version française)

Contexte : L'épizoochorie est reconnue comme un mode de dispersion longue distance sélectif, important pour la migration rapide des plantes. La connaissance reste pourtant lacunaire sur le rôle des comportements fins de déplacement et de la structure du paysage sur les kernels de dispersion épizoochore des plantes.

Objectifs : Nous avons évalué l'influence d'aspects spécifiques du comportement de déplacement du cerf (les limites du domaine vital, la sélection de l'habitat, les caractéristiques de déplacement dépendant de l'habitat) sur les distances de dispersion et l'habitat de dépôt des graines.

Méthodes : Nous avons combiné des *step selection functions* ajustées avec des localisation GPS de femelles de cerf élaphe dans le Domaine National de Chambord (France) et dans le parc national de la forêt bavaroise en Allemagne avec une distribution des temps de rétention externe des diaspores d'une plante épizoochore modèle, *Xanthium strumarium*, pour comparer les kernels de dispersion épizoochore sur le court terme (i.e. 5 jours) dans deux paysages contrastés.

Résultats : La distance moyenne de dispersion est plus courte dans le site de Chambord, plus petit et plus structuré (moyenne 462.4 m) que dans le site plus étendu et homogène de Bavière (moyenne 809.2 m). Entre nos modèles simulés, les estimations de distance de dispersion étaient systématiquement plus élevées quand on ne tenait pas compte des limites du domaine vital. La spécificité de l'habitat de dépôt augmente quant à elle avec la proportion de l'habitat dans le domaine vital, mais s'avère aussi plus élevée qu'attendue en cas de dispersion aléatoire pour l'habitat minoritaire de milieu ouvert.

Conclusions Nos résultats montrent que les domaines vitaux sont plus importants pour le kernel de dispersion des graines que la sélection de l'habitat ou les vitesses de déplacement habitat-dépendantes au sein du domaine vital. La zoochorie est marginalement bénéfique pour la spécificité de l'habitat de dépôt des graines dispersées, mais celle-ci dépend principalement de la représentativité de l'habitat au sein du domaine vital.

Keywords: long distance dispersal (LDD), seed deposition, ungulates, ecological modeling, step selection function, individual-based model

Abstract

Context Epizoochory is recognised as a key long-distance and selective dispersal mode, important for rapid plant migration. Knowledge gaps exist on how seed dispersal kernels result from the behaviour of animal vectors and landscape structure.

Objectives We assessed the influence of specific aspects of red deer movement behaviour (home-ranging, habitat selection, habitat-specific step lengths) on seed dispersal distances and habitat specificity of seed deposition.

Methods We combined step selection functions fitted to GPS data from collared female red deer in Domaine National de Chambord (France) and in Bavarian Forest National Park (Germany) with an external seed retention time distribution of the model plant species, *Xanthium strumarium*, to compare short-term (i.e. five day) epizoochorous seed dispersal kernels in the two contrasting landscapes.

Results The mean dispersal distance was much shorter in the smaller, more structured site Chambord (mean 462.4 m) than in the more contiguous Bavaria (mean 809.2 m). Between our simulated models, dispersal distance estimates were consistently highest for the model excluding home range centre. Habitat specificity of seed deposition generally increased with an increasing area cover of a habitat type, but was higher than expected under random dispersal for the open habitat type.

Conclusions Our results show that home ranges are more important for the seed dispersal kernel than habitat preference or movement speeds within specific habitats of

the home range. Animal aided dispersal was marginally beneficial for habitat specificity of transported seeds, but the latter mainly depends on the proportion of the habitat class in the landscape.

Introduction

Habitat loss and fragmentation is one of the major drivers of biodiversity loss (Pereira et al. 2010). Plants will need to expand/shift their range and move to keep up with the changing global climate (Chen et al. 2011). Seed availability and dispersal limitation are identified as major impediments in plant dispersal at the local and regional scales, respectively (Münzbergová and Herben 2005). Where plants move is closely linked to the ability of animals to transport and deposit them in conducive habitats. Seed dispersal, thus, profoundly influences the dynamics of plant species and communities. Consequently, quantifying seed dispersal kernels, i.e. the probability distribution of seed deposition sites relative to the seed's origin (Nathan and Muller-Landau 2000), is of great importance for understanding past and predicting future dynamics in changing landscapes. Mechanistic models are key tools for explaining the spatial pattern of seed dispersal. While there are several well-established mechanistic models of seed dispersal by wind (Greene and Johnson 1996; Nathan et al. 2001, 2011), models explaining seed shadows of plants dispersed by animals are still rare.

Animal dispersers determine the quantity and quality of seed dispersal (Côtés and Uriarte 2013), e.g. the distance to which the seeds travel, and the habitat in which the seeds are finally deposited (Cousens et al. 2010; Côtés and Uriarte 2013). Both dispersal distance and habitat specificity of dispersed seeds influence the quality component of the seed dispersal 'effectiveness' (Schupp et al. 2010).

The most common approach for estimating dispersal kernels of plants dispersed by animals is combining information on gut passage time of the animal and its movement trajectory (Cousens et al. 2010). While gut passage time pertains to the seeds ingested by animals, epizoochory is concerned with the external transport of seeds. Epizoochory has been reported to be less common than endozoochory, but has been shown to have a stronger filtering effect than endozoochory, e.g. with ungulates as dispersal vectors (Albert et al. 2015).

Where animals move and how they move is largely governed by the composition and the structure of the landscape in which they move (Baguette and Van Dyck 2007; Coulon et al. 2008). Seed dispersal kernels therefore result from the interplay between animal movement behavior and the surrounding landscape. Here we aim to identify how three components of movement behavior – home ranging, habitat selection, and habitat-specific movement speed – combine with landscape structure to determine two important aspects of the seed dispersal kernel: distance and habitat specificity.

Primary seed dispersal is a tri-phasic process – emigration, transfer and deposition (Matthysen 2012). In the emigration phase seeds are picked up by animals either by external attachment on the body or internally via consumption. Large animals play a pivotal role in carrying diaspores away from parent plants during the transfer phase of dispersal (Couvreur et al. 2004; D'hondt et al. 2012), and allow the diaspores to escape density-dependent mortality (Howe and Smallwood 1982). Seeds transported by large vertebrates generally travel longer distances than those transported abiotically, by wind or water (Vittoz and Engler 2007), and the trajectory is essentially dependent on the behavior and habitat preferences of the animal disperser. Seed deposition site is linked

to successful survival, establishment and recruitment; it is determined by dispersal distance, and its quality depends on habitat specificity and the spatial clustering of dispersed seeds (Muller-Landau and Hardesty 2005). Animals may move a disproportionate number of seeds into habitats similar to that of the parent plant, i.e. a favourable environment for establishment (directed dispersal hypothesis, Wenny 2001). This may be either due to preferential movement of animals to these habitats, or different seed deposition rates in different habitats (Nathan and Muller-Landau 2000; Revilla et al. 2004).

Behavioural decisions made by animals influence the shape of the dispersal curves (Westcott et al. 2005; Russo et al. 2006). For seeds dispersed by animal vectors, the characteristics of their movement drive the dispersal kernel of the dispersed seeds (Damschen et al. 2008). Home range sizes, seed retention times and movement rates of animals are key parameters in predicting dispersal distances (Muller-Landau and Hardesty 2005). Spatial heterogeneity within the home range of an individual animal, the perception of the available resources and activity-dependent habitat selection influence where an animal moves within the landscape (Zollner et al. 2000). Animal habitat preference (selection) within heterogeneous landscapes also influences the dispersal kernels (Börger et al. 2008; Levey et al. 2008). Plants in open areas are known to especially benefit from this non-random space use by ungulates, and are more likely to be deposited back in open areas than would be expected by chance (Heinken and Raudnitschka 2002; Heinken et al. 2002; D'hondt et al. 2012).

In temperate regions, ungulates are some of the largest seed dispersers. Their habitat preference and movement between different habitats aids long distance seed dispersal

(Pellerin et al. 2016). For example, red deer (*Cervus elaphus*) move through several different habitats within a single day. They mostly prefer forest areas for cover and use open areas for feeding in the dark and crepuscular zones (Schaefer et al. 2008; Godvik et al. 2009). However, there is less difference in day and night habitat usage when there is enough cover and fewer disturbances (Náhlik et al. 2009).

As large-bodied animals with several metres to kilometres of movement within a day, red deer produce specific seed shadows of plants they disperse and influence their seed dispersal kernel. In this study, we were mainly interested in how three aspects of red deer movement behavior affect the short-term (five days) 'effective dispersal kernel' (Nathan et al. 2012) of epizoochorously dispersed plants: 1) home ranging behaviour, 2) attraction to specific habitats, and 3) speed of moving in different habitats. We expected that home ranging behaviour would result in shorter seed dispersal distance compared to movement trajectories with no home ranging behaviour. We also expected that attraction to certain habitats within the home range would increase the habitat specificity of the dispersed seeds from these habitats; and that a slow speed of movement through preferred habitats would increase habitat specificity of the seeds but decrease dispersal distance.

We follow the simulated seeds for a maximum of five days post attachment to the animal, which encompassed the home range crossing time of the majority of the analysed red deer individuals. We take the example of *Xanthium strumarium* as a model seed type dispersed epizoochorously by red deer; retention times for this plant species have been estimated by Liehrmann et al. (2018) in a previous study. We assess the dispersal distance and habitat specificity of seed deposition; and use forested and open areas as the primary habitats for assessment. To increase the generality of our results, we

compare two different landscapes with different deer densities and landscape composition and compare the resulting seed dispersal kernels.

Methods

Study area

The study was carried out in Domaine National de Chambord (Chambord) in France and Bavaria Forest National Park (Bavaria) in Germany (Fig.4.1). The site Chambord is located in north-central France (47°36 N, 1°31 E) at low elevation (72–128 meters above sea level). It is predominantly a game hunting reserve, with added emphasis on biodiversity conservation. It is a highly spatially structured forest, mainly of oaks (*Quercus petraea* and *Quercus robur*) and conifers (mostly *Pinus sylvestris*), with few mixed stands including species such as *Betula pendula* and *Carpinus betulus*. The forest boundary is demarcated by a 32 km long wall on all sides. It covers a total area of 5400 ha (54 km²). The red deer population within Chambord is about 700 animals, i.e. 13 individuals/ km².

The site Bavaria, located in south-east Germany (48°58 N, 13°23 E) covers a total area of 24,250 ha (242.5 km²) and is contiguous with the Šumava National Park (690 km²) in Czech Republic. It covers three main forest types along a wide elevation gradient. Hunting management has to consider the objectives of the park and is banned from the core zone of the park, which comprises 75% of the area. Natural migration of red deer into lowlands during winters is restricted by the use of winter enclosures. The red deer population (in spring) within Bavaria is estimated around 400 animals, i.e. 1.7 individuals/ km² (Heurich et al. 2011).

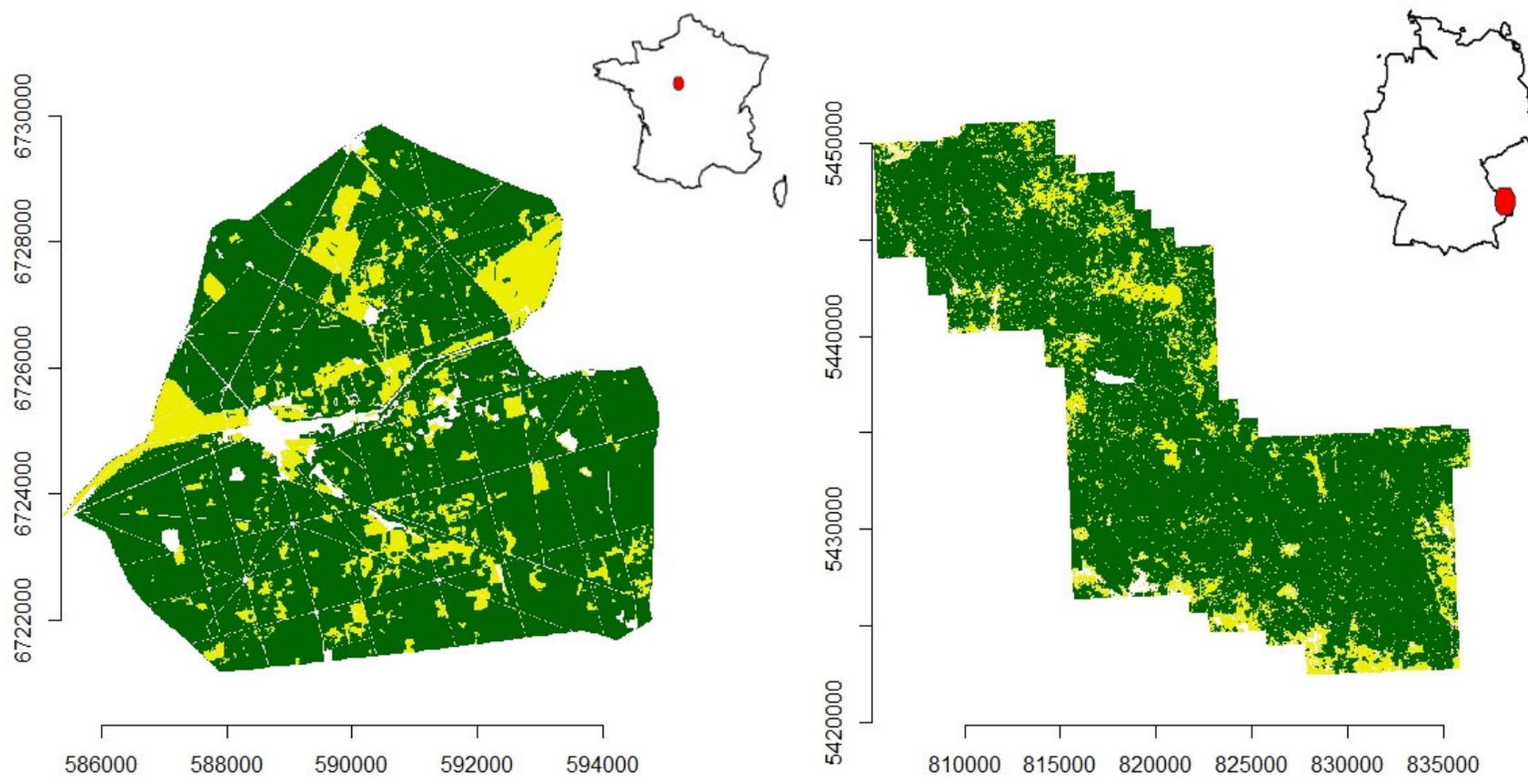


Figure 4.1: Map of study areas. Chambord to the left, bavaria to the right. Forest areas in green, open areas in yellow. Position of study area in the country is marked with a red circle. Units on axis are UTM coordinates for each site. Total area: Chambord = 54 km², Bavaria= 242.5 km²

These two landscapes contrast in landscape configuration, management, and animal vector density (eight times higher in Chambord), making it interesting to compare potential consequences for the seed dispersal kernels. While Bavaria represents a large, contiguous forest area, Chambord represents a spatially-structured, restricted forest area with extremely high ungulate density maintained for hunting, and an intensively managed forest. While animals in Chambord roam the forests all year round, Bavaria restricts deer movements to enclosures in winters. Chambord has a hunting pressure between mid-November to end-February each year, where hunters are permitted to shoot once a week, with four to six hunt-drives per day (each drive lasting about 60 mins, (Chassagneux et al. 2020)). Whereas in Bavaria population control is carried out when animals are entering enclosures at the beginning of winter, and in the management zone of the park (25% of the area).

Movement data: GPS collar data

This study included collared red deer females in both study areas, 12 for Chambord (captured and collared between 2015-17) and 17 for Bavaria (captured and collared between 2013-14). To make the data comparable, we included only location data from the period between 15th May and 5th of Dec (to exclude the period when animals are likely to be in enclosures in Bavaria). The location data were collected every two hours for each individual. Our study period also includes the main shedding period for most seeds in the two sites (Manzano and Malo 2006). Home range sizes of each individual were calculated with an auto-correlated kernel density estimator (akde) using the ctmm (Calabrese et al. 2016) package in R.

GIS layers

We used digital forest maps provided by the respective Forest office at both sites to create raster maps of 10 m x 10 m resolution. We used the ‘rasterize’ function of the package raster (Hijmans 2019) in R for this purpose. We included only the forest and open areas within each study site, i.e., we did not distinguish between different types of forest or open areas and combined several different sub-types of these habitats into one. All other layers (water bodies, buildings, etc.) were masked from further analyses. In the simulations, the animals were “allowed” to walk on roads, but any seeds landing on roads were removed from further analyses, as seeds landing on roads are unlikely to germinate and are thus lost from the system. We used the raster maps to annotate each location with the habitat type for all animals. The proportion of open areas (9.25% and 14.4% in Bavaria and Chambord respectively) was much lower than forest habitats (78.5% and 89.7% in Bavaria and Chambord respectively) in both sites.

Step Selection Function (SSF)

We fitted an integrated step selection function (iSSF) to the movement trajectory of each animal (Avgar et al. 2016), with conditional logistic regression using the ‘amt’ package (Signer et al. 2018) in R. Each realised step was compared against 200 alternative steps along the trajectory drawn from an exponential distribution for step lengths and uniform distribution for turning angles. We used a 2-hour interval to meet the assumption of uncorrelated movement velocities between steps.

For each animal, we fitted an iSSF model (“full model”) representing all movement behaviors under investigation, i.e. home ranging, habitat preference for forest vs. open habitat, differential step lengths in forest vs. open habitat, and three simplified models

where one of the three behaviors was excluded (“no_HRCentre”, “no_habitatPref”, “SpeedofMove”).

The full model included movement metrics that describe red deer movement path and had the following predictors: cosine of turning angles (which describes the tortuosity of the movement path), step length, and log(step length) as well as their interactions with habitat (forest vs. open), regression coefficients quantifying the location of the home range centre and the strength of attraction to the home range centre (i.e. the three predictors northing, easting, and $(\text{northing}^2 + \text{easting}^2)$), habitat preference (forest vs. open), and step id as strata.

Dispersal kernel

Dispersal kernels were simulated in a three-step approach (Fig. 4.2). First, for a given iSSF model, we simulated movement trajectories at the corresponding two hour time step for the period over which animals tracks were observed (15th May and 5th of Dec). Second, since according to the seed retention time model (see below), nearly half of the seeds fall off in the first 10 min and are then slowly lost over the next few hours, we interpolated the trajectories to 15 minutes intervals from the two hour time-step using ‘ctmm’. Third, we calculated the dispersal kernel statistics based on 3000 seed uptake locations chosen randomly across the trajectory of the animal that are not roads, and followed the fate of seeds from these 3000 locations for a maximum of five days (i.e. 480 steps of 15 minutes), weighting the Euclidean distance from the pickup location and habitat along the 480 steps according to the corresponding seed drop probability. We worked under the assumption that our model plant species has the same diaspore retention times in both forest and open area habitats. The seed retention probability for each seed was calculated using a

power exponential function $p(t) = a \cdot \exp(-t^b)$ (Bullock et al. 2011) with parameter estimates from Liehrmann et al. (2018), for red deer ($a=1.730$ and $b=0.095$), where p is the proportion of diaspores left on the animal and t represents time (Fig. 4.2).

As a reference point, we calculated expected seed dispersal distance for random dispersal within a given home range as the mean distance between pairs of 1000 random points in the 95% kernel of the home range estimate. We analysed whether habitat specificity of deposited seeds is related to the proportion of that habitat type within the home range of an animal using beta regression with a cloglog link (package 'mgcv' in R).

Results

Movement data and Step Selection Function

Home-range estimates of the animals within the two sites showed a large variation (Fig.4.3). While the home ranges of deer within Chambord were more or less consistently under five km² (range 0.70 - 4.4 km²), those in Bavaria were mostly higher than that (range 1.5 - 21 km²).

Visual comparison of movement trajectories estimated by different models (i.e. full model and three simplified models) indicated that the full model performed best in simulating trajectories of actual animals. To assess whether simulated trajectories resulted in similar estimates of dispersal distances and habitat specificity as actual animal trajectories, we compared, across all animals, these two estimates between actual animal trajectories and trajectories simulated with the full iSSF model. The Pearson's correlation was 0.97 in both cases (Appendix 1 - Fig.S1, Fig.S2), indicating that the full model provided a good

approximation of the actual trajectory of the animal with respect to resulting seed dispersal distances and habitat specificity.

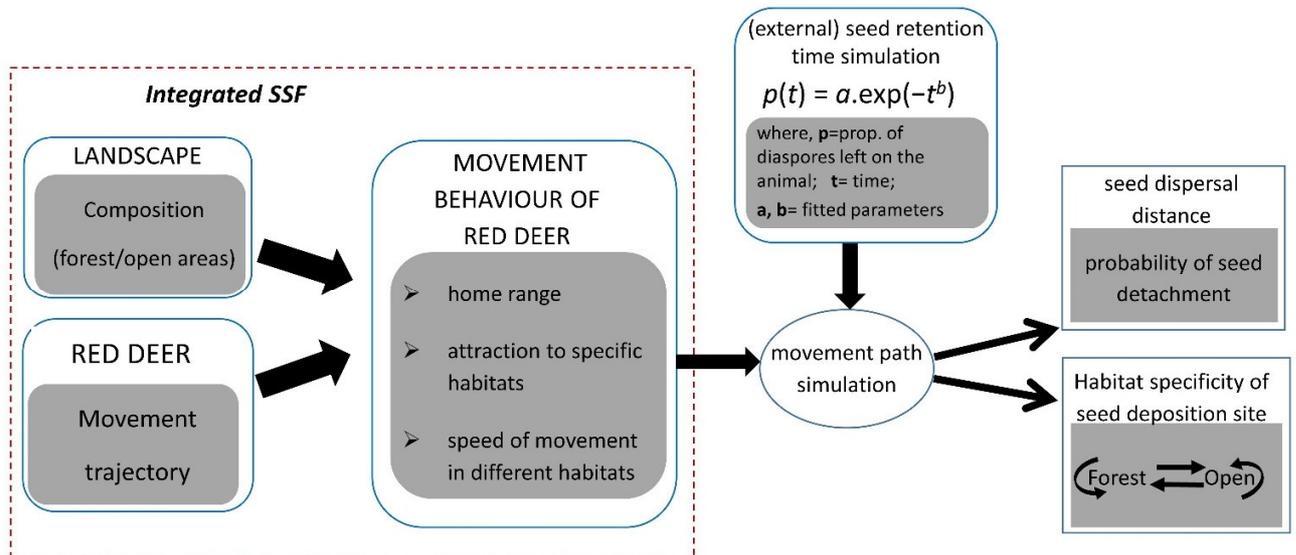


Figure 4.2: Conceptual figure illustrating our approach to estimating seed dispersal kernel of a typically epizoochorously dispersed plant, *Xanthium strumarium*.

Models that did not include the home range centre ('no_HRCentre') had consistently different movement patterns, and larger ranges of movement of the animal when compared to the other models (Fig.4.4, Fig.4.5). While the tortuosity of the path taken by the animal can be an indicator for its preferences for or within a habitat, our full model and the model without different speeds of movement through the habitats ('SpeedOfMove') behaved similarly. Also, comparing the full model to the model that did not include habitat preference of the animal ('no_habitatPref'), the latter tends to estimate slightly higher dispersal distances. However, this difference in estimates is small.

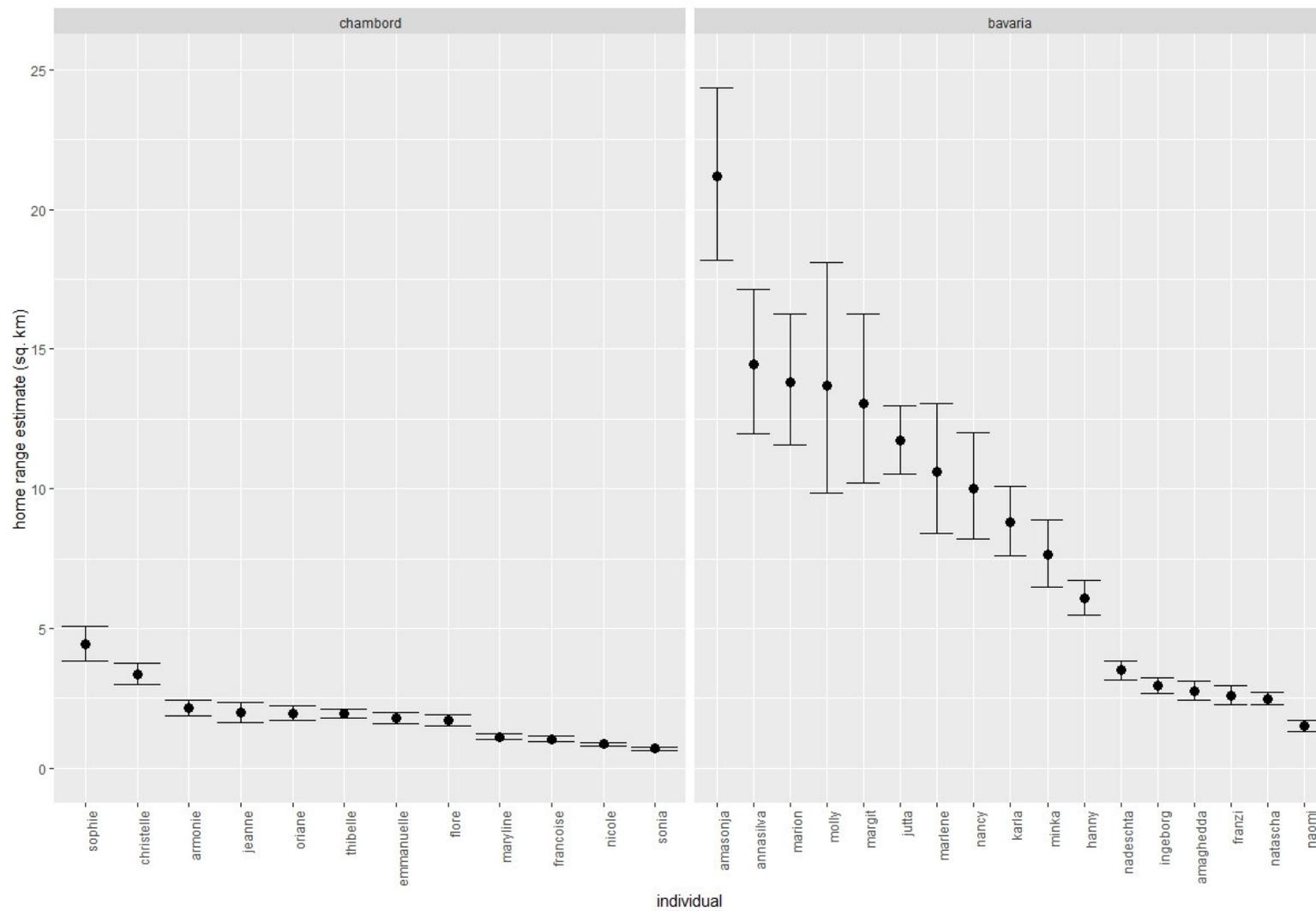


Figure 4.3: Home range estimates of individuals from both sites.

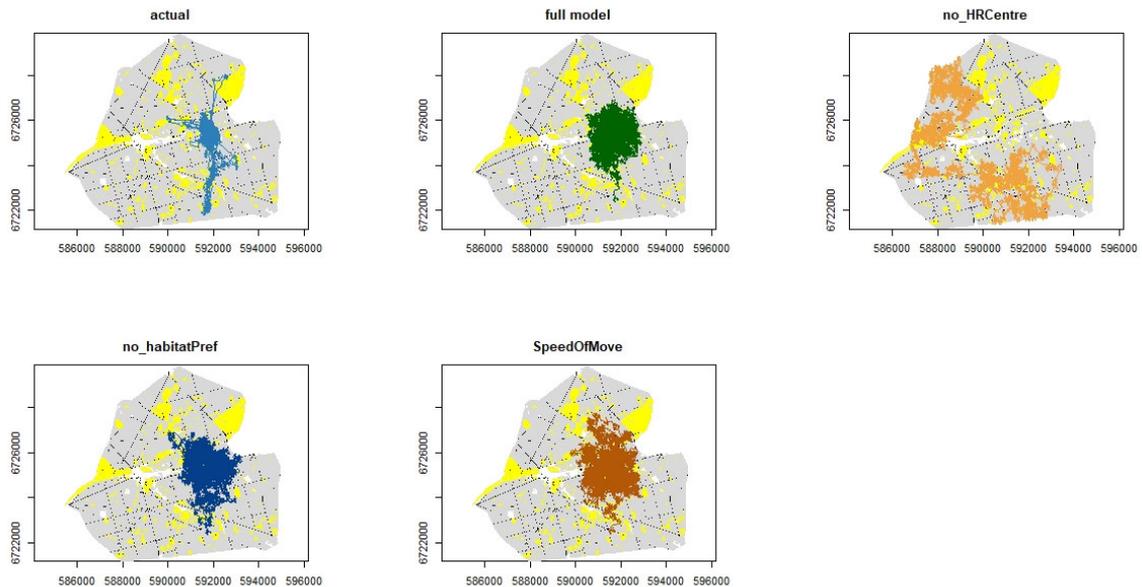


Figure 4.4: Alternate tracks from simulated models for one individual - ‘Jeanne’ from chambord. Open areas in yellow, forests in gray, black dots represent roads. All other habitat classes have been masked. (time between consecutive locations = 15 min for all tracks)

Dispersal kernel

The overall estimated dispersal kernels (Fig.4.6) showed site-specific responses. Seeds in Chambord were dispersed over smaller distances compared to Bavaria. The seeds from open areas moved into forest (“open:forest”) travelled for longer distances than the opposite direction, at both sites.

a) Dispersal Distance

To compare the results for different movement behavior models between sites, we visualised the distribution of mean seed dispersal distance across individuals with

boxplots. At site-level (Fig.4.5), the mean dispersal distances in Chambord were much lower than for Bavaria. Dispersal distance estimated by the 'no_HRCentre' model was much higher than the alternative models. Additionally, there was a weak trend shown by the model without habitat preference ("no_habitatPref") to estimate longer dispersal distances compared to the simulated full model. However, this weak trend was not exhibited by models dispersing seeds from forest:forest or open:open areas in Bavaria.

