

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

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

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

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

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

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

INTRODUCTION

Seed dispersal is a key process in determining plant populations and community dynamics. Particularly, long-distance dispersal events (> 100 m for plants, Cain et al. 2000), though rare, are crucial to maintaining the connectivity between isolated populations necessary for plant species to survive at the regional scale (Will & Tackenberg 2008). Long-distance dispersal by large herbivores also accounted for the plant migration rates during the Holocene (Pakeman 2001). Understanding long-distance dispersal mechanisms and their consequences is critical in a context of rapidly changing environments under the effects of global change (Shupp et al. 2010). Because plants are fixed, their mobility relies on vectors that may be abiotic like wind (anemochory) and water (hydrochory), or biotic (zoochory) (Ridley 1930). Wind and water disperse few species over long distances (Mouissie et al. 2005, Schmidt et al. 2004) and wind is ineffective inside forest stands (Howe & Smallwood 1982). Birds and mammals are therefore the main vectors for long-distance seed

dispersal within and among forest areas. While birds seem to disperse specific plants according to their diet (endozoochory), large herbivores, compared to small-bodied rodents, might be able to disperse many plant species in their fur due to a larger surface available for hitching seeds. For example, the role of roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) in the expansion of Green Hound's-tongue (*Cynoglossum germanicum* Jacq.) through external dispersal has recently been highlighted (Boulanger et al. 2011).

Wild ungulates provide useful models for the study of long-distance plant dispersal and distributional dynamics under changing landscapes. First, roe deer, red deer and wild boar (*Sus scrofa*) populations have been increasing in Europe, and particularly in France, since the 1970s. The number of animals killed by hunting has increased ninefold over the last forty years, reaching over 500,000 individuals for both roe deer and wild boar and 50,000 for red deer in 2010 (Source: 'Réseau Ongulés sauvages ONCFS-FNC-FDC').

Second, due to their large home ranges and high travel speed, wild ungulates move over long distances and through

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

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

a wide diversity of open and closed habitats (Heinken et al. 2002).

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

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

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

MATERIALS AND METHODS

Animal species and hunting areas

We used a cross-species comparative approach on the three most common wild forest ungulates in France and Europe, which are easily accessible through the practice of hunting: the roe deer, a browser ruminant species; the red deer, a browser/grazer ruminant species (Hoffman 1989); and the wild boar, an omnivorous-frugivore non-ruminant species.

Comparing these three species is pertinent due to their ecological differences in terms of body size, fur structure, home range and diet (see table 1), all of which may influence the dispersal process. Samples were collected on animals shot in Loiret forests (France) (fig. 1): the Domaine des Barres and the Forêt de Montargis, inhabited by both roe deer and wild boar, and the Massif de Lorris where red deer are present. The forests were chosen for the presence/absence of red deer and for variations in the abundance of both roe deer and wild boar. The Domaine des Barres and the Forêt de Montargis are dominated by sessile oak (*Quercus petraea* (Matt.) Liebl.) and hornbeam (*Carpinus betulus* L.) stands and the Massif de Lorris is composed of sessile oak and Scots pine (*Pinus sylvestris* L.) in pure and mixed stands.

Assessing epizoochorous transport

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

Comparison between transported plants and the local flora

Plant species observed in all the districts belonging to the three forests were considered to be the local flora. The list of plant species present in each district was obtained from the Conservatoire Botanique National du Bassin Parisien (available online at <http://cbnbp.mnhn.fr/cbnbp/observatoire/coll-TerrForm.jsp>). Authorship for each species is given in elec-

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

Statistical analyses

Within- and among-species variations in animals – In the Domaine des Barres, we were only able to obtain data for roe deer, though wild boar is also present in this forest.

Red deer only occurs in the Massif de Lorris. We therefore used Kruskal-Wallis tests to compare the number of transported plant species and diaspores among roe deer, red deer and wild boar in the Massif de Lorris, and between roe deer and wild boar in the Forêt de Montargis separately. We also used the same approach to compare intra-specific variations for roe deer among all three studied forests. In case of significant differences among animal species or study sites, we used Kruskal-Wallis tests to conduct pairwise comparisons.

Ecological traits of transported plants – To determine whether or not epizoochorous species were more dispersed than other plant species, we compared epizoochorous species in our samples to those present in the local flora of the Loiret. In addition, we compared the number of epizoochorous species on fur vs. hooves, and in cervidae vs. wild boar, through pairwise comparisons relying on Fisher's exact test (Crawley 2005).

