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Effects of connectivity on seed dispersal patterns in hedgerows

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Abstract

Questions

Habitat isolation is a major driver of biodiversity as it affects dispersal among local communities, especially for plants. Corridors are supposed to facilitate the movement of organisms and hence their effective dispersal, thereby increasing biodiversity. Hedgerows provide favorable habitats for forest plant establishment, but their role in dispersal among forest patches is still unknown. In addition, seeds can be more predated within hedgerows as animal movement is also encouraged by these corridors. We are testing the following question: Are plant dispersal and seed removal by animals in connected hedgerows compared to unconnected hedgerows promoted for forest plant species?

Location

Long Term Ecological Site of "Zone Atelier Armorique", Western France (ca. 150 km^2)

Methods

We analyzed seed dispersal along two pathways in 16 woodlots, connected (least cost pathways, i.e., optimal corridors) and unconnected high cost pathways, (absence of corridor). Using a trap study, we first quantified seed rain and analyzed seed composition after trapped seeds were germinated in the greenhouse. At the same sampling points, we then analyzed the rate at which two different sized seeds were removed from seed baits by animals.

Results

Our results revealed no difference in the number of trapped seeds in connected and unconnected pathways, but did reveal a difference in the number and richness of viable seeds, corridors having a positive impact. In the predation experiment, the rate of removal of small seeds was higher in connected pathways than in unconnected pathways.

Conclusion

Connectivity enhanced the dispersal of viable forest plant species but also the predation of small seeds, which possibly played a role in their subsequent dispersal. This work highlighted the effect of connectivity on seed dynamics within hedgerows and improves our understanding on their role as stepping stones for seed dispersal among forest patches.

Keywords

Ecological corridors, landscape connectivity, seed dispersal, seed predation, least-cost path analysis, plant community, hedgerow network, forest fragments

Introduction

Habitat isolation is an important driver of species assemblages as it limits dispersal among local patches and affects the structure of metacommunities (Leibold et al. 2004). In small wooded habitats, plant assemblages are particularly sensitive to habitat isolation (Grasholf-Bokdam, 1997; Cordeiro and Howe, 2001) as they are strongly driven by dispersal limitation (Honnay et al., 2002; Verheyen et al., 2003). Connectivity (*sensu* Taylor et al., 1993) provided by the landscape mosaic is assumed to promote organisms' dispersal and to offset the negative consequences of habitat isolation by enhancing gene flow and favoring the likelihood of (re)colonization of habitat patches (Young et al., 1996). However, the effect of connectivity on species assemblage has been less frequently studied in plants than in animals (Gilbert-Norton et al., 2010; Fletcher et al., 2016), with few emphasis on community-wide approaches (Uroy et al., 2019a), especially for forest plant species (but see Mony et al., 2018).

Linear woody elements, such as hedgerows have been suggested to provide favorable habitat conditions for forest species (McCollin et al., 2000; Wehling and Diekmann, 2009). Through a large European study, Litza et al. (2022) demonstrated the important role of hedgerows as refuge for many forest plant species. In addition, hedgerows provide more stable features in agricultural landscapes than the other features constituting the landscape mosaic and may promote species establishment and subsequent dispersal. They may also influence the vectors (e.g. animal, wind) involved in plant species dispersal (Uroy et al., 2019b). Because plant species may disperse through a stepping-stone process, hedgerows should then enhance connectivity among forest patches and constitute preferential pathways for species to be dispersed, especially when they are connected to source patches (Lenoir et al., 2021).

Though, species effective dispersal within hedgerows is not well-known. Recent works demonstrated that species richness in plant assemblages harbored in hedgerows, especially of forest species depends on their age (Paal et al., 2017; Lenoir et al., 2020) as ancient hedgerows harbor also species that have low dispersal capacity (Closset-Koop et al., 2016). Species composition and richness depends on their distance to the forest patch (Corbit et al., 1999; Wehling and Diekmann, 2009). One limitation of these correlative approaches is that plant communities established within hedgerows depend on both dispersal (i.e., plant recruitment via seeds) and local factors (i.e., the ability of seeds to germinate and establish in the hedgerow patch). Then, species assemblages occurring in hedgerow might not reflect the actual dispersal within the hedgerow. In addition, the efficiency of seed dispersal could also depend on predator and or

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parasitism pressure, that could lower the flow of viable seeds (i.e., able to germinate), or increase the predation rate of seeds *in situ*.