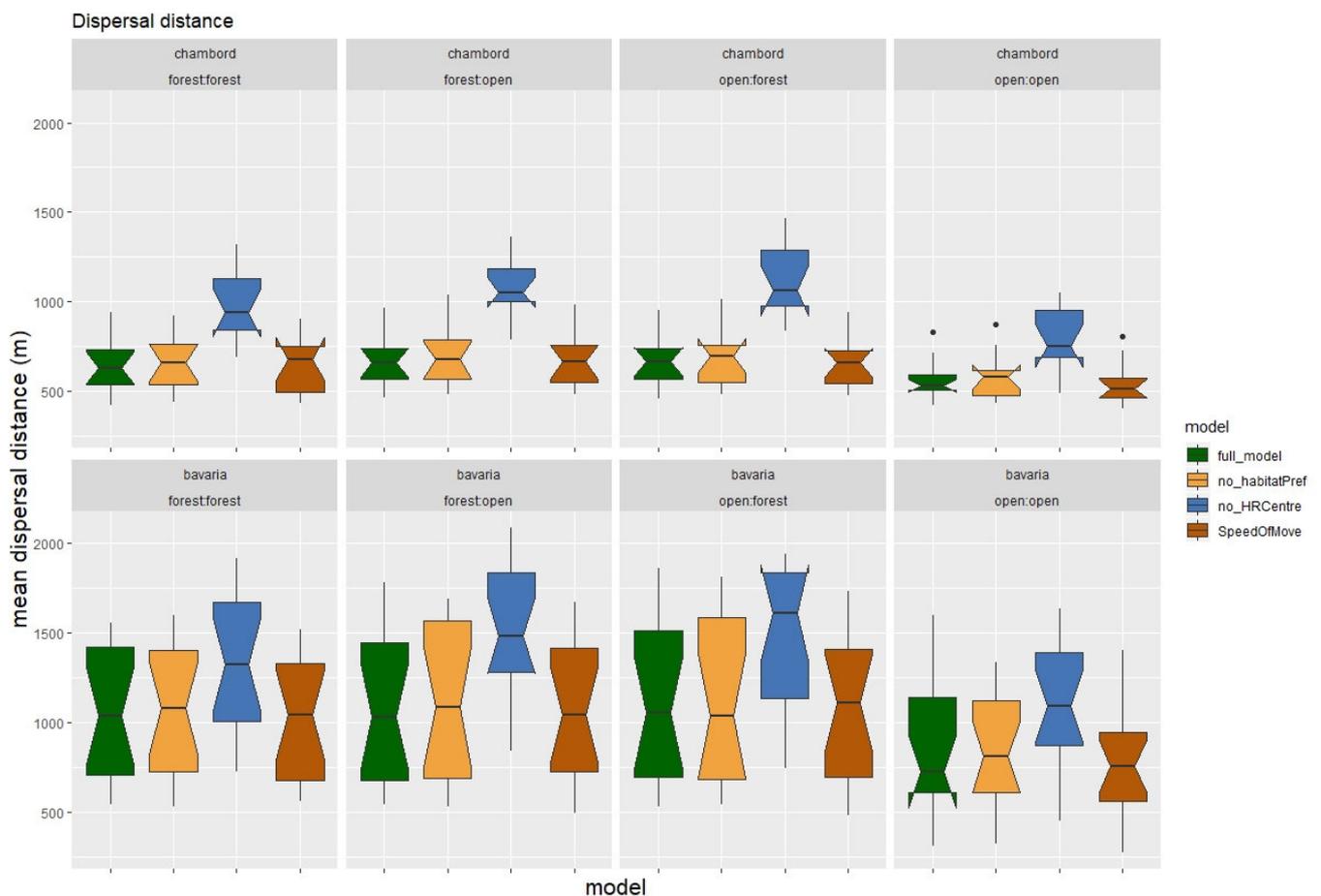


Figure 4.5: Site level- Estimated mean dispersal distance by different models

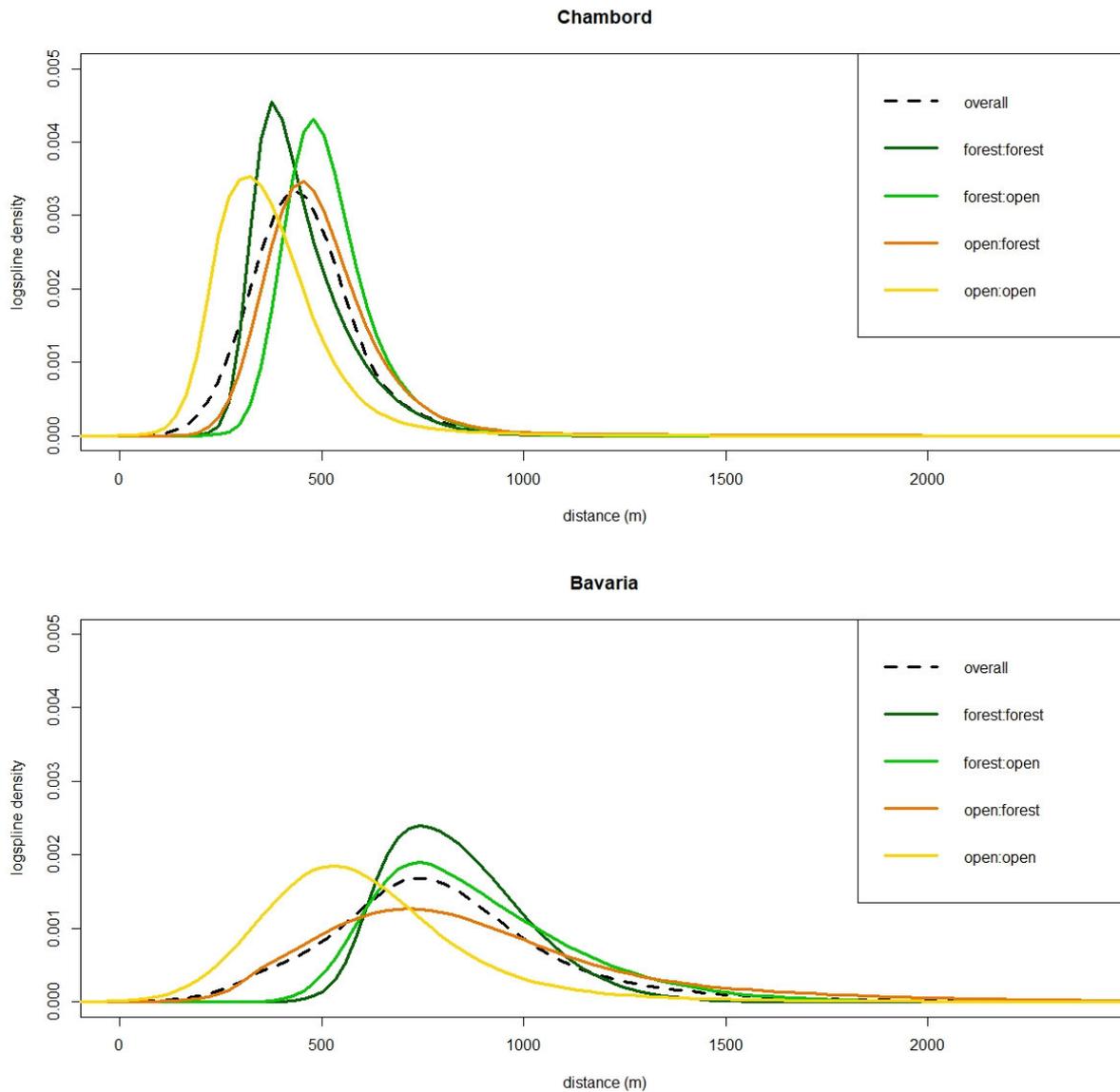


Figure 4.6: Overall dispersal kernel for sites chambord and bavaria.

At the individual level (Fig.4.7), with the exception of the individual 'amaghedda' from Bavaria, the mean dispersal distance of seeds dispersed by each individual was lower than the mean of expected distances for random dispersal within its 95% home range kernel, irrespective of the study site. The dispersal distances were also related to the size

of the home range of the animal. Individuals with larger estimated home range sizes moved seeds over longer distances.

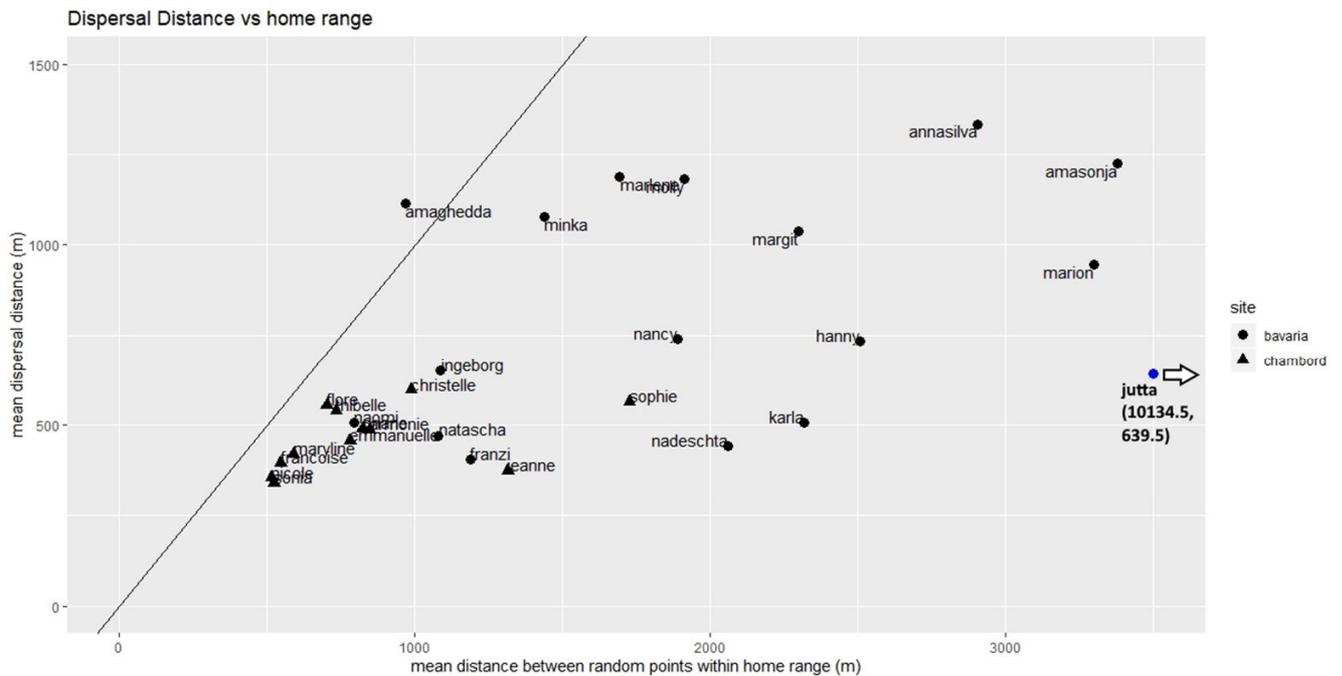


Figure 4.7: Dispersal distance vs random distances within HR. The individual 'jutta' is an outlier due to its large home range.

b) Habitat specificity

Similar to the dispersal distance, to compare the spread of values for different models between the sites, we created boxplots of the mean value of habitat specificity for each individual animal. At the site level (Fig. 4.8), the seeds from open areas in Chambord showed higher specificity than in Bavaria, i.e. the seeds from open areas in Chambord are more likely to be deposited back to open areas. Once again, the model that did not

account for home range centre of the animal was different in its specificity from the other models. The specificity for 'no_HRCentre' was lower than all other models except for the open area seeds in Bavaria.

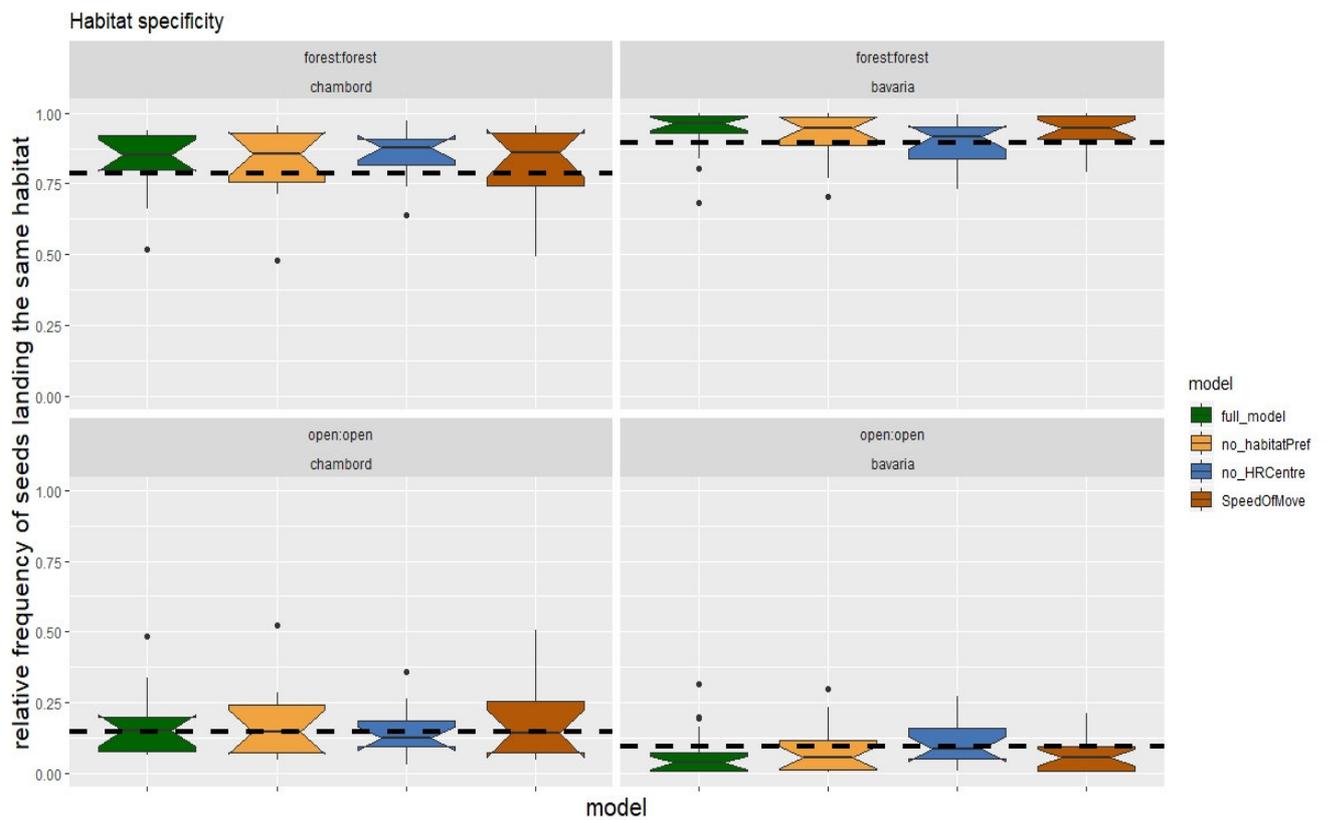


Figure 4.8: Site level- Estimated habitat specificity of seed deposition by different models. Dashed line showing the proportion of habitat class (forest/open) in the landscape.

The results of the beta regression model indicate that the habitat specificity of forest seeds was highly correlated with the proportion of forest within the home range of the individual animal (Fig.4.9), a pattern that would also be expected for a complete spatially-random dispersal of seeds. However, at high proportions of forest, habitat specificity levelled-off,

and consequently, at low proportion of open area within the animal home range, the habitat specificity of dispersed seeds tended to be higher for open area seeds.

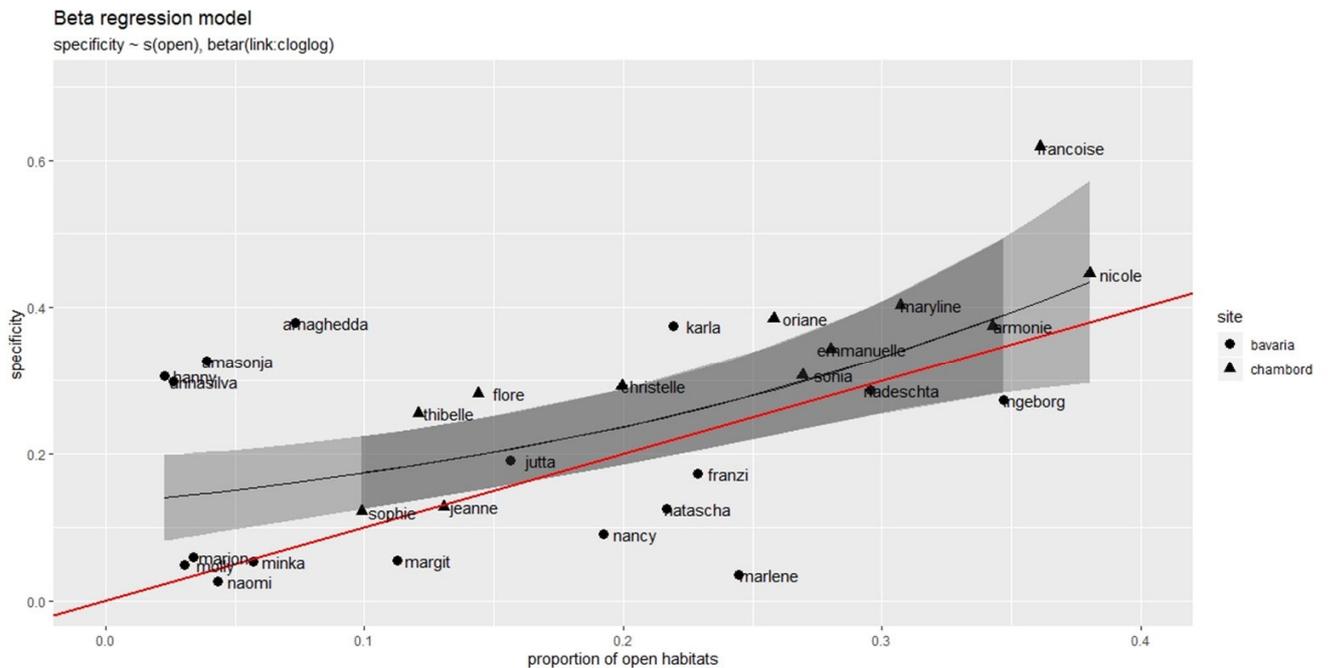


Figure 4.9: Beta regression model to assess whether habitat specificity of deposited seeds is related to the proportion of that habitat type within the home range of an animal (overall model fit, $R^2 = 0.33$). Area in gray shows the prediction from the model with 95%CI.

Discussion

In this study, we consider the effect of home ranging behaviour, habitat preference within the home-range, and of the speed of movement through different habitats by red deer on seed dispersal kernel of an epizoochorously dispersed plant species. Our results stress the importance of accounting for home range behaviour of animal vectors. Habitat

selection and habitat-specific movement speed within the home range were less important for red deer in affecting the seed dispersal kernel. Our approach makes use of empirical estimations of seed retention times by Liehrmann et al. (2018) for the common cocklebur, *Xanthium strumarium*, and movement information from GPS collars fitted on deer in two landscapes. While this approach does not allow for plant species-specific estimates of dispersal kernels, we consider it a useful first step in understanding a complex ecological process where occurrence of events are difficult to predict (Sorensen 1986). We focused on dispersal distance as well as habitat specificity of seed deposition, both of which are important to assess the quality of dispersal and disperser effectiveness (Schupp et al. 2010).

Red deer movement and space use

The home range emergence of animals is associated with having predictable environmental conditions (Riotte-Lambert and Matthiopoulos 2020). A previous study comparing movement patterns of four ungulates (Mueller et al. 2011), reported that species moving in landscapes with predictable vegetation availability, moved in shorter, more predictable ways and showcase range residency. Yearly and seasonal home range of red deer is overall constant with high site fidelity (Richard et al. 2014). Red deer hinds have larger summer ranges, and the size of individual home ranges is related to the food availability in their home range as well as their reproductive status (Clutton-Brock et al. 1982). Home ranges of red deer are reportedly smaller in areas that have substantial supplementary feeding during winters (Reinecke et al. 2014). Between our study sites, the ungulates in Chambord are regularly provided with supplementary feeding to support high game population management for hunting, whereas in Bavaria animals are only fed

inside the winter enclosures. Additionally, habitat selection within the home range is associated with the proportion of the different habitats (Catt and Staines 1987; Godvik et al. 2009) and is related to the home range size. When availability of food resources is clustered and more evenly spread out, the home ranges tend to be smaller as compared to the areas where food resources are more scattered across the landscape (Tufto et al. 1996). It is perhaps not so surprising then that the home ranges within Chambord (with overall smaller, spatially structured and intensively managed landscape) are much smaller than those in Bavaria.

a) There are other factors related to space use that can affect the effective seed dispersal by red deer. While adult and sub-adult red deer males show longer natal dispersal rates, adult and sub-adult females and juveniles tend to be more philopatric (Prévot and Licoppe 2013). Hamman and Klein (unpublished data) have previously reported a natal dispersal of 60 km for a male compared to just under 10 km for females. Females with calves tend to use open areas and forest edges (Licoppe 2006; Náhlik et al. 2009). These sexually dimorphic and age-related differences will likely produce different seed shadows. Moreover, in areas with intense hunting pressure, female red deer are known to spend twice as much time away from the home range centre than in periods without hunting (Jarnemo and Wikenros 2014; Chassagneux et al. 2020). Additionally, there might be seeds being transferred between animals during social interactions leading to change in animal vector that carries the seed to its final deposition site (Liehrmann et al. 2018). However, testing for all these fine-scale differences is beyond the scope of the present study. They should be considered for future studies to test their specific effects on the consequent seed dispersal kernels.

Seed dispersal kernel: epizoochory and red deer

a) Dispersal distance

Overall, our results indicate that seeds in contiguous landscapes (Bavaria) are moved over longer distances than in smaller, spatially-structured landscapes (Chambord). This is in agreement with previous studies that reported dispersal distances to be shorter in heterogenous landscapes (Levey et al. 2008). Also, animals move for longer distances in homogenous landscapes (Tucker et al. 2018). The overall dispersal distances in Chambord are much shorter and show lower variation than Bavaria across all tested models, and associated to higher density of deposited seeds.

Epizoochory is reported to be more selective than endozoochory in filtering plant species based on traits (Albert et al. 2015). A frequency (of use) index i.e., browsing pressure from both roe and red deer has been associated (Boulanger et al. 2011) with the spread of a rare plant species, *Cynoglossum officinale* via epizoochory. Liehrmann et al. (2018) estimated the half-life dispersal distance of *Xanthium strumarium* to be between 237-2437 m depending on which body part of the deer the seeds were attached. Higgins et al. (2003) estimated potential and realised dispersal distances by considering barriers to movement through a landscape. They assessed dispersal distances for *Xanthium strumarium* via epizoochory by the Iberian Lynx (*Lynx pardinus*), with a reported mean realised dispersal distance of 572 m, and a realised and potential migration rate of 968 m/yr and 2186 m/yr, respectively. The overall mean dispersal distance for the *Xanthium strumarium* seeds estimated by our simulated model (Fig.4.6) was 462.4 m for Chambord and 809.2 m for Bavaria which is well over the arbitrary 100 m threshold to classify LDD events (Cain et al. 2000).

b) Habitat specificity

A previous study described the simulation model 'SEED' (Will and Tackenberg (2008)) and used the movement data from a red deer collared in lowlands of Germany to parameterise the model jointly for epi- and endozoochory of *Achillea millefolium*. They found that seeds dispersed by endozoochory had a higher probability of being deposited in unsuitable habitats when compared to seeds transported by epizoochory. Endozoochorously dispersed seeds might have lower habitat specificity of seed deposition because the gut passage times might well exceed the time taken by the animal to cross a certain habitat (D'hondt et al. 2012). There is therefore a trade-off between dispersal distance and habitat specificity of dispersed seeds, which can vary between dispersal modes given that most seeds dispersed by epizoochory are detached relatively soon.

The attachment of seeds on the body of an animal (the emigration phase of dispersal) depends on the spatial distribution pattern of the plant (Bullock and Primack 1977), its fecundity (Hovstad et al. 2009) and the probability of contact between the animal and plant (Will et al. 2007). Since we focus only on the transfer stage of the seeds, these additional factors have not been considered, although they will most likely have a strong influence on the final seed deposition site.

The ability for seeds to be deposited in different patches depends on clustering, inter-patch distance, configuration and patch size (Levey et al. 2008). Open areas in both our study sites are present in smaller proportions compared to forested areas, and thus can be considered as patches of (open area) seed sources. Our results indicate that seeds from open areas in Chambord showed higher specificity than in Bavaria. This could at

least partially be linked to their spatial configuration as the open areas in Bavaria are more spread out over the landscape than in Chambord. The effect of the clustering and configuration of the open areas on the eventual dispersal kernel remains to be tested.

Animals preferentially move between similar habitats resulting in 'directed dispersal' of seeds (Wenny 2001). This has implications for the long distance dispersal, as it avoids seeds landing in unsuitable habitats the further they move from their parent plants (Spiegel and Nathan 2007). Our results indicate that animal dispersal conferred a slight advantage in habitat specificity relative to random dispersal for seeds originating from rare habitats. However, in absolute terms habitat specificity increased with the within home-range dominance of that habitat type.

Conclusions

Red deer are one of the largest mammals in the temperate regions, capable of transporting seeds over long distances by attachment in its fur. In increasingly fragmented landscapes, with increasing heterogeneity of the forests, it can play a crucial role in the transport of seeds. However, this is largely dependent on the landscape configuration and its ability of navigating the change in structure of its habitats. Our study stresses the importance for accounting for home range sizes of range-resident species when quantifying different aspects of the effective seed dispersal kernel. While there have been numerous previous studies combining animal movement and gut passage times through animals to estimate seed dispersal kernels, ours is one of the few that estimate the kernel for an epizoochorous plant species. In this study, we show that in smaller, more spatially-

structured areas, where the home ranges of the deer are smaller compared to more contiguous forests, seed dispersal distances are much shorter.

The seed dispersal kernel can be influenced by many aspects of individual movement behavior, sex- and age-specific differences, social interactions, animal cognition as well as changes in landscape configuration and composition. The combination of simulating trajectories with integrated step selection functions and seed retention time distributions provides an adaptable toolbox to quantitatively explore epizoochorous seed dispersal kernels.