The whole analysis was carried out using the R software (R Development Core Team 2010, stats package), with a $p = 0.05$ threshold.

RESULTS

Altogether we identified 651 diaspores corresponding to 41 plant species. Ten percent of the seeds could not be identified. Only certain plant species (24%) were found in the cleft of the hoof. The five most abundant species identified in fur were, in decreasing order, *Chenopodium* sp., *Betula pendula*,

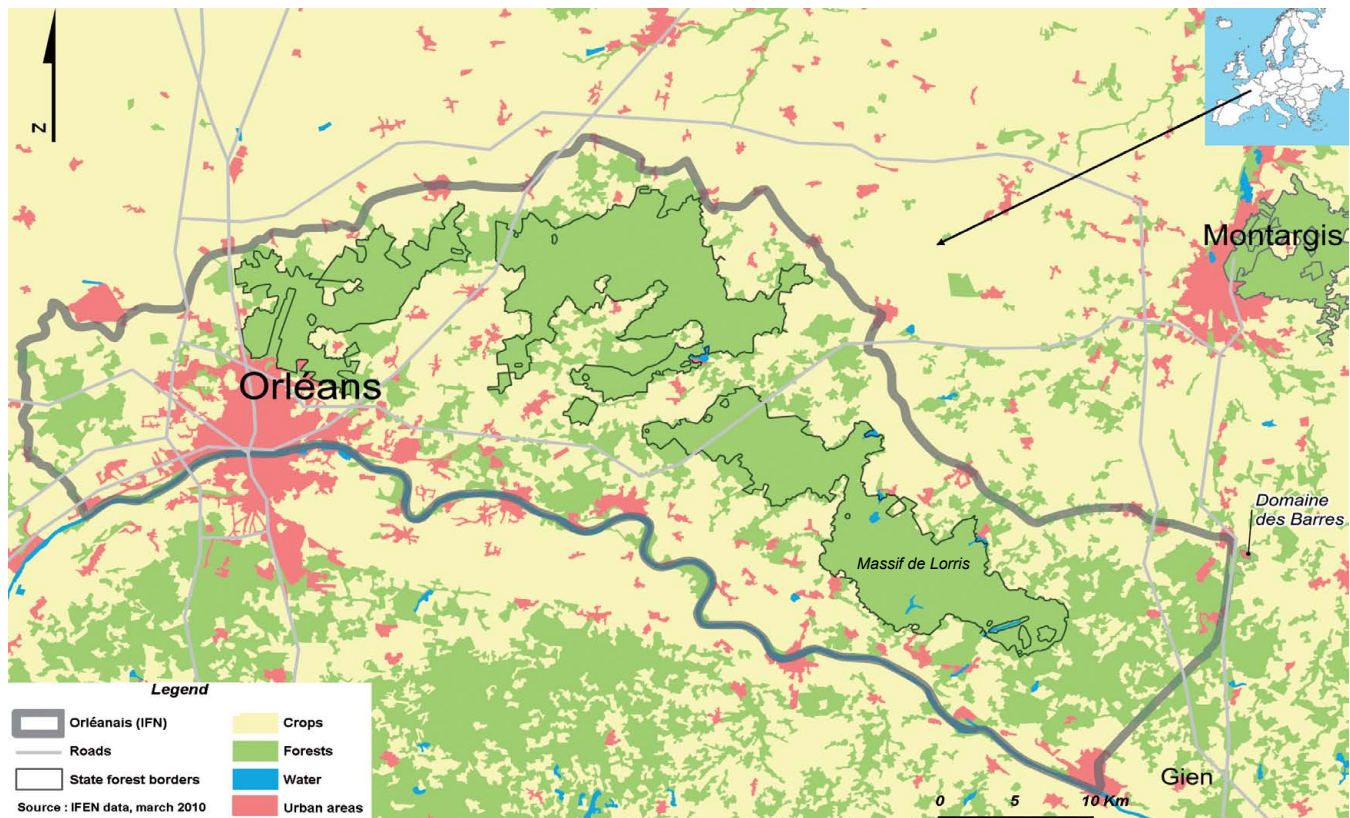


Figure 1 – Location of the three forests where the animals were shot: Domaine des Barres, Forêt de Montargis and Massif de Lorris, Loiret, France.

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

Massif de Lorris							
<i>Capreolus capreolus</i> (Cc), <i>Cervus elaphus</i> (Ce) and <i>Sus scrofa</i> (Ss)							
		Plant species			Total number of seeds		
		χ^2	df	p	χ^2	df	p
Fur	Cc-Ce-Ss	15.3	2	0.0005	15.5	2	0.0004
	Ce-Ss	5.7	1	0.02	7.1	1	0.008
	Cc-Ss	12.3	1	0.0005	12.7	1	0.0004
	Cc-Ce	4.3	1	0.04	3.1	1	0.08
Hooves	Cc-Ce-Ss	6.0	2	0.05	5.2	2	0.07
Forêt de Montargis							
<i>Capreolus capreolus</i> (Cc) and <i>Sus scrofa</i> (Ss)							
		Plant species			Total number of seeds		
		χ^2	df	p	χ^2	df	p
Fur	Cc-Ss	7.0	1	0.008	9.05	1	0.003
Hooves	Cc-Ss	10.1	1	0.002	10.9	1	0.0009

Rubus fruticosus, *Brachypodium sylvaticum* and *Geum urbanum*, and they were essentially dispersed by wild boar. *Betula pendula* was the only species encountered on all three animal species, both on the fur and in the hooves. Ninety-four percent of the wild boar sampled carried seeds on their fur and 88% carried seeds in their hooves, thus revealing that wild boar is an important dispersal vector. When we pooled all the samples, wild boar transported 85% of the 41 species identified, while roe deer transported 34% and red deer only 7%.

Within- and among-species variations in animals

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

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

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

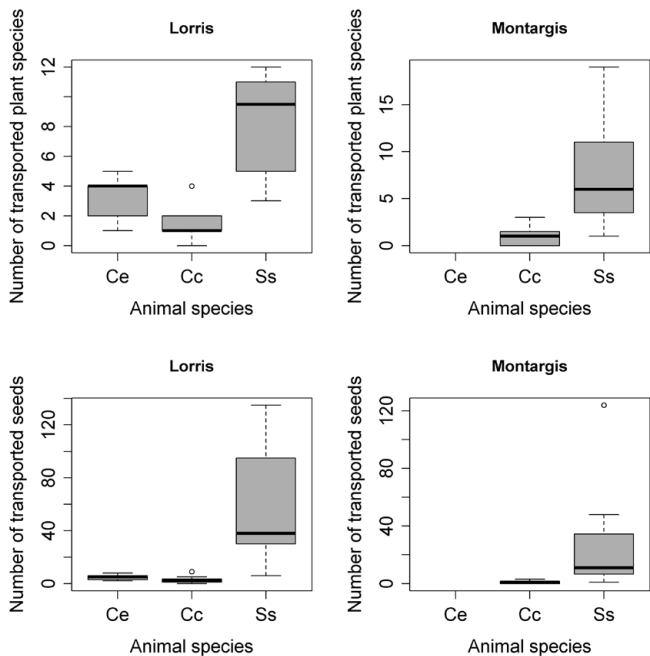


Figure 2 – Number of plant species (top) and seeds (bottom) transported by one animal, for each animal species (Cc = *Capreolus capreolus*, Ce = *Cervus elaphus* and Ss = *Sus scrofa*) in the Massif de Lorris (left) and the Forêt de Montargis (right).

Ecological traits of transported plants

The majority of transported plants were epizoochorous (n = 19), while other modes of dispersal were less represented (see table 3). We found no significant differences in the

Table 3 – Number of species by main dispersal mode and main habitat, and L-Ellenberg index for plant species both transported by the brushed animals and present in the local flora.

A: anemochory, Au: autochory, B: barochory, D: diszoochory, En: endozoochory, Ep: epizoochory, H: hydrochory, M: myrmecochory. Plants for which the ecological traits could not be obtained were not used in the analyses.