Acknowledgements

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Appendix 1

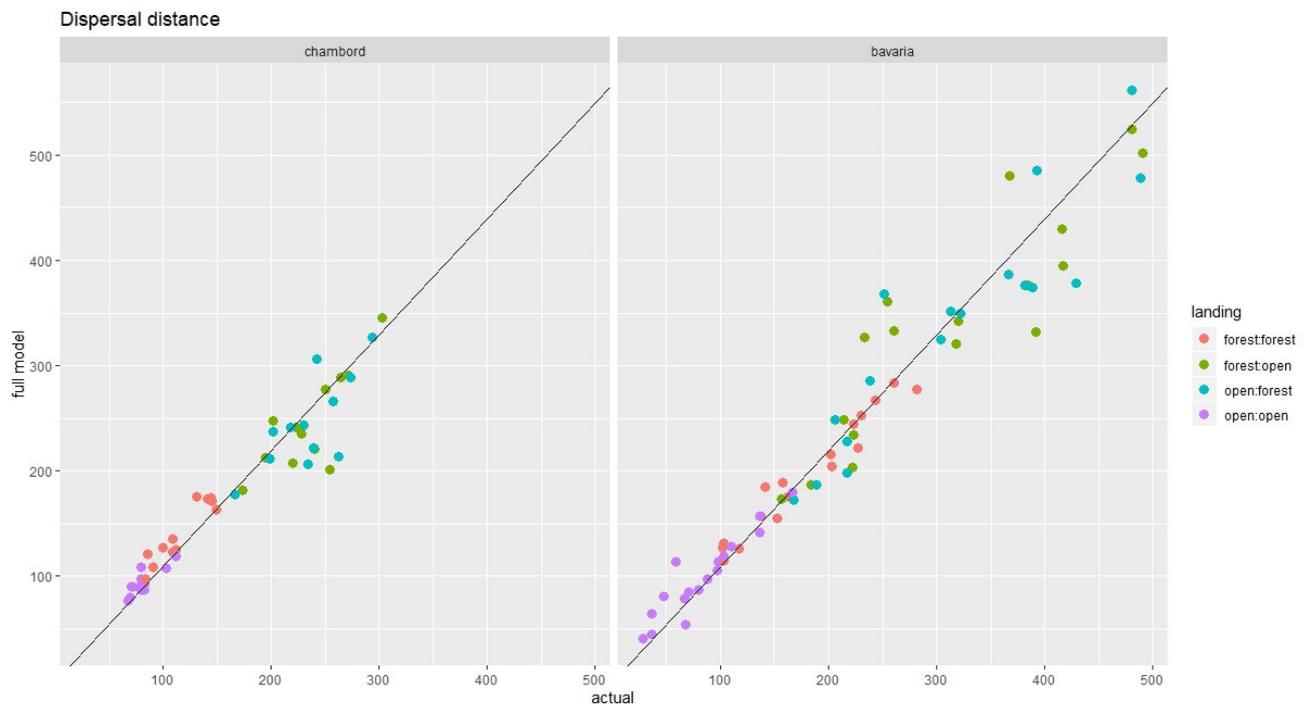


Fig S1: Simulated seed dispersal distance (combining animal trajectories and seed retention times), using either actual animal trajectories or trajectories simulated from the full iSSF model. Pearson correlation=0.97. ('landing' = initial habitat: final habitat of seed attachment and deposition)

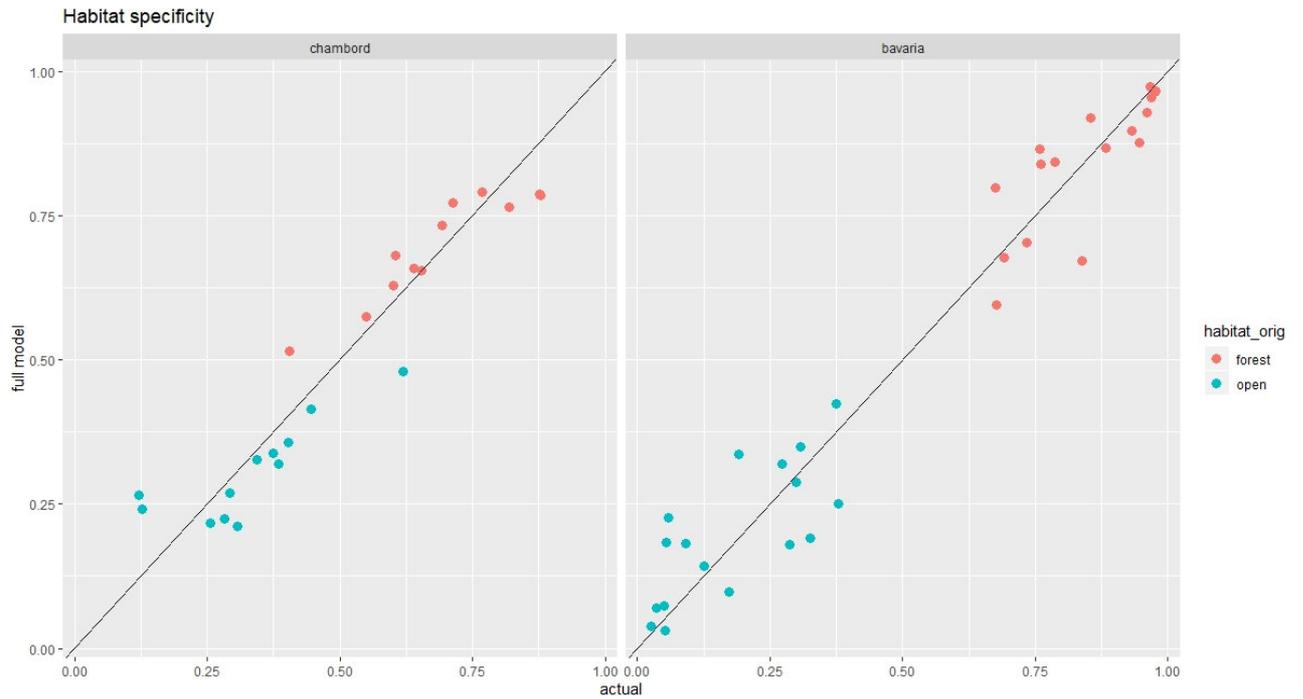


Fig. S2: Simulated habitat specificity of deposited seeds (combining animal trajectories and seed retention times), using either actual animal trajectories or trajectories simulated from the full iSSF model. Pearson correlation = 0.97. ('habitat_orig' = initial habitat in which seeds were attached to the animal).

CHAPTER 5

Complementarity of dispersal processes by red deer (*Cervus elaphus*)

Résumé (version française)

Contexte : Les mammifères sont des vecteurs privilégiés de dispersion à longue distance des plantes. Ils peuvent prendre en charge les diaspores de différentes manières, soit par voie interne (endozoochorie), soit par voie externe (épizoochorie). Les caractéristiques des graines et des plantes dont elles sont issues qui favorisent la dispersion par ces animaux dépendent de ces différents modes de dispersion. Jusqu'à présent la complémentarité en termes de diversité taxonomique et fonctionnelle des plantes dispersées a été rarement étudiée et principalement abordée à l'échelle du site d'étude, sans tenir compte du vecteur individuel et de la charge totale (par tous les modes de dispersion) en graines véhiculées.

Objectifs : Dans cette étude, nous avons cherché à mettre en évidence la part des plantes spécifiquement dispersées par endozoochorie et épizoochorie par des vecteurs individuels de dispersion, et à mettre en évidence les traits des plantes et des graines impliqués.

Méthodes : Nous avons tiré profit d'un jeu de données récemment publié (Petersen et Bruun, 2019), et en accès libre, pour des individus de cerfs prélevés à la chasse, et pour lesquels trois prélèvements ont été réalisés (fèces, pelage et sabots) dans 4 forêts du

Danemarck, pour évaluer la charge en graines par individu. Des données similaires ont été prélevées en France et en Allemagne dans le cadre de cette thèse, mais le jeu de données, similaire à celui analysé, n'est pas encore disponible du fait de doutes persistants sur l'identification taxonomique de certaines graines et germinations. Nous avons utilisé des courbes d'accumulation d'espèces, et une approche multivariée pour mettre en évidence la complémentarité taxonomique des cortèges d'espèces dispersées par les différents modes de dispersion.

Résultats : Nous montrons que ni le nombre de diaspores, ni le nombre d'espèces transportées, à l'échelle de l'individu, ne diffèrent que l'on considère la dispersion endozoochore, la dispersion épizoochore dans le pelage ou la dispersion épizoochore sous les sabots. Par contre, la composition spécifique des plantes dispersées diffère entre modes de dispersion endozoochore et épizoochore avec très peu de chevauchements, indiquant une complémentarité de ces modes de dispersion.

Conclusion : Pour la première fois, nous avons pu mettre en évidence que les ongulés sauvages, en particulier le cerf élaphe, disperse des cortèges floristiques différenciés en fonction du mode de dispersion considéré, soulignant ainsi l'importance de considérer la charge totale de graines dispersées par chaque vecteur de dispersion. Contrairement à des études antérieures, nous montrons également que le cortège floristique dispersé par épizoochorie peut être plus important que celui dispersé par endozoochorie. Par ailleurs, l'évaluation ponctuelle de la charge totale constitue probablement une sous-estimation du potentiel de dispersion de l'individu considéré.

Keywords: endozoochory, epizoochory, dispersal traits, taxonomic complementarity, functional complementarity

Introduction

In terrestrial ecosystems, seed dispersal by large herbivores can cover longer distances than dispersal via wind or even birds (Vittoz and Engler, 2007). This ability to transfer viable diaspores over long distances plays an important role in helping plants migrate to new habitats in keeping up with climate change (Corlett and Westcott, 2013), help persist in fragmented habitats, escape density-dependent mortality and kin-competition (Howe and Smallwood, 1982) and help overcome constraints such as seed limitation. Conversely, this same ability enables rapid spread and propagation of invasive plants (Dovrat et al., 2012).

Complementarity in seed dispersal can be either 1) between different animal species dispersing the same plant or 2) between different dispersal modes by the same animal species (Baltzinger et al., 2019). Seed dispersal by animals can follow endo- or epizoochorous dispersal modes. Previous studies have reported endozoochory outweighing epizoochorous dispersal (Brochet et al., 2010; Costa et al., 2014), sometimes with transported seed numbers differing by orders of magnitude. A recent study by (Petersen and Bruun, 2019) showed that when gut, fur and hooves were sampled together from an individual animal, there were no significant differences in number of transported diaspores between the two main dispersal modes. Additionally, plant traits are expected to be associated with specific dispersal modes, making it interesting to compare the specific plant species transported by individual animals by

different dispersal modes. Here, we are interested in assessing the overlap (i.e. same plant species dispersed by different dispersal modes) and the complementarity (i.e. different plant species dispersed by different dispersal modes, with few overlaps) of plant species dispersed by red deer. Previous studies on complementarity of dispersal modes concentrated on differences in plant species composition transported by different dispersal modes (Benthien et al., 2016; Couvreur et al., 2005). While they considered taxonomic and functional overlaps between dispersed species, no study has compared specific dispersal modes at the level of the individual animal.

Diaspores with dispersal-enabling traits are more likely to be transported by animals and may influence the diaspore retention times and the consequent dispersal distance. These set of phenotypic modifications are referred to as 'dispersal syndromes' (Ronce and Clobert, 2012). Endozoochory is, by default, associated with fleshy fruits; and frugivorous animals like birds, primates, mustelids are more likely to disperse such diaspores (Corlett, 1998). However, this does not seem to be the case when considering other dispersal vectors such as water birds (Figuerola and Green, 2002) or ungulates (Albert et al., 2015a). For large herbivores, such as ungulates, smaller seeds with hard seed coats with the ability to withstand gut passage may also be dispersed endozoochorously (Traveset, 1998). This happens when the animal inadvertently ingests seeds while eating palatable foliage of the parent plant (Janzen 1984). On the other hand, epizoochory is associated with diaspores bearing modified appendages such as hooks or bristles that increase the likelihood of the diaspores remaining on the fur of the animal. However, a majority of diaspores without such adaptations are also transported epizoochorously by animals (e.g.

(Picard and Baltzinger, 2012), thus making the case for reconsideration of the 'morphological dispersal syndromes' paradigm, especially for predicting LDD potential.

Ungulate-mediated plant dispersal by both epi- and endozoochory at the same site has been studied for domestic species such as sheep ((Benthien et al., 2016; Schoenbaum et al., 2009); goat (Benthien et al., 2016); cattle (Chuong et al., 2016) and donkeys (Couvreur et al., 2005). Also, a few studies have been undertaken taking wild ungulates species into account - wild pig (Dovrat et al., 2012) and roe deer (Heinken et al., 2002; Heinken and Raudnitschka, 2002b; Picard et al., 2016; Picard and Baltzinger, 2012); bison (Eyheralde, 2015; Rosas et al., 2008) and red deer (Petersen and Bruun, 2019; Picard et al., 2016; Picard and Baltzinger, 2012). While they compare the dispersal modes by a single/multiple vectors at a site, the data collected for each dispersal mode comes from different individuals (except in the case of Petersen and Bruun, 2019), leaving room for potential bias in inferring the relative importance of the dispersal modes considered.

Red deer is one of the largest mammals in the temperate region with an unprecedented level of population increase in the recent years (ONCFS, 2018). Red deer can disperse seeds via different modes, namely gut, fur and hooves (Petersen and Bruun 2019), and can even regurgitate some of them (Delibes et al., 2019). It is an intermediate mixed feeder with short, straight hair (Baltzinger et al., 2019; Picard and Baltzinger, 2012) and thus consumes varied food resources staggered over time and space. They move from tens to thousands of meters each day in a varied and diverse set of habitats and can thus move seeds over long distances effectively. Moreover, specific behaviours of individual deer such as trampling, grooming, rubbing against barks of trees can all influence detachment of diaspores on the body of the animals into specific habitats. Recently,

Liehrmann et.al. (2018) reported a case of transfer-epizoochory, i.e., transfer of diaspores attached in the fur among conspecifics from red deer hinds.

In this study, we were mainly interested in looking at taxonomic and functional complementarity of plant species dispersed by red deer individuals by different dispersal modes. Specifically, we were interested in a) assessing the differences in species dispersed by endo-, fur-epi or hoof-epi zoochory within the dispersed species pool in a landscape and b) if dispersed plants of a particular mode show common set of dispersal enabling traits. We took advantage of the uniqueness of the dataset, containing information on total seed load (gut, fur and hooves) and plant species dispersed by all three dispersal modes (endo-, fur-epi and hoof-epi zoochory) for each individual red deer.

Petersen and Bruun (2019) compared compositional differences between dispersal modes and the probability of dispersal predicted by five traits (seed mass, release height, seed number per ramet, variance in seed shape, and landscape occupancy index). However, they did neither consider the individual deer level information in their approach nor take into account additional traits previously identified as important in enabling dispersal (Albert et al., 2015a).

Methods

Study area and field data collection

The study was carried out at four sites of different sizes in Denmark, of which Lille vildmose (3,993 ha) and Jægersborg Dyrehave (1,100 ha) were fenced reserves, while Oksbøl (2,745 ha) and Torbenfeldt (1,632 ha) were unfenced.

The sample size includes 57 individuals of red deer - 22 from Oksbøl; 21 from Lille vildmose; 4 from Torbenfeldt and 10 shot in Jægersborg Dyrehave. The samples were collected from individuals shot during hunting season of Sep.-Dec. 2015. All individuals were brushed with metal combs of two different sizes to get the diaspores from the fur. For hooves, the seeds were brushed along with mud and debris using toothbrushes. All seeds were identified using microscopes with the aid of regional flora and other published literature. For the seeds in the gut, faecal material was collected from the shot animals and planted in greenhouse trays. The faecal material was dried at 25°C for 10 days and then cold stratified for 6 weeks. The trays were kept in greenhouse with 15 hours of sunlight. The samples were monitored between Dec-Jun of 2015/16 and emerging seedlings were identified and removed (see Petersen and Bruun 2019, for more details).

To assess taxonomic complementarity, we compared the species composition of the dispersed plants by the dispersal modes. First, we compared the species richness of the dispersed plants by each of the dispersal modes by plotting species accumulation curves. For this, we used the number of seeds dispersed for each plant species by each individual deer. We used the function 'specaccum' from package vegan in R to calculate the species accumulation curves across all sites for- a) all dispersed species, b) species dispersed solely by (combined fur- and hoof-) epizoochory and c) species dispersed solely by endozoochory. Similarly, we compared the species accumulation curves between endozoochory and (combined fur- and hoof-) epizoochory for two sites- Oksbøl and Lille vildmose, which had more than 20 individual deer samples. The other two sites were excluded from this comparison due to low sample sizes. The individual deer (samples)

were added randomly while estimating the species accumulation curves for 200 permutations.

We assessed the differences in frequency of occurrence of seeds dispersed by endozoochory and (combined fur- and hoof-) epizoochory on the sampled animals with a χ^2 test. Due to the low sample sizes, we used the Monte-Carlo simulation to estimate p-values. Additionally, the difference in number of plant species dispersed by endozoochory and epizoochory was assessed with a Mann-Whitney test. All statistical analyses were carried out in R (R Core team 2019).

To analyse functional complementarity of the dispersal modes, we performed a Principal Component Analysis ('PCA') on morphological and ecological plant traits. The species-level traits information was taken from the published database of Albert et al. (2015a) and complemented with data from Picard et.al. (2016), LEDA and Bioflor databases for the remaining species. We used information on Ellenberg values for Light ("EV_L") and nitrophily ("EV_N") and general Plant Habitat of each species (Forest- "PH_F" and Open- "PH_O"; which we marked as simply present/absent i.e. 1/0, in lieu of the 0, 0.5, 1 scale used by Albert et al. 2015a). Seed level information included diaspore mass ("DM"), diaspore length ("DL") and diaspore width ("DW"). And finally, we included information on presence/absence of diaspore appendage and appendage type (hooked / elongated / flat / balloon). For the traits-level information, we used only those species that were definitely identified up to species level, and thus used a subset of 60 species (from a total of 71 dispersed species) to build the PCA.

We compared traits between 1) exclusively epizoochorously dispersed species 2) exclusively endozoochorously dispersed species, and 3) species dispersed by both endo-

and (combined fur- and hoof-) epi zoochory. Kruskal-Wallis and multiple comparison tests were used to compare continuous and ordinal variables and Pearson's χ^2 tests for the categorical ones.

Results

Taxonomic complementarity

Overall, the observations include a total of 958 seeds from 33 plant species dispersed by 41 individual red deer through endozoochory (with 16 instances of no data); 3883 seeds from 36 plant species and 47 individuals by fur-epizoochory (with 10 instances of no data); and 733 seeds from 35 plant species and 45 individuals by hoof-epizoochory (with 12 instances of no data) (Fig.5.1).

A comparison of the two main dispersal modes indicates that endozoochory is more frequent in occurrence than (fur- and hoof-) epizoochory for the seeds collected from individual animals ($\chi^2(1)= 4.69$, $p=0.03$). However, when comparing each fur- and hoof-epizoochory separately (Fig.5.2), differences vanished between the modes (endo vs. hoof-epi $\chi^2(1)=3.62$, $p=0.07$; endo vs. fur-epi $\chi^2(1)=0.85$, $p=0.47$; fur-epi vs. hoof-epi $\chi^2(1)=2.62$, $p=0.19$).

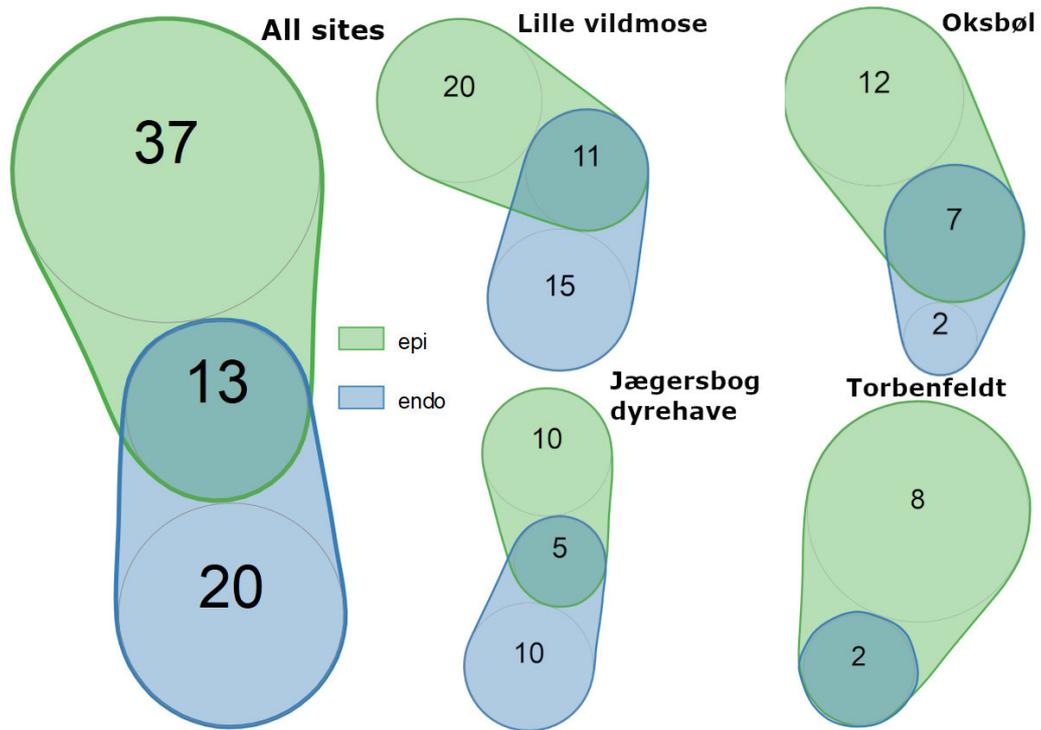


Figure 5.1 Venn diagram showing overlap in number of dispersed plant species for the four study sites. 'epi' represents plants dispersed via (combined) fur- and hoof- epizoochory, 'endo' represents plants dispersed via gut of the deer.

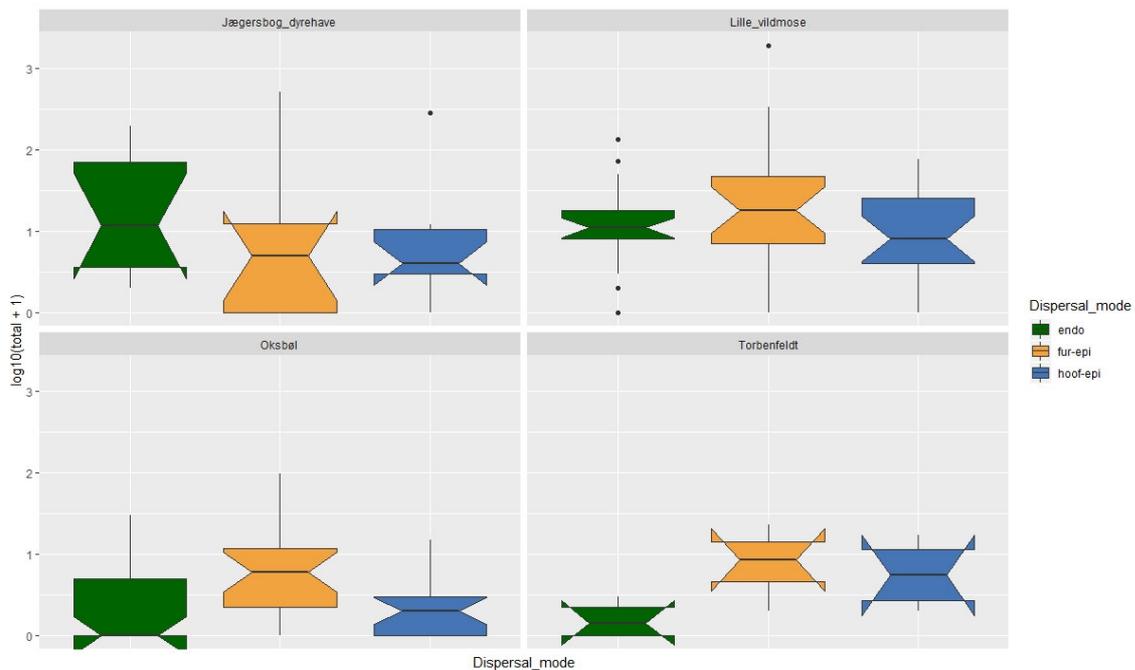


Figure 5.2: Site-wise boxplots showing the number of diaspores measure by each dispersal mode

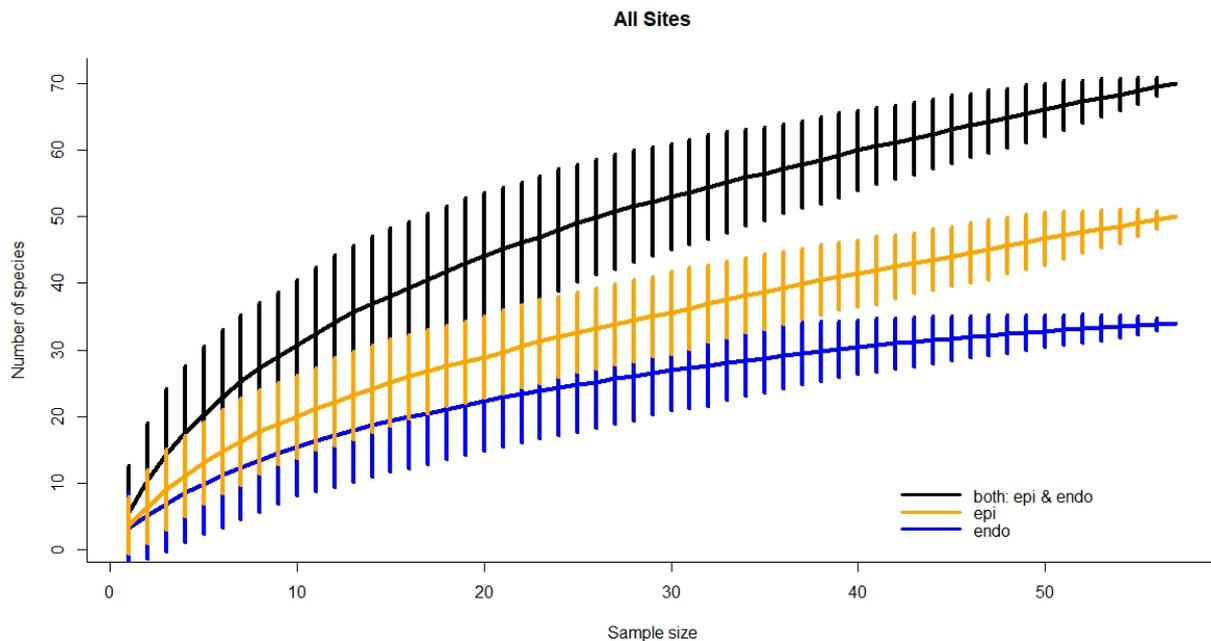


Figure 5.3: Species accumulation curve for all study sites combined. 'epi' represents species that are dispersed by fur or hooves, 'endo' represents species that are dispersed via gut and 'both' represents endo as well as (combined hoof- and fur-) epizoochory.

Similarly, comparing the overall number of plant species dispersed by each of the dispersal modes, we found none of modes to be significantly different from each other (Mann Whitney test: endo vs. hoof-epi $W=2380$, $p=0.74$; endo vs. fur-epi $W=2345$, $p=0.61$; fur-epi vs. hoof-epi $W=2485$, $p=0.87$). However, when combining fur- and hoof-epizoochory into a single category for epizoochory, the difference with endozoochory becomes significant (Fig.5.3, Mann Whitney test: $W=1855$, $p=0.004$). Comparing site-specific species composition of dispersed plants, the two sites had more species dispersed by (combined fur- and hoof-) epi- than endozoochory (Fig.5.4a, Fig. 5.4b). However, the fenced 'Lille vildmose' site had a higher species richness than the unfenced Oksbøl.

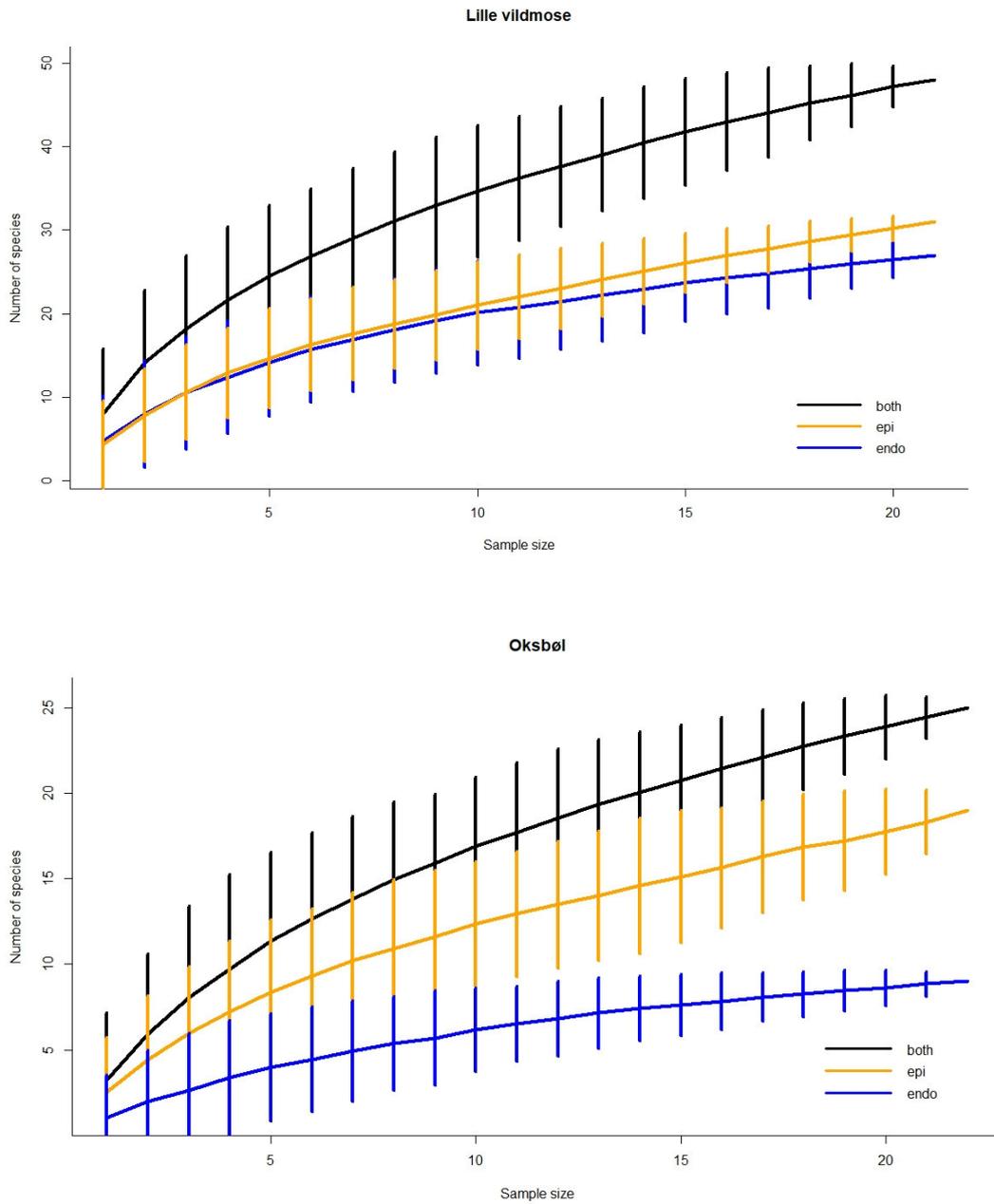


Figure 5.4: Species accumulation curves of dispersed species for a) Lille vildmose and b) Oksbøl ('epi'=plants dispersed by fur and hoof epizoochory; 'endo'= plants dispersed by gut; both= plants dispersed by both epi and endo modes)

Functional complementarity

The first two dimensions of the PCA (Fig.5.5) explain 46% of the variance (27% and 19%). The first axis was positively correlated with diaspore mass (loading: 0.37), presence of elongated appendage (0.36) and diaspore length (0.32). The second axis was positively correlated with presence of balloon structures (0.53), presence of elongated appendage (0.42) and Ellenberg-Light values (0.32).