	Main dispersal mode								Main habitat			L-Ellenberg index		
	A	Au	B	D	En	Ep	H	M	Forest	Peri-forest	Open	Hygrophile	1 to 5	6 to 9
Transported plants	6	0	9	0	1	19	3	0	5	11	20	2	6	33
Local flora	219	3	202	11	62	187	55	45	103	229	359	91	124	602

number of epizoochorous species dispersed among the three animal species (Fisher Exact tests: Cc vs. Ce $p = 0.27$, Cc vs. Ss $p = 0.89$ and Ce vs. Ss $p = 0.31$). Among these epizoochorous species, the majority was found on the animals' fur. Other plant species dispersed by wild boar belonged to more varied modes of dispersal ($n = 5$ modes, epizoochory, barochory, anemochory, endozoochory, hydrochory) than the ones found on roe deer ($n = 3$) and red deer ($n = 2$). The proportion of epizoochorous species was higher in our samples than in the local flora (transported plants vs. local flora, Fisher Exact tests: $p = 0.00079$). In terms of main habitat and L-Ellenberg index, plant species were dispersed according to their representation in the local flora (transported plants vs. local flora, Fisher Exact tests: main habitat $p = 0.70$, L-Ellenberg $p = 1$; table 3). In our samples, light-demanding plant species and those from non forest and periferest dominated. The few forest-specific species that we encountered in our samples were essentially tree species such as *Betula pendula*, *Carpinus betulus* and *Pinus sylvestris*.

DISCUSSION

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

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

Methodological insights

The methodology we chose allowed us to determine seeds that were effectively transported on the animal's body. This method proves to be efficient and not very time consuming. However, our seed counts were probably biased due to the difficulty in identifying all the seeds. We have therefore planned to place the seeds collected in growth chambers under controlled conditions and will later transplant the seedlings into greenhouses (Cosyns 2004) to confirm the species

identified under stereo microscope and to identify the unknown species. This second process will involve much more time and require more expensive equipment. However, combining microscopic observations and germination tests will no doubt improve the identification process, even though all the seeds are not likely to germinate and an underestimation of the number of dispersed seeds will still remain.

Within- and among-species variations in animals

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

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

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

Ecological traits of transported plants

The most dispersed plant species we found are similar to those in other studies: *Betula pendula*, *Rubus fruticosus*, *Brachypodium sylvaticum*, *Geum urbanum*, *Galium odoratum*, *Deschampsia flexuosa*. *Betula pendula* was the only species transported by all three animal species, even though its main dispersal mode is anemochory. For this species, epizoochorous transport acts as a secondary dispersal mode. *Betula pendula* was also the species most frequently found

on wild boar individuals, followed by *Chenopodium* sp. and *Geum urbanum*. Epizoochorous species, like Poaceae, were the plants most frequently transported by red and roe deer. As expected, the plant species we found on ungulates' bodies were mainly epizoochorous (Poaceae, *Geum urbanum*, *Deschampsia flexuosa*...) and were more frequent on fur than in the hooves.

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

However, species with other modes of dispersal were also transported by the animals we brushed, particularly in the hooves (*Amaranthus* sp., *Chenopodium* sp...). Indeed, we identified seeds from nearly all dispersal classes (epizoochory, barochory, anemochory, endozoochory, hydrochory) and, again, these seeds were mainly found on wild boar, followed by roe deer. Our results agree with Fischer et al. (1995) and Mrotzek et al. (1999) who demonstrated that plant species are more easily carried when they produce small seeds rather than large ones. Therefore, we supposed that any type of seed could be dispersed in hooves and wild ungulates could play a role in the distribution of the entire flora even though epizoochorous species should be more dispersed than other plant species. Our final hypothesis was that the diversity of the seeds collected on hunted individuals should reflect the diversity of the habitats present within their home range. Our results are in contradiction with that statement. We mainly collected light-demanding plant species that originated from periferest and non forest habitats. This result agrees with the fact that woodland plants are only rarely dispersed (Heinken & Raudnitschka 2002). Indeed, most woodland species do not possess morphological adaptations and generally produce few seeds (Bierzychudek 1982); this negatively affects the likelihood that they will be dispersed by animals. The fact that wild ungulates more actively search for food in open areas may also enhance the likelihood that ruderal and grassland species will be transported.

Consequences for plant population dynamics

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

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

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

SUPPLEMENTARY DATA

Supplementary data are available at *Plant Ecology and Evolution*, Supplementary Data Site (<http://www.ingentaconnect.com/content/botbel/plecevo/supp-data>), and consist of the following: (1) table summarizing data concerning the brushed animals (pdf format) and (2) ecological traits of the plant species identified as being transported by the animals sampled (pdf format).

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