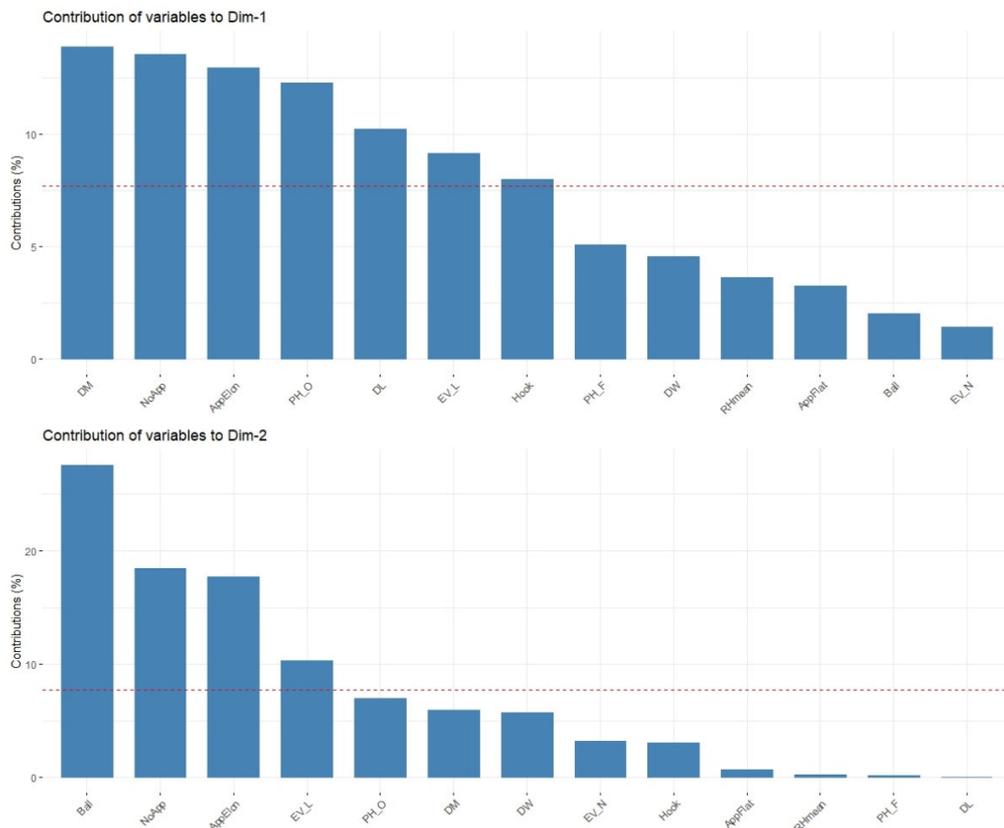


Figure 5.6: Barplot of contribution of plant traits to the first two axis of the PCA. (DM=diaspore mass; NoApp=no appendage; AppElong=elongated appendage; Hook=hooked appendage; Ball=Ballon-like appendage; Flat= flat appendages; DL=diaspore length; DW=diaspore width; RHmean=mean diaspore release height; EV-L/EV-N=Ellenberg values for light and nitrophily; PH_O/PH_F= open or forest plant habitat

Overall, based on absolute values of factor loadings of the PCA, the three most important variables on the first axis are by decreasing order, diaspore mass > diaspores with no appendages > diaspores with elongated appendage, whereas on the second axis the three most important variables are- diaspores with balloon-shaped appendage > diaspores with no appendage > diaspores with elongated appendage (Fig. 5.6).

Ellenberg-Nitrophily has a significant association with dispersal mode (Table 5.1a). In addition, presence of elongated appendage is significantly associated with the dispersal mode (Table 5.1b).

Discussion

We found no significant difference in the number of diaspores dispersed by both endo and (combined fur- and hoof-) epizoochory (Fig.5.2). However, the species composition of the dispersed plants is different between the dispersal modes (Fig.5.3), with some overlaps. This is an indication for the complementary nature of the dispersal modes. Comparing the site-level species accumulation plots between two out of the four studied sites that had more than 20 individuals sampled, we find that the number of plant species dispersed by endo and (combined fur- and hoof-) epizoochory is higher in the fenced reserve (Lille vildmose) compared to the unfenced (Oksbøl) one (Fig.5.4a, Fig.5.4b).

Additionally, when comparing diaspores retrieved from individual animals, simultaneously for all dispersal modes, we found no difference in the number of seeds carried by the three modes (endo-, fur-epi and hoof-epi). This differs from previous findings generally showing that endozoochory largely outweighs epizoochory with respect to both numbers and species of diaspores transported by animals (Couvreux et.al., 2005; Dovrat et.al., 2012).

Table 5.1: Overview of plant traits associated with dispersal mode(s). ‘both’ represents plants dispersed by both (combined fur- and hoof-) epi- and endo-zoochory; ‘endo’ represents plants dispersed only by endozoochory; ‘epi’ represents species dispersed only by (combined fur- and hoof-) epizoochory.

a) Kruskal Wallis tests (with dunn tests for multiple comparisons)

	kW	both vs. endo	endo vs. epi	both vs. epi
Ellenberg-Light (EV_L)	2.66 <i>ns</i>	1.55 (0.06)	-1.17 (0.12)	0.65 (0.26)
Ellenberg-Nitrophily (EV_N)	11.38*	-3.11 (0.0009)*	2.61 (0.0046)*	-1.08 (0.14)
Release height (RHmean)	2.95 <i>ns</i>	1.62 (0.052)	-1.26 (0.10)	0.64 (0.26)
Diaspore length (DL)	0.79 <i>ns</i>	0.23 (0.39)	-0.88 (0.19)	-0.45 (0.32)
Diaspore width (DW)	2.18 <i>ns</i>	-1.03 (0.15)	-0.45 (0.32)	-1.47 (0.07)
Diaspore mass (DM)	1.17 <i>ns</i>	-0.46 (0.32)	-0.65 (0.26)	-1.04 (0.15)

b) Pearson’s χ^2 tests

	χ^2	both	endo	epi
Open habitat	1.90 <i>ns</i>	1.2	-1.0	-0.2
Forest habitat	3.01 <i>ns</i>	-1.8	-8.0	-5.2
Diaspore appendage: no appendage	3.41 <i>ns</i>	-5.8	-7.0	-17.2
Diaspore appendage: balloon	5.02 <i>ns</i>	0.6	-4.0	3.4
Diaspore appendage: flat	3.05 <i>ns</i>	-0.6	-1.67	2.27
Diaspore appendage: elongated	4.96*	-0.8	-3.33	4.13
Diaspore appendage: hooked	(0.814) ⁺⁺			

- *significant at $p \leq 0.05$; *ns*= non-significant
- ++ p-value from Fisher’s exact test due to low sample sizes
- Kruskal Wallis test: kW= group average; pairs of dispersal modes in column with Z-scores from dunn test and associated p-values
- Pearson’s χ^2 test: χ^2 values when category is “present” ; numbers under dispersal mode columns are the difference between observed and expected χ^2 values (Couvreur et al., 2005), positive values indicate more than expected presence of the trait in the group, negative indicates the opposite.

However, for endozoochory, the seeds found in samples can be restricted by what is present in the gut of the animal at the time of capture and may actually be a subset of the total plant species dispersed by the animal. Similarly, the seed retention time in the fur of the animal is strongly related to the features of the animals such as fur-type and shoulder height (Picard and Baltzinger 2012, Albert et.al., 2015), and some of the seeds may already be shed before or during the hunt and capture.

Additionally, hoof-epizoochory is less specific i.e., the probability of seed attachment is more often based on chance, than the other two dispersal modes, and therefore it is nearly impossible to completely determine the entire seed community transported by this mechanism. In short, it is highly likely that the number of plant species transported by each different dispersal mode is underestimated and recorded plant species by each of the dispersal modes is also likely to be sensitive to the time of sampling (also if we refer dispersal mode, we did not find the same result. This is possible due to the overgeneralization of plant habitat type we used - open vs. forest species, including those that occur in both habitats simultaneously. Conversely, to differential seed shedding period of the different plants).

The dispersed species data are dominated by grasses. Previous studies on ungulate-mediated dispersal have also found low numbers of trees and shrubs among zoochorously dispersed plants. This can be attributed to specific foraging behavior of red deer that prefer feeding in open areas on highly palatable grasses and other forbs in the herbaceous layer. One particular plant species, *Juncus effusus* was present in large quantities across all dispersal modes in the dataset. While the species has no obvious modifications on diaspores for transport by animals, the staggeringly high numbers could

be explained by several factors such as – high abundance in study area (Petersen and Bruun 2019), high fecundity of species (Schurr et.al., 2008) with small round seeds; palatable foliage that attracts animals towards the plant (Janzen 1984), as well as presence of mucilage on diaspores that stick to animal body parts. In turn, seeds are dispersed by various modes based on the interaction between plant and individual animal.

While Petersen and Bruun (2019) reported habitat of plant species as an important association with while they did not find diaspores with appendage as a significant trait related to dispersal, we find diaspores with elongated appendage to be positively associated with epizoochory (Table 1b, Fig.6). Our finding is in agreement with previous studies associating diaspores with potential attachment-enabling appendages with transportation by animals over longer distances (Albert et.al., 2015). However, the presence of appendages alone is not the only important factor in explaining seed dispersal modes.

Ellenberg-Nitrophily values show a strong association with dispersed plant species between epi- and endozoochory. Nitrophily values could be an important association for ungulate-mediated plant dispersal as these animals could come into contact with the plants while searching and foraging on plants with high nutritious value (“foliage is the fruit hypothesis”, Janzen 1984). Surprisingly, diaspore release height did not show a significant association with dispersal mode in our results (Albert et al., 2015b). This could partially be due to the high prevalence of ruderals and grassland species recorded in the dataset.

The results from the PCA indicate a cluster of species that are associated with diaspores that lack appendages. This cluster includes more species dispersed by endozoochory

than by epizoochory (Fig. 5.5). Previously, (Pakeman et al., 2002) have suggested that plant species dispersed by ungulates via endozoochory could be found in diaspores lacking modified appendages. Couvreur et.al. (2005) suggested that edibility of plant species is an important enhancer of both epi- and endozoochorous dispersal modes.

The probability of a diaspore getting dispersed depends strongly on behavior and habitat preferences of the animal. The retention time of the diaspores, both internal and external, are influenced by specific behaviours such as selective feeding on certain species, grooming behavior, interaction with co-occurring neighbouring plants (Shukla et al. submitted). Red deer are large bodied, intermediate mixed feeder with strong habitat preferences within its range. A recent review by Baltzinger et al. (2019) found intermediate mixed feeding species (e.g. red deer and goat) to disperse the least number of plant species compared to other concentrate eater (roe deer), grass/roughage eaters (bison, sheep, cattle) and omnivores (wild pig). Intermediate mixed feeders disperse the least proportion of similar species by endo- and fur-epizoochory compared to other feeding regime groups. They are thus, more likely to be complementary with respect to dispersed plant species.

Red deer populations are reaching unprecedented levels in temperate forests of Europe. As large herbivores within the guild of ungulates in these landscapes (e.g. (Jaroszewicz et al., 2013), red deer populations manage plant community composition in the ecosystems. This study shows when taken into account together, that there are no real differences between the dispersal modes in terms of numbers of plant species and diaspores conveyed. However, the species composition between dispersal modes varies. The number of diaspores dispersed by an individual animal is an important component in

determining its effectiveness as a disperser (Schupp et al., 2010). The findings from this study underline the importance of comparing individual-level data and indicate the need to reassess the effectiveness of red deer as a seed disperser in temperate ecosystems.

CHAPTER 6

Ungulates as dispersal vectors of non-native plants

Résumé (version française)

Les ongulés sont répandus à travers le monde avec 257 espèces inventoriées, incluant les espèces domestiques. Ils couvrent différents gradients fonctionnels, en terme de régime alimentaire, de stratégie digestive, de taille et masse corporelle, de caractéristiques du pelage ou de socialité. Toutes ces caractéristiques peuvent intervenir dans les différentes phases de la zoochorie. Les ongulés déplacent les diaspores de plantes natives et exotiques, par endo- et épizoochorie. Initialement introduites par les activités humaines, les plantes exotiques portant des traits spécifiques peuvent être dispersées sur de longues distances et dans de nouveaux environnements par les ongulés. Ces vecteurs peuvent aussi libérer des ressources nécessaires à la germination et à la croissance ultérieure des graines dispersées. Nous avons d'abord étudié l'évolution des traits à l'échelle des communautés végétales en présence de différentes espèces d'ongulés sauvages et sur différents pas de temps.

Nous avons aussi réalisé une revue systématique de littérature pour identifier les plantes exotiques dispersées par endozoochorie, régurgitation et épizoochorie. Nous avons ainsi réalisé une évaluation globale par zone biogéographique et mode de dispersion des plantes exotiques dispersées en nous intéressant au type de croissance des plantes et

au vecteur impliqué. Nos résultats concernent 4 familles d'ongulés: Cervidae, Bovidae, Suidae et Equidae. Pour chaque famille, nous présentons nos résultats soit par espèce d'ongulés (e.g. *Odocoileus virginianus*, *Bison bison*, *Bos taurus*) ou par groupe d'espèces. En cohérence avec leur régime alimentaire, les ongulés pousseurs dispersent essentiellement herbacées et graminées, alors que les omnivores dispersent d'autres types de plantes (i.e. cactus, lianes, arbustes et arbres). De nombreuses plantes exotiques sont dispersées par les ongulés, mais seulement 12% des espèces d'ongulés ont été étudiées jusqu'à présent, suggérant que leur contribution à la dispersion des plantes exotiques est probablement sous-estimée.

Keywords: plant functional traits, invasives, exotic plants, Cervidae, Bovidae, Suidae, Equidae

Abstract

Ungulates are present worldwide with 257 recorded species, including livestock. They cover different functional gradients, be it feeding regime, digestive strategy, body size, body mass, fur characteristics or sociality. All these specificities may intervene at different stages of animal-mediated plant dispersal. Ungulates move diaspores from both native and non-native plants, through endo- and epizoochory. Initially introduced by humans, non-native plants bearing specific traits can be carried over long distances and to new environments by ungulates. These vectors can further free local resources necessary for the germination and the subsequent growth of the released diaspores. We first looked at trait-based plant community changes at different time scales in the presence of different native ungulates. We then reviewed the literature on endozoochory, regurgitation and fur-epizoochory assisted by ungulates, focusing on the dispersal of non-native plants. We made an overall assessment of ungulate-mediated non-native plant dispersal by biogeographical zone and dispersal mode, and then provided additional information on plant growth form and taxonomy, vectors and associated modes of dispersal. Results are presented for four main ungulate families: Cervidae, Bovidae, Suidae and Equidae. For each family, we highlighted our findings either by ungulate if sufficiently represented (e.g. *Odocoileus virginianus*, *Bison bison*, *Bos taurus*) or by group of species. According to their feeding regime, grazers dispersed solely forbs and graminoids whereas omnivores also dispersed plants from other growth forms (i.e. cactus, vine, shrub and tree). Numerous non-native plants are dispersed by ungulates around the world, but this is

probably the visible part of the iceberg, as only 32 ungulates (i.e. 12%) have been studied as vectors so far, suggesting their overall contribution is certainly underrated.

Introduction (of non-native plants)

"It is both interesting and troubling to note that not only do feral pigs [...] create disturbed sites where non indigenous plants can establish, but they both further enhance the naturalization process by dispersing seeds to the site they disturb" (Schifmann, 1997).

Non-native invasive plants displace and replace local, native plants, being one of the main causes of biodiversity erosion. Plant invasions generally occur in two phases. The first includes the introduction of the non-native species, through a long-distance dispersal event, often facilitated or associated with anthropic activities. The second phase involves its naturalisation and expansion. Non-native plants can expand their ranges in recipient ecosystems, resulting in different patterns of spread (Hui and Richardson, 2017). One of the reasons why non-native plants are generally successful in invading recipient ecosystems concerns the Enemy Release Hypothesis (Keane and Crawley, 2002). Ecosystems are enemy-free for non-native newcomers, providing them a competitive advantage over local species. Numerous vectors can drive introduction, naturalization and expansion of non-natives.

Plants can benefit from ungulates for dispersal distance, seed germination (deinhibition, scarification and fertilization effect through endozoochory) and establishment (see Chapter 5, this volume). For instance, by its toxicity at certain development stages (seeds and first leaves), common cocklebur (*Xanthium strumarium*; Botha *et al.*, 2014) escapes

ungulate herbivory and gains competitive advantage over more palatable plants, consumed by large herbivores.

Some native ungulates, contrary to other large mammals, are relatively abundant (Russell *et al.*, 2001). They generally have highly diverse plant-based diets, meaning that they regularly interact with plants during feeding bouts, and can thus consume diaspores that they release remotely. They generally cover long distances, from hectometres to kilometres, on a regular basis within their home ranges (Pellerin *et al.*, 2016). Historically, domestic ungulates also dispersed plants over exceptional distances via ancient transhumance routes (Manzano and Malo, 2006).

Interactions between ungulates and plants fit in the general framework of ecosystem engineering effects (Wilby *et al.*, 2001). They include transport (seed dispersal), physical and chemical engineering processes affecting soil properties and germination of seeds present on the ground or in the soil seed bank. This framework also includes trophic interactions that modulate the spatial distribution of plants, plant community composition and other taxonomic groups (insects, birds) by cascading effects. Ungulates are dominant interacting agents and their management is of great interest for plant community dynamics and ecosystem functioning.

Ungulates are involved in diverse internal and external plant dispersal mechanisms that include primary mechanisms: endozoochory, regurgitation and fur-epizoochory; and several secondary dispersal mechanisms: hoof-epizoochory, transfer-epizoochory (Liehrmann *et al.*, 2018) and seed dispersal by dung beetles. Each of these mechanisms or pathways (Liddle and Elgar, 1984) differentially affect the fate of the conveyed diaspores (Baltzinger *et al.*, 2019).

In a recent review, Albert *et al.* (2015a) showed that ungulate-mediated seed dispersal was a generalist ecological process, affecting an important part of the accessible flora (~44%) dispersed by temperate ungulates. Different ungulates dispersed the same plants by similar or diverse dispersal mechanisms. However, they also showed that different mechanisms of ungulate-mediated dispersal relied on the interplay between plants/diaspores and dispersal vector traits (diaspore releasing height and ungulate body size for fur-epizoochory, or diaspore morphology and ungulate feeding guild for endozoochory; Albert *et al.*, 2015b).

The high taxonomic (257 species, Baltzinger *et al.*, 2019) and functional diversity of native, introduced and domestic ungulates along with the diversity of plant dispersal mechanisms determine the characteristics, diversity and abundance of plants dispersed (Fig. 6.1). Fur characteristics, body size, and use of open versus forested areas are main predictors in fur-epizoochory. For transfer-epizoochory, the more frequent the degree of social interactions, the higher the probability of transfer from one individual to another. Endozoochory is more a matter of feeding regime, digestive strategy and animal body mass. Seed regurgitation by ruminants concerns mostly fleshy-fruited plants, and seeds too large to pass through the orifice between the rumen and the omasum. Ungulates, on a world scale, contribute to the dispersal, range expansion and success of non-native plants.

Spatio-temporal changes in plant communities and characteristics of winner species

Once introduced, plants can spread at different spatial scales depending on the time scale considered. This expansion is linked to dispersal events. The use of retrospective approaches (Wang and Smith, 2002) helps infer the underlying ecological processes that explain current plant distribution patterns compared with their historical distributions. Longitudinal approaches are based on long-term vegetation resurveys of permanent plots (Boulanger *et al.*, 2011; Box 1). They allow the assessment of changes in plant abundance, occurrence and spatial expansion. Coupled with censuses of ungulate abundance (hunting bags, browsing indices) or with erection of fences excluding ungulates, they can provide indirect evidence of the role ungulates play in the observed plant community changes. To date, there are relatively few studies linking plant distribution patterns to ungulate-mediated long distance dispersal events (Vickery *et al.*, 1986).

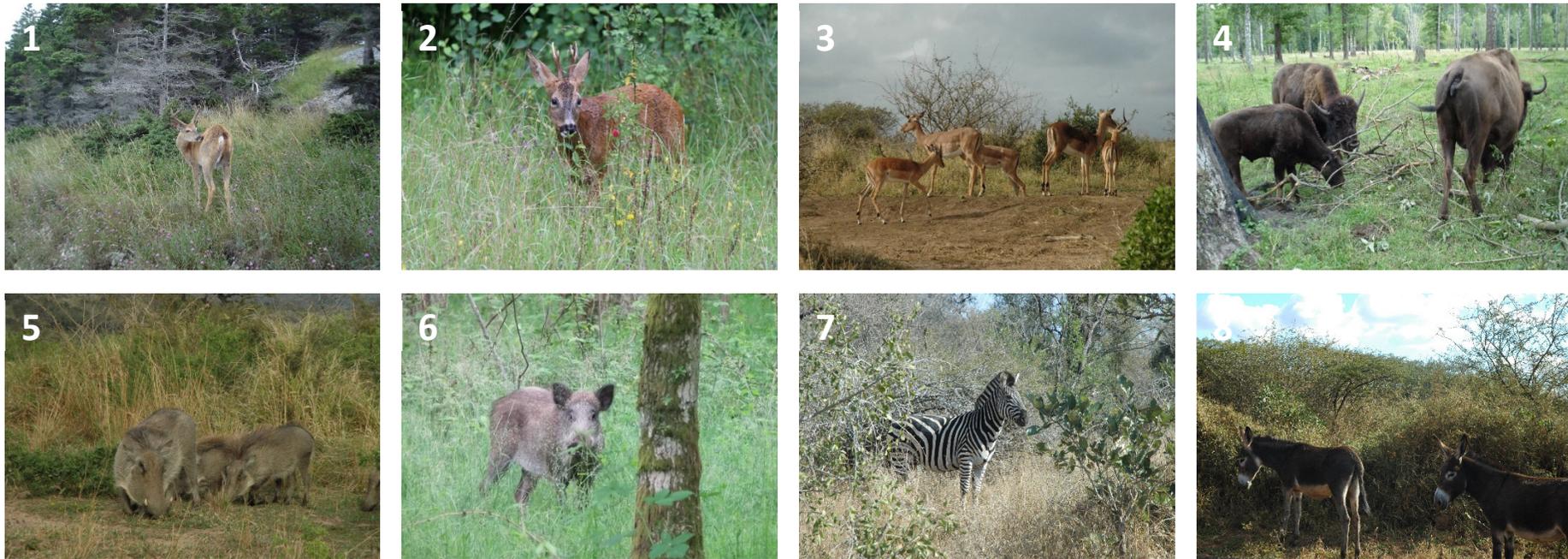


Figure 6.1: Ungulate seed dispersers e.g. Cervidae (1) white-tailed deer, *Odocoileus virginianus* (Anticosti Island, Canada) (2) roe deer, *Capreolus capreolus* (Sologne, France); Bovidae (3) impala, *Aepyceros melampus* (Hluhluwe-iMfolozi Park, South Africa) (4) European bison, *Bison bonasus* (Prioksko-Terrasny Nature Reserve, Russia); Suidae (5) warthog, *Phacochoerus africanus* (Hluhluwe-iMfolozi Park, South Africa) (6) wild pig, *Sus scrofa* (Sologne, France); Equidae (7) Plain zebra, *Equus quagga* (Kruger National Park, South Africa) (8) donkey, *Equus asinus* (Mkhuze, South Africa). Pictures by Christophe Baltzinger.

The spatial scale of these community changes is partly dependent on initial interplot distances and is not necessarily optimal to highlight animal-mediated dispersal events. Longitudinal approaches have been used to detect winners and losers (McKinney and Lockwood, 1999), identify their associated attributes and the potential causes of the observed changes. Winners are species that increase in abundance, and expand their spatial distribution. They generally share specific traits, including small size, high fecundity, rapid dispersal, being generalist species, although, this is not always the case (Box 1, hound's tongue *Cynoglossum germanicum*, a rare and specialist plant species). A contrary set of traits characterizes loser species. In agreement with McKinney and Lockwood (1999), we thus expect specialist plants with a restricted ecological niche to be more sensitive to habitat changes than more widespread ubiquitous plants that should cope better with various environmental conditions.

Temporal windows chosen to track modifications in plant communities allow us to assess the speed of changes and generally cover decades (10-yr and 30-yr in Boulanger *et al.*, 2011, 2018; 50-yr in Vidl *et al.*, 2017). These authors undertook studies to infer the potential role of varying deer population abundance in shaping plant communities.

Following a 10-yr period, using a network of 82 pairs of fenced and unfenced plots covering all major forest types at the French national scale, Boulanger *et al.* (2018) demonstrated an increase in ruderal and epizoochorous plants in the presence of red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and wild pig (*Sus scrofa*), at intermediate densities. However, no non-native plants were detected as winners.

Box1. Hound's tongue (*Cynoglossum* sp., Boraginaceae), plants advantaged in the presence of ungulates



Fig1. Box1 *Cynoglossum officinale*, Domaine National de Chambord, France, June 2017 (© C. Baltzinger). *Cynoglossum* sp. are **epizoochorous** plants, locally both rare (*C. germanicum* in France) and invasive (*C. officinale* in British Columbia; De Clerck-Floate, 1997). For instance, *C. virginianum*, is a native plant in Virginia (USA) known to be dispersed by white-tailed deer (Shen *et al.*, 2016). Couvreur *et al.* (2004) showed that donkeys dispersed *C. officinale* within a network of nature reserves connected by grazing domestic ungulates. *Cynoglossum* sp. all share common attributes favouring their expansion in the presence of biotic dispersal vectors, they bear glochids on their seeds that cling to animal fur. Seeds from *C. creticum* can remain a long time in animal fur (60% of remaining seeds on sheep and 10% on goat after 48 hours; Shmida and Ellner, 1983). However, Whigham *et al.* (1993) mentioned that most of the seeds remain attached to the plant and disperse at a maximum distance matching the plant height. These plants are also unpalatable to deer, known as highly **toxic** to cattle and horses because of their high content of pyrrolizidine alkaloids, which are hepatotoxins (De Jong *et al.*, 1990). Moreover, seedling germination and seedling establishment of *C. officinale* is favoured on **disturbed sites** (De Jong *et al.*, 1990); specifically *C. germanicum* individuals frequently occur on deer bed sites below oak trees. These plant traits (epizoochorous, toxic and ruderal) led to the amazing range expansion of *C. germanicum* in the 88 km² Arc-en-Barrois forest in France, within a 30-yr time (Boulanger *et al.*, 2011).

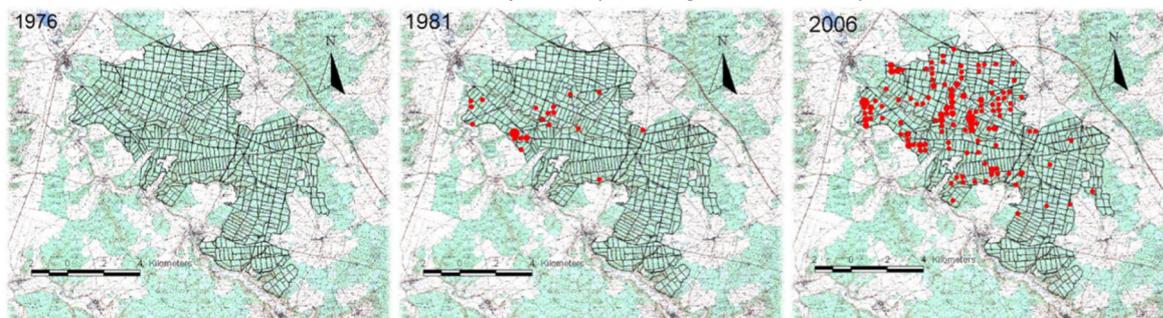


Fig2. Box1 *Cynoglossum germanicum* spatial distribution patterns in 1976, 1981 and 2006, based on the long-term monitoring of permanent plots, one plot every 10 ha on a square grid. A red circle indicates the presence of the species, its size varies with its local abundance. The plant was absent from the plot network, when the monitoring began in 1976 (Boulanger *et al.*, 2011). (Fig2aBox1 - map_cyno_1976; Fig2bBox1map_cyno_1981, Fig2cBox1map_cyno_2006)

C. germanicum had been probably introduced with exogenous soil during forest plantation sometime between 1976 and 1981. The presence of the *C. germanicum* was further significantly associated with a deer frequentation index. These plant characteristics are typical of what would define an invasive species (Vavra *et al.*, 2007) in the presence of deer. A rough assessment of the yearly dispersal distance fitting the distribution pattern of *C. germanicum* in 2006, averages 360m.yr⁻¹. Highlighting such changes in plant spatio-temporal distribution patterns rely on the long-term monitoring of permanent plots (see **section 2**).

Following a 30-yr period, Boulanger *et al.* (2011) showed the expansion of *Cynoglossum germanicum* (Box 1), a rare plant species, epizoochorous, toxic and dependent on soil disturbance for germination and establishment. Other plants also increased their frequency over this time period, lots of them being epizoochorous (graminoids *Brachypodium sylvaticum*, *Bromus benekenii*, *Carex sylvatica*, *Hordelymus europaeus* and forbs *Galium odoratum*, *Geum urbanum*, *Stachys sylvatica*). Of 169 native plants censused, we recorded 57 winners, 27 losers, and the remnants showed no change. Moreover, the temporal changes observed in plant communities depended on a reduction in deer herbivory (Boulanger, 2010).

Two studies, in the Czech Republic (Vild *et al.*, 2017) and in the USA (Wiegmann and Waller, 2006) looked at changes in vegetation community over a 50-yr period. Vild *et al.* (2017) showed an increase in ruderal, nitrophilous and light-demanding species. Among the winners, they highlighted four non-native plants, three endozoochorous and hemerochorous forbs (*Amaranthus retroflexus*, *Conyza canadensis*, *Solanum nigrum*). Nevertheless, contrary to short-term studies, there was a reduction in epizoochorous plants while ruderal and early successional plants benefitted. Wiegmann and Waller (2006) identified five non-native plants: 3 forbs (*Galeopsis tetrahit*, *Hieracium aurianticum*, *Veronica officinalis*) and 2 graminoids (*Poa nemoralis*, *Poa pratensis*) among the 21 winners (~25% non-native species). These non-native plants, present at the start of the monitoring, expanded over the 50 years. Authors suggested that white-tailed deer (*Odocoileus virginianus*) was probably a major driver of the changes observed over the 50 years as most winners were either browsing resistant or tolerant in comparison with the more sensitive to deer loser species. Shen *et al.* (2016) also concluded « chronic high

deer density facilitated increased abundances of several non-native invasive plants » that were browse tolerant. Similarly, Knight *et al.* (2009) demonstrated that two highly invasive plants (*Alliaria petiolata* and *Microstegium vimineum*) were favoured in the presence of white-tailed deer (see also examples in Chapter 5, this volume). However, although often winners, non-native plants do not explain the main changes observed in plant communities.

Fluctuating resources in plant communities and ungulate-mediated non-native plant dispersal

The way ungulates locally modulate the abundance and spatial heterogeneity of resources explains how they can shape plant assemblages. The regional plant species pool is sieved into local plant communities (Lortie *et al.*, 2004) via four major ecological filters namely *i*) the ability of the plant to reach a new environment (dispersal phase), *ii*) the environmental filter (tolerance to local abiotic conditions), *iii*) plant-plant interactions and *iv*) other biotic interactions. Davis *et al.* (2000) proposed a theory of invasibility based on the fluctuations of resources in plant communities, which offers a general framework to integrate different ungulate-mediated ecological processes within ecosystems. This theory also provides a convincing framework of how ungulates might favour non-native plant invasion.

Invasion of plant communities by newcomers depends on three main elements: the **diaspore arrival**, the **characteristics of the novel individual** and the susceptibility of the local environment to be colonised by this novel individual. This last element relies on the **transient release or addition of local resources** for the establishment and growth of the novel individual. Olf and Ritchie (1998) proposed such an outline to describe the

effects of herbivores in grasslands. Additionally, this invasibility scheme is generic and applies to any arriving individual, whether a native coloniser or a non-native invader.

For Davis *et al.* (2000), the novel environment is never at equilibrium, subject to regular fluctuations in resource availability, and thus hosts transient communities. A plant community is therefore prone to invasion anytime resources are released or added (light, nutrients, water or even physical space). The susceptibility of local environments to be colonised fluctuates with time, matching windows of opportunities (Myster, 1993), and should be highest immediately after resource release, especially because resident vegetation requires time to use resources efficiently. Resources become available following various events, whether the temporary reduction in resource uptake by the resident vegetation, the addition of external resources, or a combination of both (see Fig. 1 in Davis *et al.*, 2000). Introducing grazers is recognised as one favourable situation increasing opportunities for newcomers to colonise (Rico *et al.*, 2014). In a meta-analysis on seed addition experiments, Myers and Harms (2009) showed that the addition of similar number of different diaspores of various sizes increased local species richness and that this effect was even stronger in previously disturbed sites.

Diaspore arrival

The capacity for diaspores to be dispersed is a critical step in biological invasions (Pyšek and Richardson, 2010). Wild ungulates can convey diaspores over long distances through different dispersal mechanisms (see examples in Chapter 5, this volume). Through endozoochory, diaspores can be clumped into faeces, with diverse and numerous diaspores, whereas they may be more isolated, assumed less diverse and without faecal matrix through regurgitation or fur-epizoochory (Baltzinger *et al.*, 2019). Diaspore arrival

mediated by ungulates is considered directed dispersal (Wenny, 2001). Ungulates are selective herbivores, searching for preferred food items. Picard *et al.* (2016) found that plants dispersed by endozoochory came from open habitats where dispersal vectors used to feed. Ungulates generally display high within home range spatial fidelity (red and roe deer; Richard *et al.*, 2014), regularly using the same paths or core areas. Regurgitation often occurs at ruminating sites (cleaned bed sites) where diaspores are released (Delibes *et al.*, 2019). Hoof-epizoochory can be an advantage to colonise novel environments as diaspores are released in specific microhabitats (scraped ground, or within hoof prints).

Characteristics of dispersed diaspores

Characteristics of diaspores conveyed by ungulates also depend upon the dispersal mechanisms (Albert *et al.*, 2015a; see Chapter 5, this volume). In their review, they compared ten characteristics between dispersed and non-dispersed plants. They first showed that five characteristics were common to endozoochory, fur-epizoochory and hoof-epizoochory: ungulates preferentially dispersed nitrophilous plants, with persistent seed bank, from open habitats, bearing elongated diaspores or dry fruits. In contrast with regurgitation, which concerned plants bearing fleshy fruits with large seeds (Delibes *et al.*, 2019).

In comparison with endozoochory, epizoochory (fur- and hoof-) was more likely for diaspores released relatively high in the vegetation. More specifically, fur-epizoochory advantaged diaspores with a hooked or an elongated appendage, whereas hoof-epizoochory targeted relatively light diaspores without hooked appendages. Zoochory is an interactive process, which depends on specific interactions between the ungulate

vector and the dispersed plant and diaspore traits (Albert *et al.*, 2015b). Plant trait selectivity through ungulate-mediated dispersal was stronger for epizoochory (fur- then hoof-) than for endozoochory (Albert *et al.*, 2015a).

Box2. Pathways in diaspore dispersal for the epizoochorous common cocklebur (*Xanthium strumarium*, Asteraceae)



Fig1box2. *Xanthium strumarium*, banks of the Loire river, Gien, France, 8 September 2019 (©C.Baltzinger). Common cocklebur *Xanthium strumarium* is an alien invasive species in Europe, largely distributed along the banks of rivers like the Loire (France, **fig1box2**). It produces large amounts of large hooked diaspores (see Fig.1 in Liddle and Elgar, 1984), with adaptations for epizoochorous transport. They usually bear more than 50 hooks and release their diaspores high above ground (~0.75 m). Liehrmann *et al.* (2018) assessed the external retention time of these diaspores in relation to the fur characteristics of different social ungulate vectors (red deer, dwarf goat and donkey), their intraspecific interactions and individual grooming behaviour.

Cocklebur diaspores can be dispersed through multiple pathways (see Fig.6 in Liddle and Elgar, 1984): barochory, hydrochory (e.g. flooding events) and fur-epizoochory (in the mane and tail of horses, or any body part of sheep). They can also be released as a catapult from the long plant stalk (diaspore releasing height). Water can also move diaspores secondarily when burrs lay on the ground.

Hydrochory can move diaspores downstream for long distances, whereas ungulate-mediated dispersal can potentially transport diaspores in any direction (including upstream). Liehrmann *et al.* (2018) experimentally

showed that a red deer hind released a burr nearly 3 km from its attachment site. Liddle and Elgar (1984) showed that burrs remained in the fur of different domestic ungulates (cattle, sheep and horses), and diaspore retention functions fitted generated fat-tailed distributions, and potential long-distance dispersal (Liehrmann *et al.*, 2018).

This plant is also toxic at certain stages of its development. Only, the two encapsuled seeds in the burrs and the cotyledonary leaves contain a toxic compound, the carboxyatractyloside. The seeds and the burrs are thus rarely consumed by the ungulates. Botha *et al.* (2014) concluded that it « rarely causes poisoning in cattle », which confers a competitive advantage for this plant over palatable neighbouring plants. Various studies report *Xanthium sp.* being dispersed by different ungulates (American bison, cattle, horse and various southern African bovids, see **Tables 6.5, 6.6, 6.7 and 6.9**). Liehrmann *et al.* (2018) further proved for the first time that intraspecific interactions in the three ungulates they studied allowed diaspore transfer from one individual to another one, diversifying its dispersal pathway and potential distance covered in relation with the group size. Although, Liddle and Elgar (1984) did not specifically test if trampled burrs would further germinate, they experimentally showed that horses contributed to the burial of 18% of the burrs left on animal tracks, suggesting that ungulates may secondarily favour their germination and seedling recruitment

Local transient availability of resources in the novel environment

Ungulates can lower or constrain the use of local resources by the resident vegetation. They feed upon aboveground vegetation (leaves, buds, bark pieces) or belowground parts (roots, bulbs, rhizomes). They can also damage saplings through fraying or break woody stems. They thus limit resource uptake but also indirectly provide access for light to the understory lower stratum by lowering the physical obstruction of the upper layers.

They also reduce competition for resources, when they scrape the ground for food (mushrooms, roots), thermal comfort (bed sites) or territorial marking at the expense of the resident vegetation, damaged or even killed. Other disturbances (e.g. wild/controlled fires) can have similar effects and plant regrowth be attractive to herbivores. Freed space acts as physical trap (e.g. hoofprints) for arriving diaspores offering specific microclimatic

and competition-free conditions. Deer tracks are considered preferential colonisation paths (Lefcort and Petoello, 2012).

Ungulates also release nutrients through defecation and miction, and this can be reinforced if animals feed in fertilised croplands (Seagle, 2003). Milotić and Hoffmann (2016a,b) showed that the addition of faeces lowered the germination rate of grassland species but later favoured their growth and flowering. Abundant domestic cattle defecation can also kill resident vegetation in constrained areas and release more nutrients in the longer term.

Different pathways for introduction and dispersal of non-native plants

Non-native diaspores are introduced to novel environments by numerous human-induced and long-distance pathways (Schifmann, 1997). Some introductions are accidental by contamination of seed lots, fodder or potted seedlings (Box 1) or by adherence to a mobile vector (livestock, vehicles, travellers). Other introductions are intentional by the use of non-native ornamental or cultivated plants, for erosion control, for medicinal use or timber production.

Domestic herbivores are considered mobile links connecting different reserves via external seed dispersal (Couvreur *et al.*, 2004). Rotational shepherding explained patch connectivity for 27 plants, zoochorous or not (Rico *et al.*, 2014). Domestic ungulates could act as potential rewilding tools and non-native vectors in grazed habitats. Wild boars conveyed non-native plants from agricultural lands to conservation areas, but few established (Dovrat *et al.*, 2012); in Iran, only wild boar dispersed a non-native plant (Karimi *et al.*, 2018).

Table 6.1: List of the dispersal vectors by family of ungulates, species name and common name, associated with their feeding regime (CS Concentrate Selector, IMF Intermediate Mixed Feeder, GRE Grass and Roughage Eater) and the dispersal mechanism they are involved in : endozoochory (endo), regurgitation (regu), fur-epizoochory (fur-epi).

Species name by family	Common name	Feeding regime**	Dispersal mechanism
Cervidae			
<i>Axis porcinus</i>	hog deer	IMF	endo
<i>Cervus elaphus</i>	red deer /American elk	IMF	endo
<i>Cervus nippon</i>	Sika deer	IMF	endo
<i>Dama dama</i>	fallow deer	IMF	endo
<i>Odocoileus virginianus</i>	white-tailed deer	CS	endo
<i>Odocoileus hemionus</i>	mule deer	CS	endo
<i>Rusa marianna</i>	Philippine sambar	IMF	endo
<i>Rusa unicolor</i>	sambar	IMF	endo
Bovidae			
<i>Aepyceros melampus</i>	impala	IMF	endo
<i>Alcephalus buselaphus*</i>	red hartebeest	GRE	endo
<i>Antidorcas marsupialis*</i>	springbok	CS	endo
<i>Antilope cervicapra</i>	blackbuck	GRE	endo
<i>Bison bison</i>	American bison	GRE	endo, fur-epi
<i>Bos taurus</i>	domestic cattle	GRE	endo, fur-epi
<i>Capra hircus</i>	goat	IMF	endo
<i>Cephalophus natalensis</i>	red duiker	CS	endo
<i>Connochaetes gnou, C. taurinus</i>	wildebeest	GRE	endo
<i>Damaliscus dorcas*</i>	bontebok	GRE	endo
<i>Oryx gazella*</i>	gemsbok	GRE	endo
<i>Ovis aries</i>	sheep	GRE	endo, fur-epi
<i>Pelea capreolus*</i>	grey rhebok	CS	endo
<i>Philantomba monticola</i>	blue duiker	CS	endo, regu, fur-epi
<i>Sylvicapra grimmia</i>	grey duiker	CS	endo, regu, fur-epi
<i>Taurotragus oryx</i>	eland	IMF	endo, regu, fur-epi
<i>Tragelaphus angasii</i>	nyala	CS	endo, regu, fur-epi
<i>Tragelaphus scriptus</i>	bushbuck	CS	endo, regu, fur-epi
<i>Tragelaphus strepticros</i>	greater kudu	CS	endo, fur-epi
Suidae			
<i>Sus scrofa, S. s. lybica</i>	wild pig	OM	endo, fur-epi
<i>Potamochoerus larvatus</i>	bushpig	OM	endo
Equidae			
<i>Equus asinus</i>	donkey	GRE	endo
<i>Equus caballus, E. c. ferus</i>	horse, feral horse	GRE	endo, fur-epi
<i>Equus burchelli, Equus zebra</i>	zebra	GRE	endo

* species included in the category other bovinds, Shiponeni and Milton, 2006 ** Hofmann 1989 ; Milton and Dean, 2001 ; Hempson *et al.*, 2015 ; Ahrestani *et al.*, 2016

Non-native introduction is a main concern of horse riding activities along trails within protected areas; however Gower (2008) showed no non-native plant carried by horses established in the field. Whereas for American bison in Canada, Sigaud (2018) located

the more likely introduction points at the interface between croplands and Prince Albert National Park. Ungulate paths are considered roads for plant colonisation, for better or worse (Lefcort and Pettoello, 2012). Plants with long-distance dispersal mechanisms (endozoochory, epizoochory, anemochory) were more likely to be naturalised in new areas, suggested Malo and Suárez (1997). Furthermore, endozoochory showed up as the most effective dispersal mechanism (see Chapter 5). However, plants are introduced across continents more likely by fur-epizoochory, due to the mismatch between duration of gut passage time (even though few seeds can be released seven days later, Doucette *et al.*, 2001) and length of the travel. Once introduced, authors further showed that zoochory was probably the most efficient mechanism for the spread of plants, already established or present as seeds within fodder for livestock (e.g. sheep and goats considered responsible for the spread of non-native forbs and grasses to remote oceanic islands).

Which, where, how and by whom?

An overview of ungulate-mediated non-native plant dispersal

We reviewed the existing literature on ungulate-mediated non-native plant dispersal to identify **which** plant taxa were dispersed (family, genus and species) with their growth forms; **where** they occurred (by ecozone and country); **how** they were dispersed (endozoochory, fur-epizoochory or both); and **by which** ungulate (family, species, feeding regime and fur type).

Used datasets include non-native plants dispersed by native, domestic and introduced ungulates. We did not consider studies without non-native plants or focused on a single

non-native. For instance, we excluded European studies used in the review by Ansong and Pickering (2010) on weeds dispersed by horses at the world scale, because invasive weeds cited were not non-native species. A dataset corresponds to the pool of non-native plants dispersed by a specific ungulate in a given study area. We recorded 57 datasets, concerning 26 out of 32 ungulate dispersal vectors, Cervidae, Bovidae, Suidae and Equidae (Table 6.1, Fig. 6.2), 6 ecozones and 10 countries (Table 6.2). Endozoochory largely outweighed fur-epizoochory (n=45 versus n=12, Table 6.2), already noted by Baltzinger *et al.* (2019) and Díaz-Vélez *et al.* (see Chapter 5, this volume).

Some studies were dedicated to specific interactions, white-tailed deer and honeysuckle (Vellend 2002), common cocklebur and domestic ungulates (Liddle and Elgar, 1984), hound's tongue and cattle (De Clerck-Floate, 1997) or sambar (*Rusa unicolor*) and Himalayan honeysuckle (*Leycesteria formosa*; Eyles 2002). Whereas in others, some dispersal vectors were pooled, red deer and sika deer (*Cervus nippon*; Lepková *et al.*, 2018), white-tailed and mule deer (*Odocoileus hemionus*; Bartuszevige and Endress, 2008), different bovids (Shiponeni and Milton, 2006; Haarmeyer *et al.*, 2010) whatever their feeding regimes.

We listed non-native plants dispersed by Artiodactyla and Perissodactyla from four families (Cervidae, Bovidae, Suidae and Equidae). Each subsection generally accounted for the most-studied dispersal vectors, or for vectors with endozoochory and fur-epizoochory data. Within Cervidae, the second subsection focusses on cervids introduced to Australia along with a discussion on other cervids from elsewhere in the world. Three subsections present the Bovidae, one for American bison, one for domestic cattle (*Bos taurus*) and one for the communities of South African bovids (including

blackbuck *Antelope cervicapra* in India). Wild pig, both in its native range and as an introduced species, with few mentions for bush pig (*Potamochoerus larvatus*) in South Africa, represent Suidae. Domestic horses, with few mentions of feral horses, donkeys and zebras (*Equus burchelli*, *E. zebra*) describe Equidae.

Table 6.2: Report of the datasets collected, addressing alien plant dispersal by ungulates, according to their biogeographical zone (ecozone, country) and the dispersal mode involved.

Ecozone	Country	Endozoochory	Fur-epizoochory	
Australasia	Australia	2	-	2
Afrotropic	South Africa	13	5	18
Nearctic	Canada	1	-	1
	USA	20	6	26
Neotropic	Argentina	1	-	1
Oceania	Guam (USA)	2	-	2
Palearctic	Czech Republic	2	-	2
	Finland	1	-	1
	Sweden	1	-	1
	Iran	1	-	1
	Israël	1	1	2
		45	12	

We checked plant names using the Taxonomic Name Resolution Service v4.0 ([Boyle et al., 2013](#)), providing updated information on family, genus and species. Each subsection and associated table listed the plants dispersed by growth form: cactus, forbs, graminoids (Cyperaceae, Juncaceae and Poaceae), shrubs, trees and vines; by dispersal vectors and mechanisms (endozoochory, regurgitation and fur-epizoochory) and associated references.

USA (Nearctic) and South Africa (Afrotropic) were the most studied geographic areas for non-native plant dispersal for both endozoochory and fur-epizoochory. USA was also registered as the most study geographic area in a previous chapter analysing a diverse

set of seed dispersers (see Chapter 5). Indomalaya and Antarctic were not represented. The prevalence of the USA was linked to the number of referenced studies, whereas South Africa benefitted from the diversity of ungulate communities and number of study sites (Milton *et al.*, 1990). Firstly, significantly more studies had more native plant than non-native plant taxa dispersed, both for endozoochory ($\chi^2_{(2)}=25.2$, $p=3.4 \cdot 10^{-6}$) and fur-epizoochory ($\chi^2_{(2)}=10.5$, $p=5.3 \cdot 10^{-3}$, Fig. 6.2). The proportion of non-native plants varied from 2 out of 102 (~2%) to 4 out of 4 (100%) for endozoochory and from 1 out of 17 (~6%) to 7 out of 7 (100%) for fur-epizoochory.

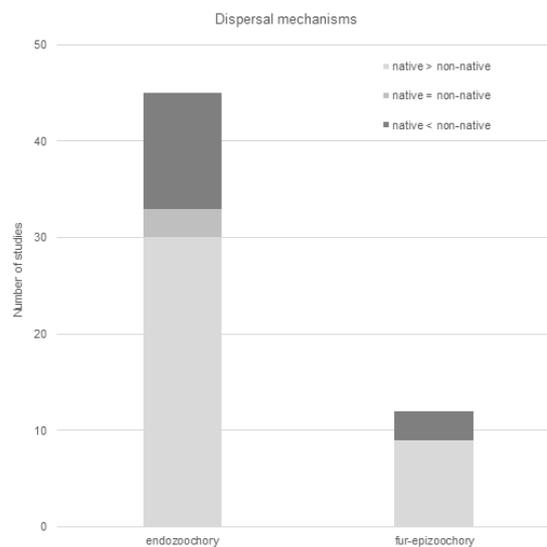


Figure 6.2: Number of studies by dispersal modes (endozoochory and fur-epizoochory) divided into three categories (native>non-native, native=non-native, native<non-native).

Secondly, in terms of fur-epizoochory and hair characteristics, non-native plants predominated native plants in only 3 out of 12 cases. These three cases included American bison, with wavy hair and domestic cattle with straight hair, whereas sheep,

with the most epizoochory efficient curled hair, systematically dispersed more native plants than non-native ones (Fig. 6.3).

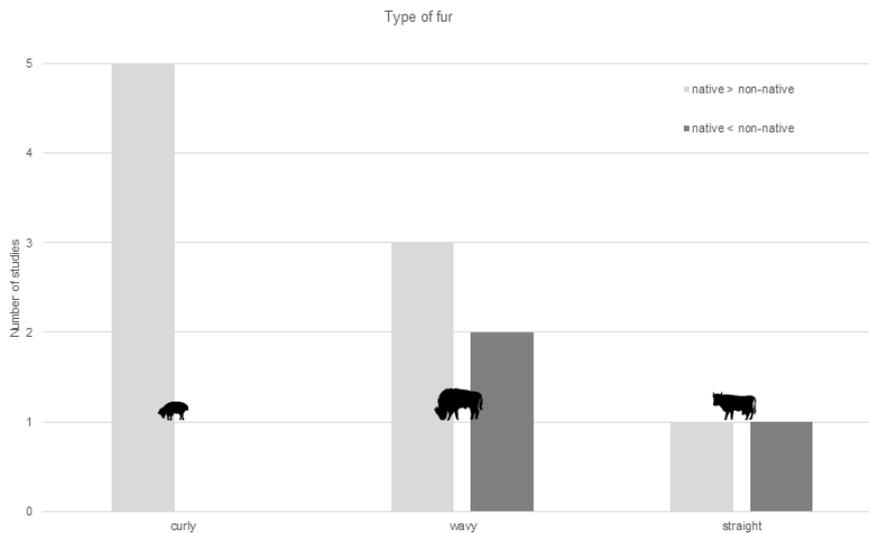


Figure 6.3: Number of fur-epizoochory studies divided into two categories (native>non-native, native<non-native) as a function of fur type (curly, wavy, straight) and associated dispersal vectors.

Thirdly, concerning endozoochory and the ungulates feeding guilds, we observed systematically more studies with more native than non-native plants dispersed (Fig. 6.4). Most datasets (n=19) concerned grass and roughage eaters (cattle, bison, wildebeest *Connochaetes gnou/taurinus*, sheep, horse, zebra); secondly (n=10) concentrate selectors (white-tailed deer, greater kudu *Tragelaphus strepticros* and bushbuck *Tragelaphus scriptus*) and intermediate mixed feeders (n=9), with nearly as many cases as different dispersal vectors, and finally omnivores (n=5).

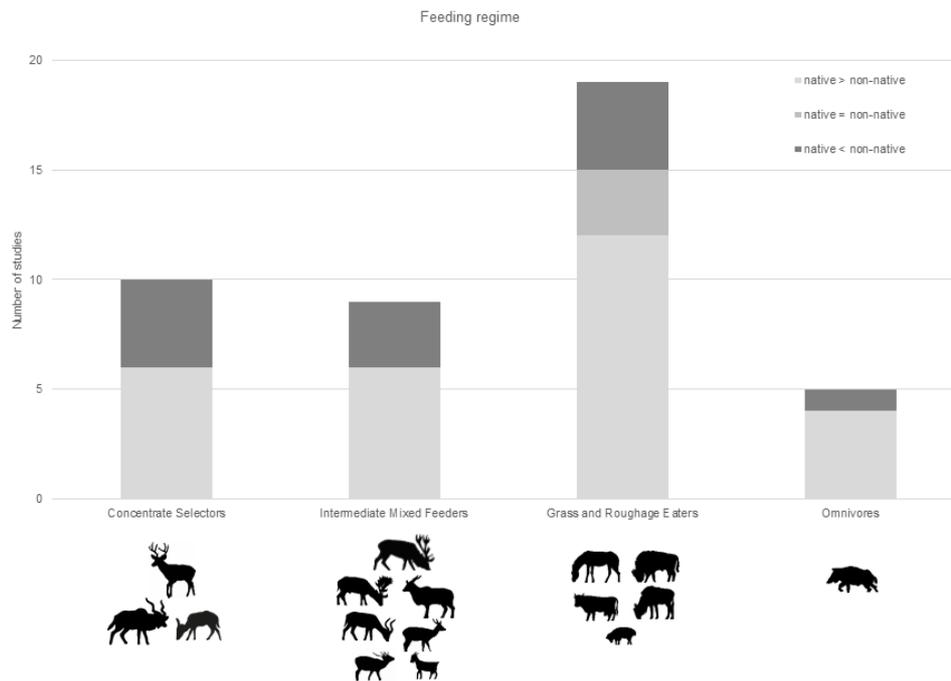


Figure 6.4: Number of endozoochory studies divided into three categories (native>non-native, native=non-native, native<non-native) as a function of the dispersal vector feeding regime. Concentrate selectors are represented by white-tailed deer, greater kudu and bushbuck ; intermediate mixed feeders by red deer, sika deer, fallow deer, hog deer, Philippine deer, goat, eland and impala ; grass and roughage eaters by bison, cattle, sheep, wildebeest, horse, donkey and zebra; omnivores include wild boar and bushpig. Latin names are indicated in Table 6.1.

Non-native plant dispersal by Cervidae

White-tailed deer and mule deer in the USA

Overabundant deer populations in North America have driven lots of research (Russell *et al.*, 2001) and white-tailed deer, a medium-sized browser cervid, was the most studied dispersal vector within its native range. We recorded nine studies concerning endozoochory (Table 6.3), but none on fur-epizoochory.

Table 6.3: List of alien plants referenced as being dispersed by white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus* c) by endozoochory, ordered by growth form (forb, graminoid, shrub, tree, vine) and family.

Growth form	Family	Plant species	References	
Forb	Amaranthaceae	<i>Amaranthus hybridus</i>	b	
		<i>Amaranthus palmeri</i>	h	
		<i>Amaranthus retroflexus</i>	b,e	
		<i>Amaranthus viridis</i>	g*	
		<i>Chenopodium album</i>	b,d,e,h	
		<i>Chenopodium glaucum</i>	b	
		<i>Chenopodium pumilio</i>	d	
	Asteraceae	<i>Artemisia vulgaris</i>	d	
		<i>Cirsium arvense</i>	e	
		<i>Galinsoga quadriradiata</i>	h	
		<i>Gnaphalium uliginosum</i>	b	
		<i>Leucanthemum vulgare</i>	b	
		<i>Matricaria matricarioides</i>	b	
		<i>Sonchus asper</i>	b,d	
		<i>Taraxacum officinale</i>	b,c,e	
		Brassicaceae	<i>Capsella bursa-pastoris</i>	b,d
			<i>Thlaspi arvense</i>	c
	Caryophyllaceae	<i>Cerastium fontanum</i>	d	
		<i>Cerastium glomeratum</i>	c	
		<i>Silene latifolia</i> subsp. <i>alba</i>	d	
		<i>Spergularia media</i>	b	
		<i>Stellaria media</i>	b,d	
	Commelinaceae	<i>Murdannia nudiflora</i>	g	
	Convolvulaceae	<i>Jacquemontia tamnifolia</i>	g*	
	Fabaceae	<i>Coronilla varia</i>	b	
		<i>Kummerowia striata</i>	g	
		<i>Lotus corniculatus</i>	b,e	
		<i>Medicago lupulina</i>	b	
		<i>Medicago minima</i>	g	
		<i>Melilotus officinalis</i> subsp. <i>alba</i>	b	
		<i>Melilotus</i> sp.	e	
		<i>Securigera varia</i>	d	
		<i>Trifolium dubium</i>	g	
<i>Trifolium pratense</i>		b,d		
<i>Trifolium repens</i>		d,i		
<i>Trifolium</i> sp.		d		
<i>Vicia tetrasperma</i>		b		
<i>Vicia</i> sp.		d		

	Lamiaceae	<i>Nepeta cataria</i>	d
	Lythraceae	<i>Lythrum salicaria</i>	b
	Plantaginaceae	<i>Linaria vulgaris</i>	b
		<i>Plantago major</i>	b
		<i>Veronica officinalis</i>	b,d,i
		<i>Veronica persica</i>	d
		<i>Veronica serpyllifolia</i>	b
	Polygonaceae	<i>Persicaria maculosa</i>	h
		<i>Polygonum caespitosum</i>	d
		<i>Polygonum lapathifolium</i>	b
		<i>Polygonum persicaria</i>	b,d
		<i>Rumex acetosella</i>	i
		<i>Rumex obtusifolius</i>	e
	Portulacaceae	<i>Portulaca amilis</i>	g
		<i>Portulaca grandiflora</i>	b
		<i>Portulaca oleracea</i>	b,d,h
	Rosaceae	<i>Potentilla norvegica</i>	b
		<i>Potentilla recta</i>	b,c,h
	Rubiaceae	<i>Galium mollugo</i>	b
		<i>Oldenlandia corymbosa</i>	g*
	Solanaceae	<i>Capsicum sp.</i>	d
		<i>Lycopersicon esculentum</i>	b
		<i>Petunia sp.</i>	d
		<i>Solanum dulcamara</i>	b,d
		<i>Solanum nigrum</i>	d
		<i>Solanum physalifolium</i>	d
	Urticaceae	<i>Urtica dioica</i>	h
Graminoid	Cyperaceae	<i>Cyperus compressus</i>	g*
		<i>Kyllinga brevifolia</i>	g*
	Poaceae	<i>Agrostis capillaris</i>	d
		<i>Agrostis gigantea</i>	b,e
		<i>Agrostis stolonifera</i>	b
		<i>Anthoxanthum odoratum</i>	i
		<i>Dactylis glomerata</i>	b
		<i>Digitaria ischaemum</i>	b,e
		<i>Digitaria sanguinalis</i>	b,e,g
		<i>Echinochloa crus-galli</i>	e
		<i>Elymus repens</i>	d
		<i>Holcus lanatus</i>	i
		<i>Microstegium vimineum</i>	d
		<i>Panicum miliaceum</i>	d
	<i>Pennisetum glaucum</i>	d	
	<i>Phleum pratense</i>	b	

		<i>Poa annua</i>	b
		<i>Poa compressa</i>	b,d
		<i>Poa pratensis</i>	b,c,h
		<i>Puccinellia distans</i>	b
		<i>Setaria viridis</i>	e
		<i>Sorghum bicolor</i>	b,e
		<i>Sorghum halepense</i>	d
		<i>Triticum aestivum</i>	b
		<i>Zea mays</i>	d
Shrub	Caprifoliaceae	<i>Lonicera aff. × bella</i>	a,b
		<i>Lonicera japonica</i>	d
		<i>Lonicera maackii</i>	f
		<i>Lonicera morrowii</i>	a,e
		<i>Lonicera tatarica</i>	a,e
	Elaeagnaceae	<i>Elaeagnus umbellata</i>	d,i
	Rhamnaceae	<i>Rhamnus cathartica</i>	b
	Rosaceae	<i>Rosa multiflora</i>	b,d,i
		<i>Rubus idaeus</i>	b
		<i>Rubus phoenicolasius</i>	d
Tree	Araceae	<i>Phellodendron japonicum</i>	d
	Rosaceae	<i>Malus sp.</i>	d
		<i>Pyrus sp.</i>	b
Vine	Vitaceae	<i>Ampelopsis brevipedunculata</i>	d

References: Vellend, 2002 ^a; Myers *et al.*, 2004 ^b; Bartuszevige and Endress, 2008 ^c; Williams *et al.*, 2008 ^d; Blyth *et al.*, 2013 ^e; Guiden *et al.*, 2015 ^f; Pile *et al.*, 2015 ^g (* cryptogenic origin); Guiden, 2017 ^h; Flaherty *et al.*, 2018 ⁱ

Bartuszevige and Endress (2008) did not distinguish white-tailed from mule deer, and two studies focused on invading honeysuckles (*Lonicera* sp.; Vellend, 2002; Guiden *et al.*, 2015). We recorded 104 non-native plants, dispersed across different states of the USA. These taxa were divided into five growth forms: 65 forbs, 25 graminoids, 10 shrubs, 3 trees and 1 vine (Table 6.3). Forbs dispersed belonged to 16 different families, predominantly Fabaceae, Asteraceae and Amaranthaceae. Twenty-three graminoids dispersed were Poaceae. Shrubs belonged to four families, with five different *Lonicera* species (Caprifoliaceae). *Chenopodium album* was the unique plant dispersed in four

studies, whereas seven plants appeared three times: *Taraxacum officinale*, *Veronica officinalis*, *Portulaca oleracea*, *Potentilla recta*, *Digitaria sanguinalis*, *Poa pratensis* and *Rosa multiflora*.

Cervidae introduced to Australia and other deer species

Australia hosts no native deer species. Fallow deer *Dama dama*, hog deer *Axis porcinus*, red deer, chital *Axis axis*, Philippine sambar *Rusa Marianna* and sambar have been introduced to different parts, with great invasion potential (Davis *et al.*, 2016). Non-native plants dispersed by non-native deer in Australia appeared in four different studies, focusing on three of the six introduced cervids (fallow deer, hog deer and sambar), all being intermediate mixed feeders.

Thirty-one non-native plants, mainly forbs (n=22), were dispersed by endozoochory, each of the 13 forb families represented by maximum three non-native plants. Graminoids comprised Cyperaceae, Juncaceae and five Poaceae. Only sambar dispersed non-native shrubs. Again, the current knowledge is sparse by the lack of information on the other three non-native ungulates. More information has been collected on horses (see Equidae subsection) and other herbivores (Calviño-Cancela, 2011) dispersing non-native plants.

Table 6.4: List of alien plants referenced as being dispersed by hog deer (*Axis porcinus*), red deer, American elk (*Cervus elaphus*), fallow deer (*Dama dama*), sika deer (*Cervus nippon*), sambar (*Rusa unicolor*), Philippine sambar (*Rusa marianna*) by endozoochory, ordered by growth form (forb, graminoid, shrub, tree, vine) and family.

Growth form	Family	Plant species	Dispersal vector	References
Forb	Amaranthaceae	<i>Chenopodium album</i>	fallow deer, red deer, sika deer	e,g
	Asteraceae	<i>Erigeron annuus</i>	red deer, sika deer	g
		<i>Hypochaeris glabra</i>	hog deer	c
		<i>Lapsana communis</i>	red deer, sika deer	g
		<i>Oncosiphon piluliferum</i>	hog deer	c
		<i>Tanacetum vulgare</i>	red deer, sika deer	g
		Brassicaceae	<i>Thlaspi arvense</i>	American elk
	Caryophyllaceae	<i>Cerastium glomeratum</i>	American elk, hog deer	b,c
		<i>Spergularia rubra</i>	hog deer	c
		<i>Stellaria media</i>	American elk, hog deer	b,c
	Fabaceae	<i>Medicago minima</i>	hog deer	c
		<i>Medicago polymorpha</i>	hog deer	c
		<i>Trifolium hybridum</i>	American elk	b
		<i>Trifolium repens</i>	American elk	b
		<i>Trifolium sp.</i>	fallow deer	e
	Gentianaceae	<i>Centaurium erythraea</i>	hog deer	c
	Geraniaceae	<i>Geranium pusillum</i>	red deer, sika deer	g
	Malvaceae	<i>Modiola caroliniana</i>	fallow deer	e
	Papaveraceae	<i>Papaver somniferum</i>	fallow deer	e
	Plantaginaceae	<i>Plantago coronopus</i>	hog deer	c
		<i>Plantago lanceolata</i>	hog deer	c
		<i>Veronica arvensis</i>	American elk	b
	Polygonaceae	<i>Polygonum aviculare</i>	hog deer	c
		<i>Rumex acetosella</i>	American elk, hog deer	b,c
		<i>Rumex conglomeratus</i>	hog deer	c
	Primulaceae	<i>Anagallis arvensis</i>	hog deer	c
	Ranunculaceae	<i>Ranunculus muricatus</i>	hog deer	c
	Scrophulariaceae	<i>Verbascum thapsus</i>	fallow deer	e
	Verbenaceae	<i>Verbena bonariensis</i>	fallow deer	e
		<i>Verbena sp.</i>	fallow deer	e
Graminoid	Cyperaceae	<i>Cyperus eragrostis</i>	fallow deer	e
	Juncaceae	<i>Juncus bufonius</i>	hog deer	c
		<i>Juncus tenuis</i>	red deer, sika deer	g
	Poaceae	<i>Apera interrupta</i>	American elk	b

		<i>Briza minor</i>	hog deer	c
		<i>Bromus hordeaceus</i>	hog deer	c
		<i>Bromus inermis</i>	American elk	b
		<i>Eragrostis cilianensis</i>	fallow deer	e
		<i>Festuca ovina</i>	American elk	b
		<i>Poa annua</i>	hog deer	c
		<i>Poa compressa</i>	American elk	b
		<i>Poa pratensis</i>	American elk	b
		<i>Vulpia bromoides</i>	hog deer	c
Shrub	Caprifoliaceae	<i>Leycesteria formosa</i>	sambar	a
	Rosaceae	<i>Rubus fruticosus</i>	sambar	d
Tree	Caricaceae	<i>Carica papaya</i>	Philippine sambar	f
	Lamiaceae	<i>Vitex parviflora</i>	Philippine sambar	f
Vine	Asteraceae	<i>Mikania micrantha</i>	Philippine sambar	f
	Passifloraceae	<i>Passiflora suberosa</i>	Philippine sambar	f

References: Eyles, 2002 (Australia)^a; Bartuszevige and Endress, 2008 (USA)^b; Davis *et al.*, 2010 (Australia)^c; Forsyth and Davis, 2011 (Australia)^d; Claridge *et al.*, 2016 (Australia)^e; Gawel *et al.*, 2018 (USA Guam)^f; Lepková *et al.*, 2018 (Czech Republic)^g

The other deer species are also intermediate mixed feeders, favouring endozoochorous seed dispersal (Table 6.4). However, few data were collected on non-native plants they dispersed in different areas. Plant dispersal by red deer has been well studied in Europe (Baltzinger *et al.*, 2019) but with rare mentions of non-native plants. We found 22 non-native plants, including 12 forbs, 6 graminoids, 2 trees and 2 vines dispersed by red deer, American elk, Sika deer and Philippine sambar. Some non-native plants listed are dispersed by red deer in their native range (e.g. *Stellaria media*, *Rumex acetosella*, *Poa pratensis*). Again, the potential for non-native plants dispersal by cervids is underrated by a global lack of studies, even more for fur-epizoochory. Cervidae like white-tailed deer (Table 6.3) or red deer generally have abundant populations with potential major

interactions with plant populations both antagonistic (herbivory) and mutualistic (zoochory).

Non-native plant dispersal by Bovidae

American bison in North America

American bison, a grass and roughage eater, with relatively wavy fur, was identified as dispersal vector four times, balanced between endozoochory and fur-epizoochory. All studies included non-native plants, occurred from 2005 to 2018, in the USA and Canada, in its native range as well as introduced on Santa Catalina Island (Constible *et al.*, 2005).

Table 6.5: List of alien plants referenced as being dispersed by American bison (*Bison bison*) by endozoochory (endo) and fur-epizoochory (fur-epi), ordered by growth form (forb, graminoid) and family.

Growth form	Family	Plant species	Dispersal mode	References
Forb	Amaranthaceae	<i>Amaranthus albus</i>	endo	d
		<i>Amaranthus graecizans</i>	endo, fur-epi	c,d
		<i>Amaranthus retroflexus</i>	endo	d
		<i>Axyris amaranthoides</i>	endo	d
		<i>Chenopodium album</i>	endo, fur-epi	c
	Apiaceae	<i>Daucus carota</i>	endo, fur-epi	c
		<i>Pastinaca sativa</i>	endo, fur-epi	c
		<i>Torilis arvensis</i>	endo, fur-epi	b
	Asteraceae	<i>Arctium minus</i>	fur-epi	c
		<i>Cirsium arvense</i>	endo	d
		<i>Sonchus arvensis</i>	endo	d
		<i>Taraxacum officinale</i>	endo, fur-epi	c,d
		<i>Xanthium spinosum</i>	fur-epi	a
		<i>Xanthium strumarium</i>	fur-epi	a,b,c
	Brassicaceae	<i>Capsella bursa-pastoris</i>	endo, fur-epi	b,c
		<i>Thlaspi arvense</i>	endo	d
	Caryophyllaceae	<i>Silene noctiflora</i>	endo	d
	Fabaceae	<i>Medicago lupulina</i>	endo	b,d
		<i>Medicago polymorpha</i>	fur-epi	a
		<i>Medicago sativa</i>	endo, fur-epi	a,d
<i>Medicago sp.</i>		fur-epi	a	
	<i>Melilotus officinalis</i>	endo, fur-epi	b,d	

		<i>Melilotus sp.</i>	endo	c
		<i>Trifolium pratense</i>	endo, fur-epi	c,d
		<i>Trifolium repens</i>	endo	c,d
	Geraniaceae	<i>Erodium botrys</i>	fur-epi	a
		<i>Erodium cicutarium</i>	fur-epi	a
		<i>Erodium sp.</i>	fur-epi	a
	Lamiaceae	<i>Galeopsis tetrahit</i>	endo	d
		<i>Marrubium vulgare</i>	fur-epi	a
	Plantaginaceae	<i>Plantago major</i>	endo	c,d
	Polygonaceae	<i>Polygonum convolvulus</i>	endo	d
		<i>Polygonum lapathifolium</i>	endo	d
		<i>Rumex crispus</i>	endo, fur-epi	c
	Rosaceae	<i>Potentilla norvegica</i>	endo	d
Graminoid	Poaceae	<i>Avena sp.</i>	fur-epi	a
		<i>Brachypodium distachyon</i>	fur-epi	a
		<i>Bromus inermis</i>	endo, fur-epi	c,d
		<i>Bromus japonicus</i>	endo, fur-epi	c
		<i>Bromus sp1.</i>	fur-epi	a
		<i>Bromus sp2.</i>	endo, fur-epi	b
		<i>Cynodon dactylon</i>	endo, fur-epi	b
		<i>Dactylis glomerata</i>	fur-epi	c
		<i>Digitaria sanguinalis</i>	endo, fur-epi	c
		<i>Echinochloa crus-galli</i>	endo, fur-epi	c
		<i>Festuca arundinacea</i>	endo, fur-epi	c
		<i>Hordeum sp.</i>	fur-epi	a
		<i>Phalaris arundinacea</i>	endo, fur-epi	c
		<i>Phleum pratense</i>	endo	d
		<i>Poa pratensis</i>	endo, fur-epi	c
		<i>Setaria faberi</i>	endo, fur-epi	c
		<i>Setaria glauca</i>	endo	d

References: Constible *et al.*, 2005 ^a; Rosas *et al.*, 2008 ^b; Eyheralde, 2015 ^c; Sigaud, 2018 ^d

The European bison (*Bison bonasus*), intensively studied in Poland (Białowieża; Jaroszewicz *et al.*, 2009), is a model for rewilding areas, only dispersing 178 native plants. American bison dispersed 52 non-native plants, 35 forbs (mainly Fabaceae, Asteraceae and Amaranthaceae) and 17 Poaceae, as expected from its feeding regime. Seventeen species were solely dispersed via endozoochory (~33%), 14 solely via fur-epizoochory

(~27%), but 21 by both mechanisms (~40%) with strong implications for dispersal effectiveness. Common cocklebur which bears epizoochorous diaspores (Table 6.5, Box 2) was identified three times, whereas 10 additional plants were recovered twice, seven of them dispersed by both dispersal mechanisms, and 3 by endozoochory only.

Domestic cattle

Domestic cattle, a grass and roughage eater, with straight hair (for the races studied) was studied as non-native plants dispersal vector five times; twice in the USA, once in Argentina, Sweden and Canada (focused on hound's tongue epizoochory, Box 1).

Table 6.6: List of alien plants referenced as being dispersed by domestic cattle (*Bos taurus*) by endozoochory (endo) and fur-epizoochory (fur-epi), ordered by growth form (forb, graminoid) and family.

Growth form	Family	Plant species	Dispersal mode	References
Forb	Apiaceae	<i>Torilis arvensis</i>	fur-epi	e
	Asteraceae	<i>Matricaria discoidea</i>	endo	e
		<i>Picris echioides</i>	endo, fur-epi	e
		<i>Silybum marianum</i>	fur-epi	e
		<i>Xanthium spinosum</i>	fur-epi	e
		Boraginaceae	<i>Cynoglossum officinale</i>	fur-epi
	Brassicaceae	<i>Myosotis stricta</i>	endo	b
		<i>Alyssum alyssoides</i>	endo	b
	Caryophyllaceae	<i>Capsella bursa-pastoris</i>	endo	e
		<i>Cerastium glomeratum</i>	endo	b
	Fabaceae	<i>Stellaria media</i>	endo	b,d,e
		<i>Lotus tenuis</i>	endo	c
		<i>Medicago lupulina</i>	endo	b
		<i>Medicago polymorpha</i>	endo	e
		<i>Trifolium hirtum</i>	endo, fur-epi	e
		<i>Trifolium hybridum</i>	endo	b
		<i>Trifolium repens</i>	endo	b,c
		<i>Trifolium subterraneum</i>	endo	e
		<i>Trifolium sp.</i>	endo	b
		<i>Vicia villosa</i>	endo	e
	Geraniaceae	<i>Erodium sp.</i>	fur-epi	e
		<i>Geranium molle</i>	endo	e
	Lamiaceae	<i>Mentha pulegium</i>	endo	c

	Lythraceae	<i>Lythrum hyssopifolia</i>	endo	c
	Plantaginaceae	<i>Plantago lanceolata</i>	endo	e
		<i>Veronica arvensis</i>	endo	b
		<i>Veronica chamaedrys</i>	endo	b
		<i>Veronica persica</i>	endo	e
	Polygonaceae	<i>Polygonum aviculare</i>	endo	c
		<i>Rumex acetosella</i>	endo	b
		<i>Rumex crispus</i>	endo	c
	Portulacaceae	<i>Portulaca oleracea</i>	endo	c
	Primulaceae	<i>Anagallis arvensis</i>	endo	c
	Rubiaceae	<i>Galium parisiense</i>	endo	e
		<i>Sherardia arvensis</i>	endo	e
	Urticaceae	<i>Urtica dioica</i>	endo	d
Graminoid	Poaceae	<i>Aegilops truncialis</i>	fur-epi	e
		<i>Agrostis avenacea</i>	endo	c
		<i>Agrostis gigantea</i>	endo	b
		<i>Apera interrupta</i>	endo	b
		<i>Avena sp.</i>	endo, fur-epi	e
		<i>Brachypodium distachyon</i>	endo, fur-epi	e
		<i>Bromus hordeaceus</i>	fur-epi	e
		<i>Bromus inermis</i>	endo	b
		<i>Cynodon dactylon</i>	endo	c,e
		<i>Dactylus glomerata</i>	endo	b
		<i>Echinochloa crus-galli</i>	endo	c
		<i>Elymus caput-medusae</i>	fur-epi	e
		<i>Festuca ovina</i>	endo	b
		<i>Festuca perennis</i>	endo, fur-epi	e
		<i>Festuca temulenta</i>	endo, fur-epi	e
		<i>Hordeum murinum</i>	fur-epi	e
		<i>Lolium multiflorum</i>	endo	c
		<i>Lolium perenne</i>	endo	c
		<i>Parapholis incurva</i>	endo	c
		<i>Phalaris aquatica</i>	fur-epi	e
		<i>Poa annua</i>	endo	c
<i>Poa compressa</i>	endo	b		
<i>Poa pratensis</i>	endo	b		
<i>Polypogon monspeliensis</i>	endo	e		
<i>Setaria pumila</i>	endo	e		

References: De Clercke-Floate, 1997 a ; Bartuszevige and Endress, 2008 b ; Vignolio and Fernandez, 2010 c ; Auffret and Cousins, 2013 d ; Chuong et al., 2016 e

Cattle dispersed 61 non-woody non-native plants including 36 forbs, 25 Poaceae, similar to American bison with its feeding regime. Most plants were dispersed solely by endozoochory (45 plants, ~74%), 10 (~16%) by fur-epizoochory, and 6 (~10%) by both dispersal mechanisms, which is relatively lower than for American bison. Fabaceae occurred frequently, with 9 non-native plants (5 *Trifolium* sp.) dispersed mostly by endozoochory. *Stellaria media* was dispersed at three occasions, *Trifolium repens* and *Cynodon dactylon* were dispersed at two study sites. With the present worldwide use of cattle, either for milk or meat production, the potential for native (e.g. Auffret and Cousins, 2013) and non-native plant dispersal is probably underestimated.

Native and domestic bovids in southern Africa

Southern Africa hosts very diverse ungulate communities, but information on ungulate-mediated seed dispersal is relatively scarce (Table 6.7). However, most studies published so far include non-native plants and involve different native and/or domestic bovids. Bovids communities in southern Africa are also functionally highly diverse in terms of feeding guilds (Hempson *et al.*, 2015), body size, body mass, fur type, habitat use and sociality. Consequently, they are likely to disperse a wide diversity of plants bearing different traits. Altogether, southern African bovids dispersed 46 non-native taxa including 1 cactus, 27 forbs, 7 Poaceae, 5 shrubs and 6 trees (2 Fabaceae). Non-native plants were dispersed by two domestic bovids (goat and sheep), more than 10 different native bovids of various feeding guilds (concentrate selectors, intermediate mixed feeders and grass and roughage eaters), by endozoochory, regurgitation and fur-epizoochory. Amaranthaceae with at least 4 different *Atriplex* sp. and Asteraceae with three *Bidens* sp.

dispersed by fur-epizoochory and endozoochory (*Bidens bipinnata* by impala *Aepyceros melampus*) were the most represented. Plants from all growth forms (except vines) were dispersed. Birds also dispersed *Solanum mauritianum* and *Lantana camara*, two invasive non-native fleshy-fruited plants. In South Africa, there is a great opportunity for ungulate-mediated dispersal studies, based on the functional diversity of both plant and potential dispersal vectors. In India, blackbuck, a grass and roughage eater, is also known to disperse mesquite (*Prosopis juliflora*, Fabaceae), a highly invasive non-native (Jadeja *et al.*, 2013). In South Africa, other livestock prevent pre-dispersal destruction of *Prosopis* sp. seeds by bruchids and favour their integration in the soil seed bank.

Table 6.7: List of alien plants referenced as being dispersed by native and domestic Bovidae in South Africa by endozoochory (endo), regurgitation (regu) and fur-epizoochory (fur-epi), ordered by growth form (cactus, forb, graminoid, shrub, tree) and family. Except *Prosopis juliflora* dispersed by blackbuck by endozoochory in India.

Growth form	Family	Plant species	Dispersal mode	Dispersal vector*	References	
Cactus	Cactaceae	<i>Opuntia ficus-indica</i>	endo	bushbuck	b	
Forb	Amaranthaceae	<i>Atriplex lindleyi</i>	endo, fur-epi	goat, kudu, sheep	a,c,f	
		<i>Atriplex muelleri</i>	fur-epi	sheep	a	
		<i>Atriplex semibaccata</i>	endo	goat, kudu, sheep	c,f	
		<i>Atriplex sp.</i>	endo	goat, sheep	f	
		<i>Chenopodium album</i>	endo	goat, sheep	f	
		<i>Chenopodium sp.</i>	endo	goat, sheep	f	
		<i>Gomphrena celosioides</i>	endo	impala	d	
		<i>Salsola sp.</i>	endo	goat, sheep	f	
		Asteraceae	<i>Bidens bipinnata</i>	fur-epi, endo	bushbuck, eland, grey duiker, impala	d,i
			<i>Bidens biternata</i>	fur-epi	bushbuck	i
<i>Bidens pilosa</i>	fur-epi		blue duiker, grey duiker	i		

		<i>Conyza sp.</i>	endo	wildebeest, other bovids	e
		<i>Xanthium strumarium</i>	fur-epi	bushbuck, grey duiker, kudu, nyala	i
Caryophyllaceae		<i>Drymaria cordata</i>	fur-epi	blue duiker	i
		<i>Spergularia media</i>	endo	goat, sheep	f
		<i>Spergularia sp.</i>	endo	wildebeest, other bovids	e
		<i>Stellaria media</i>	endo	eland, other bovids	e
		<i>Stellaria sp.</i>	endo	wildebeest, other bovids	e
Fabaceae		<i>Medicago polymorpha</i>	fur-epi	sheep	a
		<i>Medicago sativa</i>	endo	goat	c
		<i>Medicago sp.</i>	endo	other bovids	e
		<i>Trifolium sp.</i>	endo	wildebeest, other bovids	e
Geraniaceae		<i>Erodium moschatum</i>	endo	wildebeest, other bovids	e
Oxalidaceae		<i>Oxalis corniculata</i>	endo	eland, impala	d
Papaveraceae		<i>Argemone mexicana</i>	fur-epi	sheep	a
		<i>Argemone ochroleuca</i>	endo	kudu	c
Primulaceae		<i>Anagallis arvensis</i>	endo	other bovids	e
Graminoid	Poaceae	<i>Briza maxima</i>	endo	eland, wildebeest, other bovids	e
		<i>Bromus diandrus</i>	endo	wildebeest	e
		<i>Bromus murinum</i>	fur-epi	sheep	a
		<i>Bromus pectinatus</i>	endo	wildebeest	e
		<i>Lolium sp.</i>	endo	eland, wildebeest, other bovids	e
		<i>Poa annua</i>	endo	eland, wildebeest, other bovids	e
		<i>Vulpia myuros</i>	endo	eland, wildebeest, other bovids	e
Shrub	Verbenaceae	<i>Lantana camara</i>	endo	bushbuck, kudu, nyala	i
	Caricaceae	<i>Papaya carica</i>	endo	bushbuck	i

	Myrtaceae	<i>Psidium cattelinaum</i>	endo	bushbuck, grey duiker	i
		<i>Psidium guajava</i>	endo	bushbuck, grey duiker	i
	Solanaceae	<i>Solanum mauritianum</i>	endo	bushbuck, grey duiker	h,i
Tree	Anacardiaceae	<i>Mangifera indica</i>	regu	bushbuck, nyala	i
	Fabaceae	<i>Acacia melanoxylon</i>	endo	bushbuck	i
		<i>Gleditsia triacanthos</i>	regu	bushbuck, grey duiker, eland	i
		<i>Prosopis juliflora</i>	endo	blackbuck	g
	Meliaceae	<i>Melia azedarach</i>	endo	bushbuck, blue duiker, red duiker	i
	Moraceae	<i>Morus alba</i>	endo	blue duiker, red duiker	i
	Rosaceae	<i>Eriobotrya japonica</i>	regu	bushbuck, blue duiker	i

References: Milton *et al.*, 1990 ^a; Castley *et al.*, 2001 ^b; Milton and Dean, 2001 ^c; Slater and du Toit, 2002 ^d; Shiponeni and Milton, 2006 ^e; Haarmeyer *et al.*, 2010 ^f; Jadeja *et al.*, 2013 ^g; Msweli, 2018 ^h; Nichols, 2018 ⁱ * other bovids in Shiponeni and Milton (2006) include springbok (*Antidorcas marsupialis*), bontebok (*Damaliscus dorcas*), red hartebeest (*Alcephalus buselaphus*), grey rhebok (*Pelea capreolus*) and gemsbok (*Oryx gazella*).

Non-native plant dispersal by Suidae

Suidae (wild boar and bush pig) were grouped as frugivore opportunistic, omnivorous dispersal vectors. Only Dovrat *et al.* (2012) combined endozoochory and fur-epizoochory, highlighting three forbs dispersed by both mechanisms (*Amaranthus blitoides*, *Amaranthus blitum* and *Conyza sp.*). Eight studies occurred in the native range of the Suidae concerned (Iran, Israel, Czech Republic and Spain for wild boar; South Africa for bush pig) as well as introduced on islands (Guam, USA). Altogether Suidae dispersed 30 non-native taxa, representing all growth forms (3 cactus; 12 forbs, 1 graminoid, 4 shrubs, 8 trees and 2 vines) as expected from their generalist feeding regime.

Table 6.8: List of alien plants referenced as being dispersed by Suidae, wild pig (*Sus scrofa*, *S. s. lybica*) and bushpig (*Potamochoerus larvatus*) by endozoochory (endo) and fur-epizoochory (fur-epi) ordered by growth form (cactus, forb, graminoid, shrub, tree, vine) and family.

Growth form	Family	Plant species	Dispersal mode	Dispersal vector	References
Cactus	Cactaceae	<i>Opuntia ficus-indica</i>	endo	bushpig	a
		<i>Opuntia maxima</i>	endo	wild pig	b
		<i>Opuntia sp.</i>	endo	wild pig	c
Forb	Amaranthaceae	<i>Amaranthus blitoides</i>	endo, fur-epi	wild pig	c
		<i>Amaranthus blitum</i>	endo, fur-epi	wild pig	c
		<i>Amaranthus cruentus</i>	endo	wild pig	c
		<i>Amaranthus spinosus</i>	endo	wild pig	c
	Apiaceae	<i>Daucus carota</i>	endo	wild pig	f
	Asteraceae	<i>Bidens tripartita</i>	fur-epi	wild pig	c
		<i>Conyza canadensis</i>	endo	wild pig	e
		<i>Conyza sp.</i>	endo, fur-epi	wild pig	c
		<i>Lapsana communis</i>	endo	wild pig	f
		<i>Tanacetum vulgare</i>	endo	wild pig	f
	Euphorbiaceae	<i>Euphorbia hirta</i>	endo	wild pig	c
Solanaceae	<i>Solanum lycopersicum</i>	endo	wild pig	c	
Graminoid	Juncaceae	<i>Juncus tenuis</i>	endo	wild pig	f
Shrub	Asteraceae	<i>Chromolaena odorata</i>	endo	wild pig	d
	Myrtaceae	<i>Psidium cattelinaum</i>	endo	bushpig	g
		<i>Psidium guajava</i>	endo	bushpig	g
	Solanaceae	<i>Solanum mauritianum</i>	endo	bushpig	g
Tree	Caricaceae	<i>Carica papaya</i>	endo	wild pig	d
	Fabaceae	<i>Acacia cyclops</i>	endo	bushpig	a
		<i>Acacia saligna</i>	endo	wild pig	c
		<i>Leucaena leucocephala</i>	endo	wild pig	d
	Moraceae	<i>Ficus benghalensis</i>	endo	wild pig	c
		<i>Ficus religiosa</i>	endo	wild pig	c
		<i>Morus sp.</i>	endo	wild pig	c
Rutaceae	<i>Citrus sinensis</i>	endo	wild pig	h	
Vine	Cucurbitaceae	<i>Coccinia grandis</i>	endo	wild pig	d
	Passifloraceae	<i>Passiflora suberosa</i>	endo	wild pig	d

References: Castley *et al.*, 2001 (South Africa) ^a; Padrón *et al.*, 2011 (Spain) ^b; Dovrat *et al.*, 2012 (Israel) ^c; Gaweł *et al.*, 2018 (USA Guam) ^d; Karimi *et al.*, 2018 (Iran) ^e; Lepková *et al.*, 2018 (Czech Republic) ^f; Nichols, 2018 (South Africa) ^g, Peris *et al.*, 2019 (Brazil) ^h

Diet based on plants, Suidae feed on various above- and belowground parts, being able to transport diaspores and vegetative parts like rhizomes.

Non-native plants producing fleshy fruits were dispersed (*Opuntia sp.*, *Psidium sp.*, *Solanum mauritianum*, *Citrus sinensis*, Table 6.8). European studies highlighted wild boar both as a seed predator and as a seed disperser, rarely for non-native plants. Feral pig is well-distributed worldwide, which requires more attention. Wild pig is also more effective through fur-epizoochory (Picard and Baltzinger, 2012) than endozoochory (Picard *et al.*, 2016).

Non-native plant dispersal by Equidae

Domestic and feral horses, zebra and donkey represented Equidae. They are all grass and roughage eaters with relatively straight fur. Horses have been quite intensively studied regarding non-native plant dispersal, in relation to horse riding practises, mostly in the USA and Australia, but see Törn *et al.* (2010) in Finland. Table 6.9 listed plants considered non-native in the country where they were dispersed. Weeds mentioned by Ansong and Pickering (2013) in their review and retrieved from European studies are not non-natives. Most non-native plants were dispersed by endozoochory and by domestic horses (King *et al.*, 2019 for feral horses).

We gathered 101 non-native plants dispersed by Equidae (Table 6.9), nearly twice more forbs (n=65) than graminoids (n=35, 34 Poaceae and 1 Juncaceae). Among 18 families of non-native forbs dispersed by Equidae, Fabaceae (n=15, 7 *Trifolium* and five *Medicago sp.*), Asteraceae (n=10) and Polygonaceae (n=8) were the most represented. *Trifolium repens*, *Plantago lanceolata*, *Poa annua* were identified four times versus three times for *Stellaria media* and *Bromus diandrus*, and 84 species appeared only once. Common

cocklebur was the single non-native plant dispersed by fur-epizoochory (Table 6.9, Box 2). Similar to domestic cattle, the role of Equidae (mainly domestic horses) in non-native plant dispersal is probably underrated. However, Gower (2008) showed that not a single non-native plant present in horse dung germinated, nor established in the field, questioning the real contribution of horse riding in the invasion of local plant communities by non-native plants.

Table 6.9: List of alien plants dispersed by Equidae including horse (*Equus caballus*), feral horse (*E. c. ferus*), donkey (*E. asinus*) and zebra (*E. burchelli*, *E. zebra*) by endozoochory (except *Xanthium strumarium* by fur-epizoochory) ordered by growth form (forb, graminoid, tree) and family.

Growth form	Family	Plant species	Dispersal vector	References	
Forb	Amaranthaceae	<i>Amaranthus retroflexus</i>	horse	g	
		<i>Amaranthus spinosus</i>	horse	d	
		<i>Chenopodium album</i>	horse	i	
		<i>Chenopodium ambrosioides</i>	horse	d	
	Apiaceae	<i>Daucus carota</i>	horse	d	
	Araliaceae	<i>Hydrocotyle</i> sp.	horse	c	
	Asteraceae	<i>Achillea millefolium</i>	horse	i	
		<i>Arthemis cotula</i>	horse	h	
		<i>Hypochaeris glabra</i>	horse	h	
		<i>Lactuca serriola</i>	zebra	f	
		<i>Matricaria chamomilla</i>	horse	d	
		<i>Pseudognaphalium luteoalbum</i>	horse	h	
		<i>Soliva sessilis</i>	horse	h	
		<i>Taraxacum officinale</i>	horse	d	
		<i>Tripleurospermum inodorum</i>	horse	i	
		<i>Xanthium strumarium</i>	horse (fur-epi)	a	
		Brassicaceae	<i>Alyssum desertorum</i>	feral horse	j
			<i>Capsella bursa-pastoris</i>	horse	g
	<i>Cardamine hirsuta</i>		horse	d	
	<i>Hirschfeldia incana</i>		horse	h	
	<i>Sisymbrium</i> sp.		feral horse	j	
	Caryophyllaceae	<i>Cerastium glomeratum</i>	horse	c,d	
		<i>Spergularia rubra</i>	horse	g	
		<i>Spergularia</i> sp.	zebra	f	
		<i>Stellaria media</i>	horse	c,h,i	
	Fabaceae	<i>Kummerowia striata</i>	horse	d	

		<i>Medicago minima</i>	horse	c
		<i>Medicago polymorpha</i>	horse	c,h
		<i>Medicago sativa</i>	donkey	e
		<i>Medicago truncatula</i>	horse	c
		<i>Medicago sp.</i>	zebra	f
		<i>Melilotus indicus</i>	horse	c
		<i>Melilotus sp.</i>	horse	d
		<i>Trifolium arvense</i>	horse	c
		<i>Trifolium glomeratum</i>	horse	c
		<i>Trifolium hirtum</i>	horse	h
		<i>Trifolium pretense</i>	horse	d
		<i>Trifolium repens</i>	horse	b,c,d,i
		<i>Trifolium subterraneum</i>	horse	c
		<i>Trifolium sp.</i>	zebra	f
Geraniaceae		<i>Erodium moschatum</i>	zebra	f
Lamiaceae		<i>Mentha pulegium</i>	horse	h
		<i>Prunella vulgaris</i>	horse	d
Linaceae		<i>Linum bienne</i>	horse	h
		<i>Linum usitatissimum</i>	horse	h
Lythraceae		<i>Lythrum hyssopifolium</i>	horse	h
Malvaceae		<i>Malva nicaeensis</i>	horse	h
Molluginaceae		<i>Mollugo verticillata</i>	horse	d
Oxalidaceae		<i>Oxalis sp.</i>	horse	c
Plantaginaceae		<i>Plantago lanceolata</i>	horse, zebra	b,c,d,f
		<i>Plantago major</i>	horse	d
		<i>Veronica perigrina</i>	horse	d
		<i>Veronica serpyllifolia</i>	horse	i
Polygonaceae		<i>Polygonum arenastrum</i>	horse	g
		<i>Polygonum aviculare</i>	horse	d,h
		<i>Polygonum cespitosum</i>	horse	d
		<i>Polygonum convolvus</i>	horse	d
		<i>Rumex acetosella</i>	horse	b,h
		<i>Rumex crispus</i>	horse	d
		<i>Rumex obtusifolius</i>	horse	d
		<i>Rumex sp.</i>	horse	c
Portulacaceae		<i>Portulaca oleracea</i>	horse	d,h
Rubiaceae		<i>Galium aparine</i>	horse	c
		<i>Galium murale</i>	horse	h
Scrophulariaceae		<i>Verbascum thapsus</i>	horse	d
Graminoid	Juncaceae	<i>Juncus bufonius</i>	horse	c
	Poaceae	<i>Agrostis capillaris</i>	horse	c
		<i>Aira cayophyllea</i>	horse	b,h
		<i>Avena barbata</i>	horse	c
		<i>Avena fatua</i>	horse	c
		<i>Avena sativa</i>	horse	g

		<i>Avena sp.</i>	horse	d
		<i>Briza maxima</i>	zebra	f
		<i>Briza minor</i>	horse	c
		<i>Bromus diandrus</i>	horse, zebra	b,c,f
		<i>Bromus inermis</i>	horse	g
		<i>Bromus hordeaceus</i>	horse	b
		<i>Bromus pectinatus</i>	zebra	f
		<i>Bromus rubens</i>	horse	c
		<i>Bromus tectorum</i>	horse, feral horse	g,j
		<i>Cenchrus sp.</i>	horse	c
		<i>Dactylis glomerata</i>	horse	b,g
		<i>Digitaria ischaemum</i>	horse	d
		<i>Digitaria sanguinalis</i>	horse	d
		<i>Eleusine indica</i>	horse	d
		<i>Festuca arundinacea</i>	horse	d
		<i>Holcus lanatus</i>	horse	b,c
		<i>Hordeum marinum</i>	horse	h
		<i>Hordeum sp.</i>	horse	c
		<i>Lolium multiflorum</i>	horse	h
		<i>Lolium perenne</i>	horse	b,c
		<i>Lolium rigidum</i>	horse	c
		<i>Lolium sp1.</i>	zebra	f
		<i>Lolium sp2.</i>	zebra	f
		<i>Phalaris paradoxa</i>	horse	c
		<i>Poa annua</i>	horse, zebra	c,d,f,h
		<i>Poa pratensis</i>	horse	g,h
		<i>Setaria viridis</i>	horse	g
		<i>Vulpia bromoides</i>	horse	b
		<i>Vulpia myuros</i>	horse, zebra	f,h
Tree	Fabaceae	<i>Prosopis sp.</i>	donkey	e

References: Liddle and Elgar, 1984 ^a; Whinam *et al.*, 1994 ^b; Weaver and Adams, 1996 ^c; Campbell and Gibson, 2001 ^d; Milton and Dean, 2001 ^e; Shiponeni and Milton, 2006 ^f; Wells and Lauenroth, 2007 ^g; Quinn *et al.*, 2008 ^h; Törn *et al.*, 2010 ⁱ; King *et al.*, 2019 ^j

Conclusions

Shiponeni and Milton (2006) stated « antelopes could play a role in restoration via seed dispersal from natural vegetation to abandoned fields » in southern Africa, and « also

influence the rate of vegetation recovery in disturbed ecosystems by supplying seeds of both indigenous and non-indigenous species ». The debate remains open whether ungulate-mediated plant dispersal is more an opportunity than a threat.

Although numerous non-native plants are dispersed by native, introduced and domestic ungulates, non-native plant dispersal and invasion mediated by large ungulates are certainly underrated. Potential ungulate vectors are distributed worldwide as livestock, abundant deer populations in their native range or introduced in areas devoid of native ungulates like New Zealand or Australia (Davis *et al.*, 2016). Wilson and Reeder (2005) censused 257 native ungulates, in comparison with the 32 (~12.5%) reviewed species known to be involved in non-native plant dispersal. Some families are not even mentioned (Rhinocerotidae and Giraffidae). Their effectiveness in plant dispersal is also linked to their own population dynamics and range expansion, with both expanding and declining ungulates.

This review also highlighted the low number of studies dedicated to either epizoochory, or both mechanisms, acting as complementary pathways for plant dispersal. Albert *et al.* (2015a) demonstrated that epizoochory applied the most selective filter on the regional flora requiring more attention in future studies.

Some non-native plants are known to be dispersed in their native range by ungulates, suggesting that plant and diaspore traits identified by Albert *et al.* (2015a) and Picard *et al.* (2016) might be relatively similar between non-native and native plants. This remains to be tested.

Identifying the effects of such vectors in non-native plants long-distance dispersal and invasion is not an easy task and requires combining long-term vegetation surveys with

spatially explicit modelling. Moreover, most plants are dispersed by multiple vectors, and assessing their relative effectiveness is challenging. Finally, ungulates act not only as dispersal vectors but also as selective herbivores, physical and chemical engineers (Wilby *et al.*, 2001), and non-native plant invasion can result from the combination of these actions (Box 1).

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CHAPTER 7

Synthesis

(version française)

Dans cette thèse, nous avons évalué le rôle des ongulés sauvages, en particulier du cerf élaphe, dans la structuration des communautés de plantes à la fois à l'échelle de la communauté et de l'individu cerf. Les ongulés jouent un rôle pivot dans les forêts tempérées en contribuant à certaines fonctions écosystémiques, notamment en modifiant les conditions locales d'habitat (Hobbs 1996). Ils interviennent aussi comme vecteurs de dispersion des graines, par endo- et épizoochorie, transportant des graines dans leur tractus digestif, leur pelage et sous leurs sabots (Albert et al. 2015a, Chapitre 5). Dans cette thèse, en complément de revues systématiques de littérature (Chapitres 2 et 6), nous avons utilisé une combinaison d'observations de terrain, de simulations basées sur des données empiriques des approches basées sur les traits pour répondre aux questions suivantes :

- 1) Quelle est la complémentarité taxonomique et fonctionnelle entre des espèces sympatriques d'ongulés et entre modes de dispersion pour un ongulé en particulier ?
- 2) Quelle est l'influence des ongulés dans la structuration des communautés végétales ? Est-ce que les traits des plantes interviennent dans la réponse des plantes à la présence des ongulés ?

3) Quelles caractéristiques fines du déplacement individuel du cerf élaphe et de la structure et composition du paysage affectent le kernel de dispersion épizoochore ?

4) L'endo- et l'épizoochorie sont-elles des modes de dispersion complémentaire, à l'échelle du vecteur individuel ? Et quels traits des plantes et des graines sont importants pour la dispersion des plantes par le cerf élaphe ?

5) Quel rôle joue les ongulés sauvages, introduits et domestiques dans la propagation des plantes exotiques ?

Principaux résultats

En présence d'au moins deux ongulés sympatriques, le chevauchement taxonomique des plantes dispersées est très variable, oscillant entre 11.76% et 87.3% par endozoochorie, alors qu'il est plus faible en épizoochorie, avec 40% au maximum (Chapitre 2). De plus, concernant le chevauchement entre modes de dispersion pour des vecteurs de dispersion uniques, les ongulés domestiques

dispersent entre 37 (vache) et 132 espèces (mouton) par endo- et épizoochorie dans le pelage, alors que le chevauchement pour les ongulés sauvages est plus faible et varie entre 8 espèces pour le chevreuil et 71 espèces chez le sanglier. Pour la gestion des milieux naturels ainsi que pour la restauration des habitats dégradés, il est ainsi conseillé d'associer des ongulés avec des régimes alimentaires différents. Par exemple, un pousseur associé avec un brouteur ou bien un omnivore généraliste, améliorera la richesse spécifique globale (composante qualitative) et la quantité de diaspores dispersées (Chapitre 2).

Quand on considère les caractéristiques de l'habitat et d'autres variables environnementales, le filtre écologique exercé par les ongulés sauvages apparaît très faible (Chapitre 3). La présence d'appendices morphologiques sur les graines favorise la dispersion par les ongulés sauvages, comme le cerf, à l'échelle de la communauté et de celle de l'individu (Chapitres 3 et 5). A l'échelle de la communauté végétale, une masse de graine faible, une forme de graine arrondie, une hauteur de libération des diaspores élevée, ainsi que de faibles valeurs indicatrices Ellenberg pour la lumière

Influencent la réponse des plantes à la présence des ongulés (Chapitre 3). Les faibles valeurs indicatrices Ellenberg pour la lumière montrent ainsi une tendance opposée à celle généralement observée dans les études antérieures. Au niveau de l'individu cerf, la masse de la diaspore, la présence/absence d'appendices allongés, la préférence pour les milieux ouverts ainsi que la longueur de la diaspore sont les traits dont les gradients sont le plus associés avec les plantes dispersées par le cerf élaphe (Chapitre 5).

Les décisions comportementales de l'individu ont une forte influence sur les kernels des plantes dispersées. Intégrer le comportement de l'animal dans les kernels de dispersion des graines est encore en développement (Westcott et al. 2005; Russo et al. 2006; Côrtes and Uriarte 2013) et un élément important pour expliquer les modèles mécanistes de la zoochorie. Le domaine vital contraint la distance maximale de dispersion des graines (Chapitre 4). La sélection de l'habitat au sein du domaine vital est aussi importante. Cependant, nos résultats ne supportent pas trop ce dernier point. Alors que le fait d'évoluer au sein d'un domaine vital et de sélectionner certains habitats au sein du home range affectent la distance de dispersion des graines, les caractéristiques de déplacement habitat dépendantes ont moins d'influence (Chapitre 4). La spécificité

d'habitat de dépôt des graines dispersées semble être intimement à la proportion de cette classe d'habitat à l'échelle du domaine vital de l'individu et du paysage. Elle est aussi sensible à la configuration spatiale du paysage en termes de types d'habitat (Chapitre 4).

Les individus dans un site, petit et fortement structuré spatialement, dispersent les graines en fortes densités à des distances plus faibles que dans un site plus vaste et homogène, où les graines sont dispersées à plus grande distance et sont plus éparpillées. Le cerf disperse les diaspores par endo- et épizoochorie. Quelques études récentes ont étudié la complémentarité taxonomique et fonctionnelle des modes de dispersion, par exemple Picard et al. (2016) (voir les jeux de données analysés dans le Chapitre 2 pour plus de détails), cependant aucune ne réalise cette analyse en tenant compte du vecteur individuel. Comparée à l'épizoochorie, l'endozoochorie comporte moins d'échantillons sans aucune graine identifiée par les individus de cerf. Néanmoins, la séparation ultérieure entre épizoochorie dans le pelage et sous les sabots n'indique aucune différence dans le nombre de diaspores transportées ou même dans le nombre d'espèces par chaque mode (Chapitre 5). Par ailleurs, les cortèges floristiques dispersés via chaque mode de dispersion diffèrent de façon importante avec très peu de chevauchements (Chapitre 5), suggérant la complémentarité des modes de dispersion. Il existe aussi des variations dépendant des sites échantillonnés, quand on considère les courbes d'accumulation d'espèces pour l'endo- et l'épizoochorie. Pour un site, l'épizoochorie disperse plus d'espèces, et ce patron est inversé pour le second site. Cette différence site-spécifique est probablement le résultat de cortèges de plantes fonctionnellement et taxonomiquement différents sur chacun des sites.

La dispersion des graines par les ongulés a des implications dans les paysages globaux soumis à des changements rapides et brusques. La propagation d'espèces exotiques est un des 4 principaux moteurs d'érosion globale de la biodiversité (Pereira et al. 2010; McConkey et al. 2012), mais le rôle des ongulés sauvages est critiquement sous-étudié et probablement sous-estimé. Nous avons inventorié des données pour 32 des 257 espèces d'ongulés répertoriées à l'échelle du globe, pour ce qui concerne les plantes exotiques dispersées (Chapitre 6), avec des familles comme les Rhinocerotidae et Girafidae complètement absents. Alors que les pousseurs dispersent spécifiquement herbacées et graminées, les omnivores dispersent une plus grande diversité de types de plantes (e.g. lianes, cactus, arbres et arbustes).

En résumé, cette thèse contribue à et renforce notre compréhension du rôle que jouent les ongulés, notamment du cerf, dans le façonnage des assemblages de plantes. Nous nous sommes concentrés plus sur l'épizoochorie que l'endozoochorie. Nous montrons que 1) le filtre écologique exercé par cerfs et sangliers peut se révéler être un faible signal en présence d'autres variables environnementales et d'habitat comme la hauteur de la canopée, le niveau d'humidité ou encore la distance aux structures linéaires d'origine humaine, et cela particulièrement dans un contexte de populations d'ongulés chroniquement élevées. 2) Les décisions comportementales individuelles ont des implications pour les kernels de dispersion des graines, en particulier les choix de l'individu au sein de son domaine vital. 3) Les distances de dispersion et la spécificité de l'habitat de dépôt des graines transportées par épizoochorie sont sensibles à la configuration paysagère. 4) Considérées à l'échelle de l'individu, endo- et épizoochorie par le cerf sont des modes de dispersion complémentaires. 5) Il devient urgent d'étudier

et de réévaluer la contribution des ongulés sauvages à la propagation des plantes exotiques pour comprendre et prédire leur rapide expansion spatiale. 6) La combinaison des traits des plantes et des indicateurs liés à la biogéographie devrait permettre de mieux cerner le rôle des ongulés dans la dispersion des plantes.

Limites de l'étude

La dispersion des graines est un processus écologique complexe qui marque la fin du cycle de reproduction de la plante. Le processus de dispersion primaire débute avec l'attachement ou l'ingestion de la graine (phase d'émigration) et se termine avec la libération de la graine dans des conditions favorables à la germination et la croissance ultérieure (phase d'immigration). Les animaux jouent un rôle pivot dans le transport des diaspores dans de nouveaux sites (Chapitre 2). La présence sur le long terme des ongulés en forte densité est susceptible de conduire à une homogénéisation biotique des communautés végétales (Chapitre 3). Le couplage d'un indice trop simpliste de présence des ongulés et d'une faible taille d'échantillon est la cause la plus probable du très faible signal observé du rôle des ongulés sauvages (Chapitre 3). La dispersion des plantes est une interaction complexe liée aux préférences des ongulés, aux conditions d'habitat et environnementales préexistantes et au cortège régional d'espèces, cet ensemble façonne les communautés végétales localement. A l'avenir, les études doivent intégrer un plus grand échantillonnage le long d'un gradient d'abondance des populations d'ongulés pour démêler plus précisément le rôle de ces derniers.

Les temps de rétention des graines sont dépendants de la forme de la graine, de sa taille et de toute modification morphologique facilitant son adhésion au corps des animaux. Le détachement de la graine est quant à lui le résultat du contact de l'animal avec différents

éléments, ainsi que lors d'actions de toilettage solitaire ou avec des conspécifiques (Liehrmann et al. 2018).

Une approche expérimentale, basée sur des simulations (Chapitre 4) risque d'être exagérément simplifiée. Nous avons utilisé les temps de détachement de *Xanthium strumarium*, estimés par Liehrmann et al. (2018), il s'agit d'une grande diaspore avec des appendices crochus, typiques du syndrome d'épizoochorie. La présence de cette diaspore est aussi très susceptible d'irriter la peau de l'animal, augmentant les chances qu'il la découvre et cherche à l'évacuer. Pour rendre ces résultats généralisables, les futures études doivent estimer les temps de détachement de différentes espèces de graines sur un gradient de traits facilitant la dispersion (Bullock et al. 2011).

De plus, à l'échelle du paysage, nous avons utilisé une caractérisation très simplifiée des habitats avec simplement deux classes (Chapitre 4). La spécificité de l'habitat de dépôt des graines dispersées dépend de la composition et de la configuration spatiale du paysage. Nous avons essayé de dépasser ces limitations en comparant deux types de paysage, et en tenant compte de la composition du domaine vital de chaque individu, nous avons obtenu des résultats convergents dans les kernels de dispersion estimés. Les prochaines études pourront inclure ou simuler des configurations paysagères plus contrastées et tester leur influence sur les kernels de dispersion des graines.

Les mesures d'endo- et d'épizoochorie sur le terrain constituent dans la plupart des cas un échantillonnage très ponctuel d'un processus plus long, et qui de ce fait son très susceptibles de sous-estimer le cortège total des plantes dispersées par un animal donné. Pour améliorer cela, nous avons comparé 4 sites différents (Chapitre 5). Pour aller plus loin, nous aimerions comparer ces résultats à nos échantillonnages réalisés à

Chambord sur cerfs et sangliers, et en Bavière sur les cerfs. Pour tester le gradient global des types de diaspores (et de leurs adaptations morphologiques) et de leur temps de rétention, des animaux habitués avec différents types de pelage pourraient aussi être utilisés, en vérifiant régulièrement le pourcentage de graines restant sur l'animal.

Remarques de conclusion

Les résultats de cette thèse contribuent à mieux comprendre la dispersion des graines par les ongulés, notamment le cerf. Le focus initial sur l'épizoochorie est délibéré, du fait que beaucoup moins de choses sont connues et que par ailleurs ce mode de dispersion est plus sélectif que l'endozoochorie. En particulier, nous avons essayé d'évaluer l'influence des ongulés dans la structuration des communautés végétales, mais nous avons finalement montré que cette interaction est assez difficile à isoler, notamment dans le contexte particulier du Domaine National de Chambord. De plus, nous avons simulé un modèle mécaniste de kernel de dispersion incluant les décisions comportementales du vecteur dans deux sites différents. Nos résultats insistent sur l'importance de tenir compte du domaine vital de chaque individu. Finalement, nous montrons qu'endo- et épizoochorie sont des modes de dispersion complémentaires. De plus, le fait que nous ne trouvions pas de différences significatives entre les trois modes de dispersion pour le nombre d'espèces ou de diaspores transportées remet en cause l'idée généralement tenue que l'endozoochorie est plus importante que l'épizoochorie (ce qui est pourtant vrai pour les oiseaux d'eau et les passereaux). Le kernel total de dispersion d'une plante inclut tous les modes de dispersion primaire et secondaire (actifs et passifs). La complémentarité mise en lumière devrait pousser les recherches dans cette direction. Et pour conclure, nous militons pour développer les recherches sur la dispersion des plantes

exotiques, encore sous-étudiée et pourtant cruciale pour comprendre l'évolution de la biodiversité dans le futur.

Synthesis

(English version)

In this thesis, we assessed the role of wild ungulates, especially red deer, in structuring plant communities both at the community level as well as at the level of individual red deer. Ungulates play a pivotal role in temperate forests in maintaining ecosystem functions, modifying local habitat conditions (Hobbs 1996). They also play a crucial role as seed dispersers - both endo- and epizoochorously, carrying seeds in their guts, fur or hooves (Albert et al. 2015a, Chapter 5). In this thesis, in addition to assessing published literature (Chapters 2 and 6), we use a combination of observational, data-driven simulation and trait based approaches to answer the following questions-

- 1) What is the taxonomic and functional complementarity between different i) co-occurring ungulates and ii) dispersal modes for a given ungulate?
- 2) What is the influence of ungulates in structuring local plant communities? Do species-level traits intervene in plants' responses to ungulates?
- 3) Which characteristics of red deer individual movement behaviour and landscape structure affect epizoochorous seed dispersal kernel?
- 4) Are endozoochory and epizoochory complementary dispersal modes at the level of individual deer? Which plant traits are important for seed dispersal by red deer?

- 5) What is the role played by wild, introduced and domestic ungulates in spread of non-native plant species?

We discuss the main findings below.

Main findings

When two or more ungulates are sympatric, the overlap is highly variable and ranges between 11.76% and 87.3% for endozoochorously dispersed plants, whereas the overlap is lower and peaks at 40% for the epizoochory (Chapter 2). Additionally, for overlap between dispersal modes for single animal vectors, domestic ungulates are recorded to disperse between 37 (cattle) and 132 species (sheep) by both endo- and fur-epizoochory, whereas the overlap, considering wild ungulates, is lower and varies between eight plant species for roe deer and 71 for wild pig. For management of natural areas as well as for restoration of degraded areas, it is desirable to include ungulate species with complementary feeding regimes. For e.g. a grass and roughage eater introduced alongside a species from a different feeding regime such as a concentrate feeder or an omnivore, enhance the plant species richness as well as increase the quantum of dispersed diaspores (Chapter 2).

When considering habitat and other environmental factors, ecological filtering by ungulates has a rather weak signal (Chapter 3). Presence of modified diaspore appendages aids dispersal by large animals, such as red deer, both at the community as well as individual level (Chapter 3, Chapter 5). At the plant community level, lower diaspore mass, round diaspore shape, higher diaspore release height and lower Ellenberg light values were important traits influencing plant species response to ungulate

presence (Chapter 3). The lower Ellenberg light values show an opposite trend compared to previous studies. At the level of individual deer, diaspore mass, diaspore with no or elongated appendages, light demanding open-area species and diaspore length were traits whose gradients were most associated with those of plants dispersed by red deer (Chapter 5).

Behavioural decisions made by animal have a strong influence on the consequent seed dispersal kernels. Integrating animal behaviour into seed dispersal kernels is still a recent development (Westcott et al. 2005; Russo et al. 2006; Côrtes and Uriarte 2013) and an important part for explaining mechanistic models of animal-aided dispersal. Home range places constraints on the maximum distance to which an individual animals transports a seed (Chapter 4). Habitat preferences within the home range can also influence this. However, our results did not present a strong enough evidence for it. While home range centre and habitat preference within the home range affect the seed dispersal distance, the habitat-specific step lengths are less influential (Chapter 4). Additionally, habitat specificity of dispersed seeds seems to be closely related to the proportion of the particular habitat class both at the level of individual home ranges and landscape. It is also sensitive to the spatial landscape configuration of habitat types (Chapter 4). Individuals in a small, spatially-structured landscape disperse seeds in higher densities to a shorter distance compared to individuals in a more contiguous landscape that transport seeds farther and with deposited seeds more spread out.

Red deer disperse diaspores both endo- and epizoochorously. A few recent studies have looked at taxonomic and functional complementarity of dispersal modes, for e.g. Picard et.al. 2016 (see datasets in Chapter 2 for more details), but none has compared them at

the level of individual animal vector. Compared to epizoochory, endozoochory had fewer samples with no recorded seeds in the dispersed plant species by individual red deer. Nonetheless, further separation of epizoochory into fur- and hoof- epizoochory indicates no difference in either the number of transported diaspores or in the number of plant species dispersed by each mode (Chapter 5). Moreover, the dispersed plant species composition for each dispersal mode largely differ from each other with few overlaps (Chapter 5), suggesting complementarity of dispersal modes. There are also site-specific differences in species accumulation curves plotted for endo- and epizoochory. In one site, the epizoochorous species are higher in number among the dispersed plant species, and it is exactly reverse at the other site. This site-specific difference is likely to be an influence of the taxonomically and functionally different plant species pool present at each of the sites.

Seed dispersal by ungulates have implications in fast-changing global landscapes. Spread of invasive species is one of the four major drivers of global biodiversity change (Pereira et al. 2010; McConkey et al. 2012), but the role of native, wild ungulates is severely understudied. We recorded data for only 32 out of 257 species of ungulates with respect to the non-native plant species dispersed by them (Chapter 6), with families such as Rhinocerotidae and Girafidae completely missing. While grazers specifically disperse forbs and graminoids, omnivores tend to disperse a much wider range of plant growth types, including vines, shrubs and trees.

In summary, this thesis furthers and strengthens our understanding of the role ungulates play, especially red deer, in influencing plant communities. We especially focused more on epizoochorous dispersal than endozoochory. We show that 1) ecological filtering of

plant by ungulates (red deer and wild boar) could be a weak signal in the presence of other local environmental and habitat conditions such as canopy height, NDWI and distance to road that we used in this study, and specifically in the context of long-term and chronically high (human-induced) densities of ungulate populations. 2) Individual behavioural decisions has implications for seed dispersal kernels of dispersed plants, especially home ranging behaviour of a large bodied ungulate species such as the red deer. 3) Seed dispersal distances and habitat specificity of externally transported diaspores are sensitive to landscape configuration and composition. 4) Taken at individual animal level, endo- and epizoochory by red deer are complementary dispersal modes. 5) There is an urgent need to study and reassess dispersal of non-native plant species by ungulates to understand and predict how they contribute to the fast spatial spread of invasive plants globally. 6) Combined plant species-level traits and biogeographic indicators play an important role in enabling dispersal of plants by ungulates.

Limitations of the study

Seed dispersal is a complex ecological process that marks the end of the reproductive cycle for the plant. Primary dispersal process starts with successful seed attachment/ingestion (emigration phase) and ends with the diaspore being successfully deposited in growth-conducive conditions (settlement phase). Animals play a pivotal role in transporting diaspores to new locations (Chapter 2). Long-term presence of ungulates in high densities is likely to cause biotic homogenization of the local plant community (Chapter 3). Coupled with a simplified index of ungulate presence we used and the small sample sizes in the study, is the likely cause of the weak signal of ungulate ecological

footprint in our study (Chapter 3). Plant dispersal by ungulates is a complex interaction of ungulate preferences, prevailing local habitat and environmental conditions and regional plant species pool that together shape the local plant community. Studies in the future should include larger sample sizes along a gradient of ungulate abundance for disentangling the role of ungulates more fully.

Diaspore retention times are sensitive to seed shape, seed size and any modifications to appendage for better attachment to animal bodies. Seed detachment could be a result of contact of animal with another plant post-attachment of seed (Mouissie et al. 2005), as well as allo-grooming and social interactions between individuals (Liehrmann et al. 2018). An experimental, simulation-based approach (Chapter 4) risks being oversimplified in its details. We used the detachment times of *Xanthium strumarium*, estimated by Liehrmann et al. (2018) which is a large diaspore with hooked appendages, typical of an epizoochory syndrome. This species is likely to irritate the skin of the animal increasing chances of its discovery and detachment. To make the results generalizable, future studies need to estimate retention times on different species of diaspores with a gradient of dispersal-enabling traits (Bullock et al. 2011).

Additionally, at the level of landscape, we used simplified forest and open as habitat classes (Chapter 4). Also, habitat specificity of dispersed seeds depends on landscape composition and spatial configuration. We tried to overcome these limitations by comparing two contrasting landscape types, and taking advantage of the variable individual within home range habitat composition and found similar results in the estimated dispersal kernels. However, further studies should include or simulate different

landscape configuration and composition and test their influence on seed dispersal kernels.

Measures of endo- and epizoochory in field are in most cases a one-time sampling effort that presents a snapshot of the whole process in time. It is highly likely that the species recorded are an underestimate of the total pool of species dispersed by an animal. To overcome this we compare four different sites (Chapter 5) with respect to the dispersed plant species by individual red deer. Going further, we would like to compare these findings from additional sites from the data we collected on field from Chambord and Bavaria. To capture the whole gradient of diaspore types and range of retention times, tame animals with different fur types could be used to experimentally estimate retention times by attaching different types of diaspores and checking regularly for detachments.

Concluding remarks

The results of this thesis contribute towards further understanding of seed dispersal by ungulates, especially by red deer. The primary focus on epizoochory is deliberate, as much less is known about this specific and more selective dispersal mode compared to endozoochorous dispersal by red deer. In particular, we tried to assess the influence of ungulates on structuring plant community, but found that it is a difficult interaction to isolate, especially in a site with chronic high densities of ungulates. Additionally, we simulate a mechanistic model of seed dispersal kernel that includes particular behavioural preferences of individual animals and compare two contrasting sites. Our results stress on the importance of accounting for home range of a range resident species when estimating seed dispersal kernels. Additionally, we show that endozoochory and epizoochory are complementary processes in nature. There are no significant differences

in the number of diaspores transported by either of the dispersal modes nor in the number of plant species by each of them. This challenges the broadly-held idea that endozoochory outweighs epizoochory (which is true in the case of waterbirds and passerines). The total dispersal kernel of a plant includes all possible primary and secondary dispersal vectors as well as all active and passive dispersal modes. The complementarity of dispersal modes is thus, an important contribution in this direction. We also make the case for further research to focus on the dispersal of non-native plants, which is a highly understudied effect of seed dispersal by ungulates, but an important driver of biodiversity change in the global scenario.

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Dispersion des graines par le cerf élaphe (*Cervus elaphus*) pendant la saison de chasse : mise en place d'une expérimentation dans le Domaine national de Chambord

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Depuis plusieurs décennies, les populations de cerf élaphe (*Cervus elaphus*), de chevreuil (*Capreolus capreolus*) et de sanglier (*Sus scrofa*) présentent une forte expansion spatiale et numérique à l'échelle européenne. Cette augmentation est imputable à l'amélioration qualitative et quantitative de leurs habitats (pratiques agricoles dont la généralisation des cultures céréalières d'hiver, expansion de la forêt pendant le XX^e siècle ; Gill, 1990) et à l'abandon de l'élevage extensif en milieu forestier. En outre, l'exploitation cynégétique rationalisée mise en place dans les années 1970 (c'est-à-dire plans de gestion conservatoires) a contribué à restaurer les faibles populations après-guerre. En conjonction avec une faible présence de grands prédateurs (à l'exception du loup depuis 1992, surtout concentré géographiquement dans le quart Sud-Est de la France) et, plus récemment, avec une diminution du nombre des chasseurs, la forte plasticité écologique de ces trois espèces d'ongulés sauvages leur a aussi permis de se développer.

À l'heure actuelle, le chevreuil et le sanglier sont présents dans la quasi-totalité des forêts françaises, et le cerf élaphe dans plus de la moitié de celles-ci. L'abondance de ces animaux n'est pas sans répercussions sur les massifs forestiers qu'ils habitent. Elle accroît la pression exercée sur la végétation des parcelles boisées et contraint la croissance en hauteur des jeunes arbres. Le cerf, en particulier, peut dégrader les arbres en consommant leur écorce. Il augmente également la surface des sols piétinée (Fuller et Gill, 2001 ; Gill et Beardall, 2001). La strate arbustive forestière peut être excessivement affectée (c'est-à-dire visibilité d'une ligne d'abrouissement) et la régénération forestière retardée, voire compromise dans certains cas. Parallèlement, ces herbivores peuvent favoriser la diversité et la productivité végétale, notamment des plantes herbacées (Pellerin *et al.*, 2010 ; Vallée *et al.*, 2016 ; Boulanger *et al.*, 2018). En consommant des plantes très compétitives, en assurant la redistribution des nutriments et de certaines graines (Pellerin *et al.*, 2016), ils interagissent dans l'assemblage des communautés végétales.

Les grands herbivores forestiers sont susceptibles de récupérer et de disséminer passivement des graines dans leur pelage en se déplaçant dans la végétation et en s'alimentant (Janzen, 1984 ; Heinken et Raudnitschka, 2002 ; Couvreur *et al.*, 2005). Les facteurs qui influent sur la prise en charge des graines par un animal et la distance à laquelle elles sont dispersées sont multiples.

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La graine elle-même peut présenter plusieurs caractères morphologiques aidant à l'accroche aux poils des animaux, comme des crochets ou des substances adhésives ; bien que de nombreuses graines dispersées par les ongulés ne présentent aucune adaptation spécifique pour l'épizoochorie (Albert *et al.*, 2015). Certaines plantes dispersées par endozoochorie (c'est-à-dire transport interne) n'attirent pas activement les animaux disperseurs avec un fruit charnu, mais plutôt par un feuillage appétant (Janzen, 1984 « *Foliage is the fruit hypothesis* ») ou s'en remettent à une rencontre fortuite entre les deux protagonistes. Elles présentent généralement des périodes de fructification et des morphologies qui optimisent les probabilités de contact avec différents vecteurs de dispersion (Willson et Thompson, 1982 ; Herrera, 1995 ; Herrera et Pellmyr, 2009). En termes d'épizoochorie, la hauteur à laquelle se trouvent les graines dans la végétation est un facteur qui détermine le potentiel animal disperseur (Willson et Traveset, 2000). On observe des différences entre les vecteurs de dispersion dans l'abondance des graines et les plantes transportées dans le pelage et dans les fèces ; les sangliers sont par exemple susceptibles d'être couverts de nombreuses graines de plantes variées récupérées en se déplaçant dans les strates basses de la végétation, tandis que l'alimentation sélective et le pelage lisse des chevreuils réduisent leur potentiel de dispersion (Heinken et Raudnitschka, 2002 ; Oheimb *et al.*, 2005). Les plantes dispersées et les distances parcourues par leurs graines sont ainsi directement liées aux mouvements et à l'environnement des grands herbivores forestiers.

Nous avons profité des captures de biches lors des panneautages (photo 1, p. 373) dans le Domaine national de Chambord (Loir-et-Cher, figure 1, ci-dessous) pour réaliser une nouvelle expérimentation, visant à estimer en direct la capacité et la distance de dispersion de diaspores

Figure 1 REPRÉSENTATION DES DIFFÉRENTS TYPES DE MILIEU DANS LE DOMAINE NATIONAL DE CHAMBORD

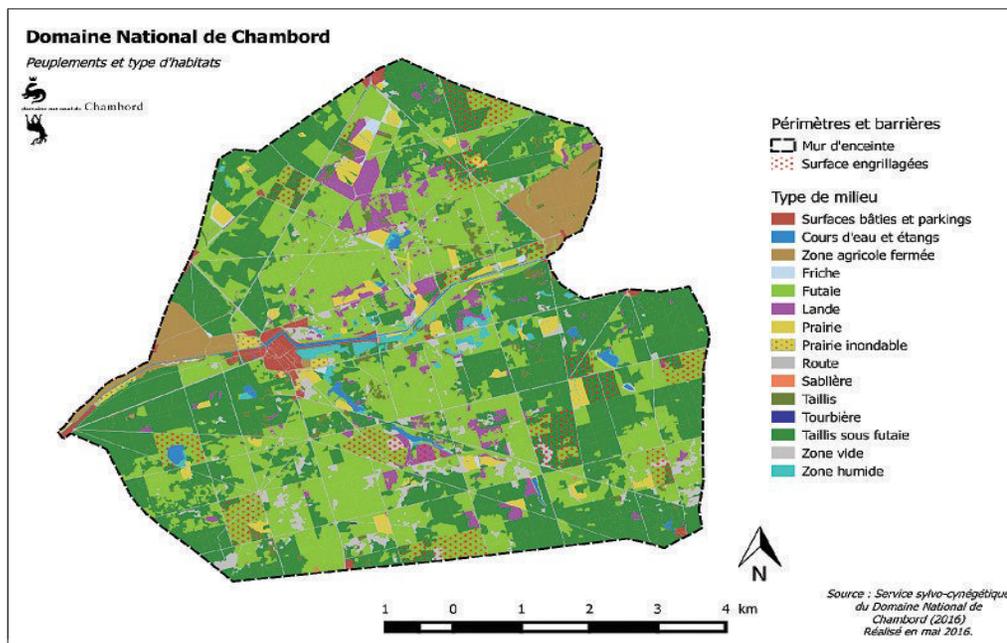




Photo 1 Un panneautage à Chambord avec 4 biches

Photo Gérard Bedarida

de lampourde (*Xanthium strumarium* L.) en milieu boisé (c'est-à-dire offrant une faible visibilité) (photo 2, p. 374). Le Domaine national de Chambord présente la particularité d'être ceint d'un mur de 32 km de long et de près de deux mètres de haut, et d'être ainsi isolé des populations d'ongulés des espaces naturels alentours, situés au-delà du mur d'enceinte.

EXPÉRIMENTATION RÉALISÉE

Des colliers GPS-GSM ont été posés sur les biches de Chambord depuis l'année 2015. Les biches sont capturées en hiver lors de panneautages (photo 1, ci-dessus), qui peuvent être assimilés à des actions de chasse. En effet, le panneautage consiste à balayer une surface forestière prédéfinie avec un cordon de traqueurs (c'est-à-dire des personnes qui se déplacent en forêt) pour guider les animaux vers des filets. Ceux-ci ont été précédemment installés et légèrement tendus à l'aide de perches plantées dans le sol. Lorsque les animaux percutent ces panneaux de filets, les perches tombent et les animaux se retrouvent piégés. Les animaux capturés sont ensuite équipés d'un collier GPS qui permettra de suivre leurs déplacements au sein du Domaine. Les colliers GPS sont programmés à l'avance pour enregistrer la position géographique des animaux à intervalles réguliers (par exemple toutes les 5 minutes dans le cadre de cette étude). Ces données GPS ont été utilisées pour étudier les déplacements des biches dans la zone d'étude (figure 2, p. 374).

Parallèlement, avant de relâcher les animaux capturés dans les filets, nous avons posé des fruits (c'est-à-dire chaque fruit contient deux graines) de *Xanthium strumarium* (photo 2, p. 374) sur le poitrail et la croupe de 5 biches (à raison de 20 fruits sur chacune de deux parties du corps de l'animal) (photo 3, p. 375). Nous avons choisi ces fruits car ils ont la caractéristique d'être de grosses tailles (entre 20 et 25 mm) et surtout pourvus de nombreux crochets bien visibles (plante épizoochore), ce qui permet une fixation plus aisée sur les biches. Ces graines ont été préalablement stérilisées à l'aide d'un four à micro-ondes et peintes de deux couleurs différentes, distinguant chaque partie du corps. La taille et la coloration des fruits choisis avaient pour objectif

d'optimiser la détection des fruits détachés le long du trajet des biches suivies. Suite au relâcher des biches, nous avons suivi le cheminement emprunté par chaque individu, en utilisant les données provenant des GPS-GSM (une localisation toutes les cinq minutes entre le moment du lâcher de la biche, vers 12 h, et 20 h le même jour). Nous avons ainsi relevé la position géographique à l'aide d'un GPS manuel et la couleur des graines retrouvées au sol ou dans la végétation.

Figure 2 EXEMPLE DES DÉPLACEMENTS MENSUELS (DE FÉVRIER À DÉCEMBRE) D'UNE BICHE DU DOMAINE NATIONAL DE CHAMBORD (1 mm = 50 m)

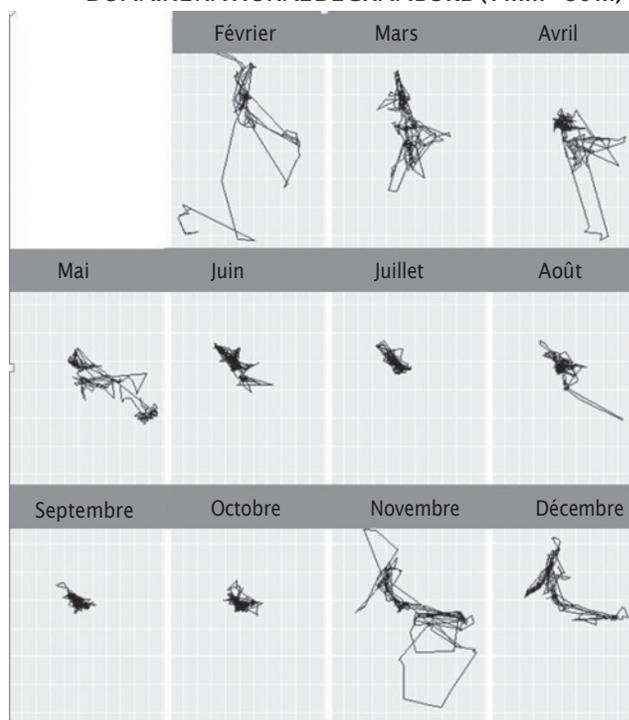


Photo 2 Fruit de lampourde (*Xanthium strumarium*), sectionné pour faire apparaître les deux graines
Photo Christophe Baltzinger



Photo 3 Fruits de lampourde (*Xanthium strumarium* L.) positionnés sur la croupe d'une biche capturée lors d'un panneautage, équipée d'un collier GPS et insérée dans un sabot avant d'être relâchée
Photo Sonia Saïd

LA DISTANCE DE FUITE ET LES CONSÉQUENCES SUR LA DISPERSION DES FRUITS DE LAMPOURDE

Le tableau I (ci-dessous) résume les résultats de l'expérimentation avec les 5 biches équipées de diaspores et de collier GPS.

Tableau I **Résultats de l'expérimentation sur les distances de dispersion épizootique évaluées *in situ*, dans le Domaine national de Chambord**

Individus	Nombre total de diaspores posées	Pourcentage de diaspores retrouvées (%)	Nombre de diaspores de poitrail retrouvées	Nombre de diaspores de croupe retrouvées	Distance moyenne des diaspores au point de lâcher (m)	Distance maximale des diaspores au point de lâcher (m)
1	40	55	17	5	13,1	41,2
2	40	48	17	2	256,4	2 846,8
3	40	5	1	1	14,0	17,1
4	40	25	7	3	9,6	9,6
5	40	35	13	1	20,3	43,2

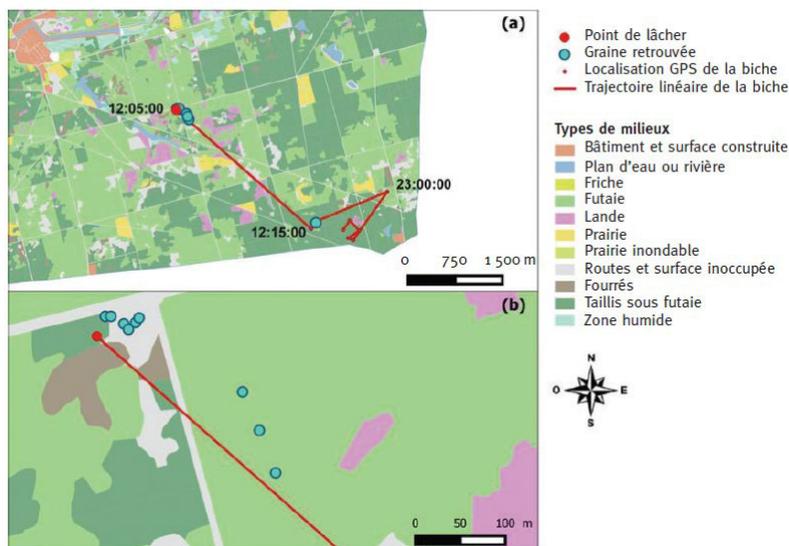
La figure 3 (p. 376) représente les localisations des diaspores sur le trajet de la biche 2 (tableau I, ci-dessus).

Cette expérimentation nous montre que la dispersion des diaspores par les biches peut atteindre des distances importantes en peu de temps. La dispersion des plantes comprend la prise en charge des graines, la phase de transfert et l'installation des plantes à distance, après germination. Dans cette expérimentation, nous nous sommes concentrés sur la phase de transfert.

Figure 3

REPRÉSENTATION DE LA MANIPULATION D'UNE BICHE, DONT UNE DES DIASPORES ACCROCHÉES A ÉTÉ RETROUVÉE À PLUS DE 2 846 MÈTRES DE SON POINT DE DÉPART

Cette biche a été capturée le 26 janvier 2016. En (a) est visible l'ensemble du trajet effectué par la biche entre le point de départ (daté à 12:05:00) et le reste de la journée. Le site de lâcher, où a été retrouvée la majorité des diaspores accrochées sur le poitrail, est agrandi en (b).



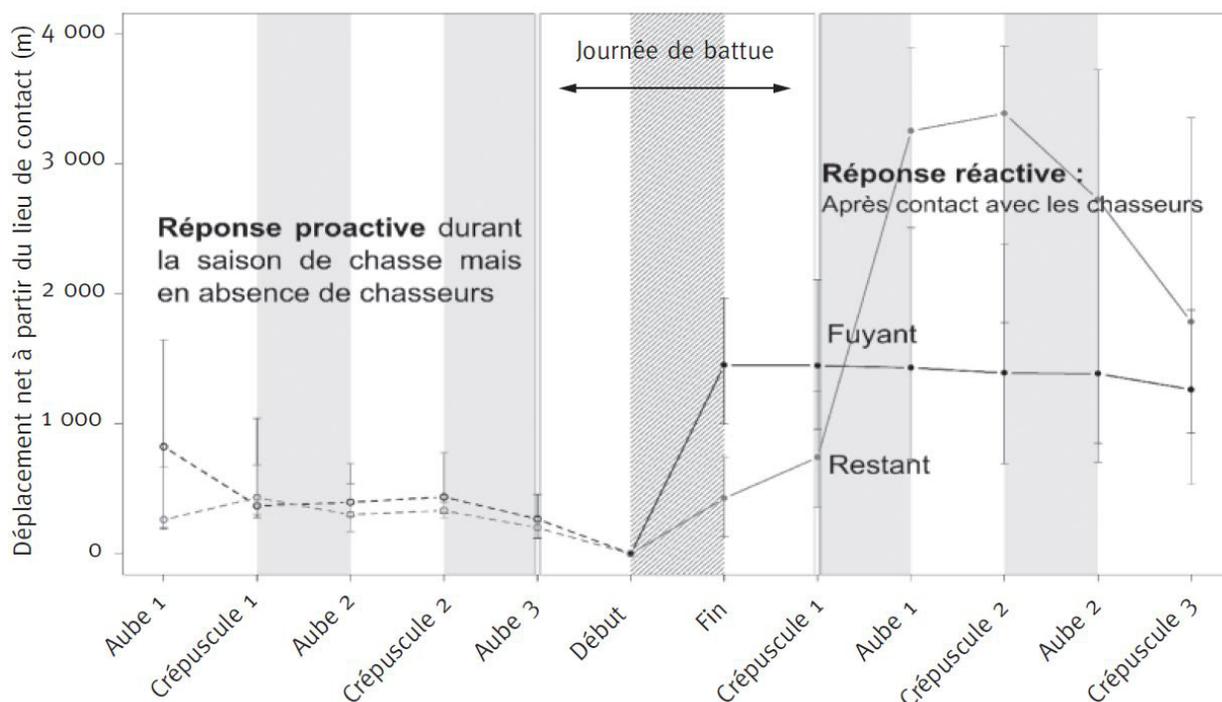
Picard et Baltzinger (2012) ont montré que la quantité et la diversité de graines transportées par le pelage et entre les sabots d'individu de l'espèce cerf élaphe sont comparables à celles des chevreuils, et moindre que celles des sangliers. Cependant, le nombre de diaspores transportées par des individus au pelage similaire (par exemple cerf et chevreuil) dépend de la surface corporelle, surface d'attache potentielle pour les diaspores (Bohème, 2012). Ainsi, les ongulés forestiers peuvent récolter des graines sur la surface de leur corps lorsqu'ils sont au contact de la végétation — en se couchant ou en se baigeant par exemple dans la litière forestière, dans les hautes herbes d'une prairie, ou en s'y alimentant. Notre expérimentation tend à montrer que ce sont les graines placées sur le poitrail, plus exposées à des frictions qui tombent le plus rapidement. Le temps moyen que peut passer une graine sur son hôte dépend de ses adaptations morphologiques à l'épizoochorie, de sa localisation sur l'animal, des mouvements et de l'environnement dans lequel celui-ci évolue (Albert *et al.*, 2015). De plus, la chasse pourrait avoir un effet, sur la distance de dispersion des graines en hiver, en augmentant les distances que les cervidés peuvent parcourir (Chassagneux *et al.*, 2020 ; figure 4, p. 377).

Ce que nous constatons sur la figure 4 (p. 377), c'est que lors des journées de battues les animaux sortent de la zone de traque, soit dès le début de la traque soit après la traque et vont

Figure 4

DÉPLACEMENT NET MÉDIAN DU LIEU DE CONTACT (c'est-à-dire la position de l'individu au début de la battue) CALCULÉ SUR UNE PÉRIODE DE CINQ JOURS

Deux réponses immédiates ont été distinguées selon que l'individu franchissait la ligne de tir et s'éloignait ou pas de la zone de traque pendant la battue. La ligne noire décrit les schémas de déplacement de biches « qui fuient » depuis le lieu de la rencontre, tandis que la ligne grise caractérise les individus « qui restent ». Les points pleins symbolisent les réponses réactives (c'est-à-dire après des contacts avec des chasseurs), tandis que les points vides correspondent au comportement proactif (c'est-à-dire pendant la période de chasse, mais en l'absence de chasseurs). Les barres verticales représentent les 1^{er} et 3^e quartiles. Les zones grises représentent les périodes nocturnes et les zones blanches les périodes diurnes. La zone gris foncé correspond à la période de battue (environ 45 minutes) (d'après Chassagneux *et al.*, 2020).



à une distance allant de 2 km à 11 km (« animaux fuyant » : 6 721 m [2 044 - 11 229], « animaux restant » : 5 027 m [2 235 - 6 660]) (Chassagneux *et al.*, 2020). Généralement, alors que l'essentiel des graines tombent très tôt, un faible pourcentage de graines reste accroché très longtemps et celles-ci peuvent se déplacer à une plus grande distance lors des battues. Nous pouvons donc nous attendre à ce que les herbivores qui partent à grande vitesse du fait du dérangement dû à la chasse aient une probabilité plus importante de perdre les graines qu'ils portent en raison de leurs mouvements brusques et de leur passage brutal dans la végétation. Dans le même temps, la fuite des ongulés sauvages encouragerait le transport d'une portion des graines accrochées à grande distance ; ceci pourrait donner l'opportunité à une espèce de plante de s'établir dans un milieu où la concurrence intraspécifique est plus faible, de coloniser des nouveaux environnements et ainsi d'influer sur la composition des communautés végétales (Boulanger *et al.*, 2011). L'intensification de la gestion cynégétique des ongulés, du fait de l'augmentation de leurs populations, avec potentiellement une augmentation du nombre de battues sur les territoires de chasse pourrait donc avoir un effet non négligeable sur le potentiel de dispersion des plantes.

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DISPERSION DES GRAINES PAR LE CERF ÉLAPHE (*CERVUS ELAPHUS*) PENDANT LA SAISON DE CHASSE: MISE EN PLACE D'UNE EXPÉRIMENTATION DANS LE DOMAINE NATIONAL DE CHAMBORD (Résumé)

Les populations d'herbivores sauvages sont en nette augmentation depuis plusieurs décennies dans l'hémisphère Nord en raison du changement des pratiques agricoles et des plans de gestion environnementaux. Cet essor est à l'origine de surpâturage, de perturbations physiques du sol par piétinement et labour du sol et de dégâts aux écorces et aux bourgeons d'essences objectif. Ces animaux contribuent aussi au fonctionnement des écosystèmes forestiers par la dispersion des plantes ou la redistribution des nutriments à l'échelle de leurs domaines vitaux. L'épizoochorie, transport externe de graines qui s'accrochent dans les phanères (par exemple pelage, plumage) des animaux, est un des principaux modes de dispersion des graines. Dans cette étude, nous nous sommes intéressés au transport des diaspores pourvues de crochets de *Xanthium strumarium* L. par le cerf élaphe (*Cervus elaphus*) dans un domaine soumis à la chasse. L'expérimentation s'appuie sur l'analyse des données de localisation de biches capturées, équipées de colliers GPS et relâchées au sein du Domaine national de Chambord.

DISPERSAL OF SEEDS BY RED DEER (*Cervus elaphus*) DURING THE HUNTING SEASON - SETTING UP AN EXPERIMENT AT THE NATIONAL ESTATE OF CHAMBORD (Abstract)

Populations of wild herbivores have significantly increased in the last decades in the Northern hemisphere due to changes in farming practises and environmental management plans. This expansion has caused over-grazing, disruption of the physical properties of soil arising from animals stamping and standing and damage to bark and buds of target species. These animals also contribute to the functioning of forest ecosystems by dispersing plants and redistributing nutrients throughout their range. Epizoochory, the external transportation of seeds attached to skin appendages of animals (e.g., fur, feathers) is one of the main vehicles for seed dispersal. In this study, we examined the transportation of *Xanthium strumarium* L. diaspores with hook appendages by red deer (*Cervus elaphus*) on a hunting estate. The experimentation relies on the analysis of location data for hinds that have been captured and equipped with GPS collars and then released again in the National Estate of Chambord.

ANNEXURE 2

Academic participation during the thesis

Poster Presentation

- **Gordon research conference. Movement ecology of Animals. Italy. (3-8 Mar 2019).**
Title: Effects of landscape spatial structure and movement behavior of red deer (*Cervus elaphus*) on epizoochorous seed dispersal kernels.
- **Gordon research seminar. Movement ecology of Animals. Italy. (2 Mar 2019).**
Title: Effects of landscape spatial structure and movement behavior of red deer (*Cervus elaphus*) on epizoochorous seed dispersal kernels.
- **5th Young Natural History Scientists' Meeting, Paris (6-10 March 2018).**
Title: The joint distribution of zoochorous plant species in the presence of wild ungulates.

Supervision

- **Hai Linh Nguyen** (Mar-Aug 2019), Internship. Master 2 Ecology, Monitoring and Management of Ecosystems. Université de Franche-Comté.
Topic: Complementarity of ungulate-mediated dispersal processes in different sites across Europe. Co-supervised with Dr. Christophe Baltzinger

Publications outside of thesis work (2016-2020)

- Naniwadekar, R., Rathore, A., **Shukla, U.**, and Datta, A. Patterns of roost site use by Asian hornbills and implications for seed dispersal. *Journal of Field Ornithology*. (Submitted)
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