The aim of the present study was to analyze the role of hedgerows in the actual dispersal of plants at different distances from 16 source forest patches in two contrasted connectivity configurations: highly connected and unconnected hedgerow pathways. These two connectivity configurations were predicted using resistance-based models (least-cost path analysis) (Adriaensen et al., 2003). We conducted two complementary experiments to evaluate actual seed dispersal by analyzing seed flows and their in-situ predation. In the first study, we analyzed the composition and richness of dispersed seeds using seed traps. This trapping study evaluated seed rains originating from plants that dispersed along the hedgerow corridor, but also seed viability through an emergence experiment in the greenhouse. The second study quantified the number of seeds eaten, which is related to predation by animals. We measured a proxy of seed-predation pressure for two model species, millet (*Panicum miliaceum*) and buckwheat (*Fagopyrum esculentum*). These species were tested because they are absent in the study landscape and their seeds are similar in size to the seeds of forest plant species that are dispersed naturally. We performed both studies in fall and winter to cover peak seed dispersal periods. More specifically, we tested the following hypotheses:

(1) Seed dispersal (i.e., number of seeds trapped) is higher in connected pathways than in the unconnected pathways, with a lower positive effect of corridors on viable seed fluxes due to enhanced parasitism and predation in corridors. Species composition and richness depend on the type of pathway present, with more species and more seeds occurring in connected pathways than in the unconnected pathways (Trapping study).

(2) More seeds are removed by animal predation along connected pathways than along unconnected pathways (Seed removal study).

Methods

Sampling design

We performed this study in the "ZA Armorique" long-term socio-ecological research (LTSER) site in Western France (48°36′N, 1°32′W). This area covers 15,000 ha and is an agriculture-dominated landscape with less than 15% of forest cover and a well-developed network of hedgerows. We selected 16 small forest patches (woodlots) based on: (1) their size (fragments ranged from 1-5 ha in size), and (2) their shape; to limit edge effects, all the plots had a low

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perimeter/surface ratio < 0.04; both criteria were around the median for the woodlots in the area. Woodlots were post-agricultural (i.e., they were established on former agricultural land) and were dominated by *Fagus sylvatica*, *Quercus robur* and *Castanea sativa*. The woodlots are extensively managed and embedded in a hedgerow network mainly composed of old hedgerows already present in historical photographs of 1952 (the oldest images available for this area).

From each woodlot, we defined two different pathway types, one corresponding to hedgerow network with few or no interconnections (hereafter called an "unconnected" pathway) and the other to a better connected network (hereafter called a "connected" pathway, and corresponding to the least cost path linking woodlots which are the source habitat patches, and found using resistance-based connectivity models) (Fig. 1). Both pathways were identified from land-cover maps, originating from photo interpreted aerial imagery (French National Institute of Geographic and Forest Information) combined with object-based, remote sensing imagery acquired by RapidEye satellites. We identified eight land-use categories, each at 5-m resolution: cropland, semi-natural grassland, managed grassland, woodlot and forest, urban cover, water body, hedgerow, and road. The hedgerow network and road categories were identified from the BDTopo® vector geographic database (2003–2006), produced by the French National Institute of Geographic and Forest Information. The permeability values attributed to each land-use category were based on Watts et al. (2010) and used successfully by Gil-Tena et al. (2014) and Mony et al. (2018) for this study area. Permeability values were fixed based on the vertical structure of the habitat, which determines its permeability to the movement of forest woodland species. Least cost paths (LCPs) were computed from the permeability map using a minimum planar graph (Graphab, Foltête et al., 2012) and calculated among all the sampled woodlots. For each woodlot, we selected the connected and unconnected pathways based on these calculations: the connected pathway was defined as LCP, whereas the unconnected pathway was selected in the area where no LCP was predicted (i.e., area with low permeability values), and at a maximum distance from the connected pathway to guarantee spatial independence (Fig. 1). Unconnected pathways comprised hedgerow fragments that were spatially discontinuous and embedded in land-use areas with high-resistance values (croplands, urban cover). In contrast, connected pathways were mostly continuous hedgerows embedded in land-use areas with low-resistance values (woodlands and grasslands).

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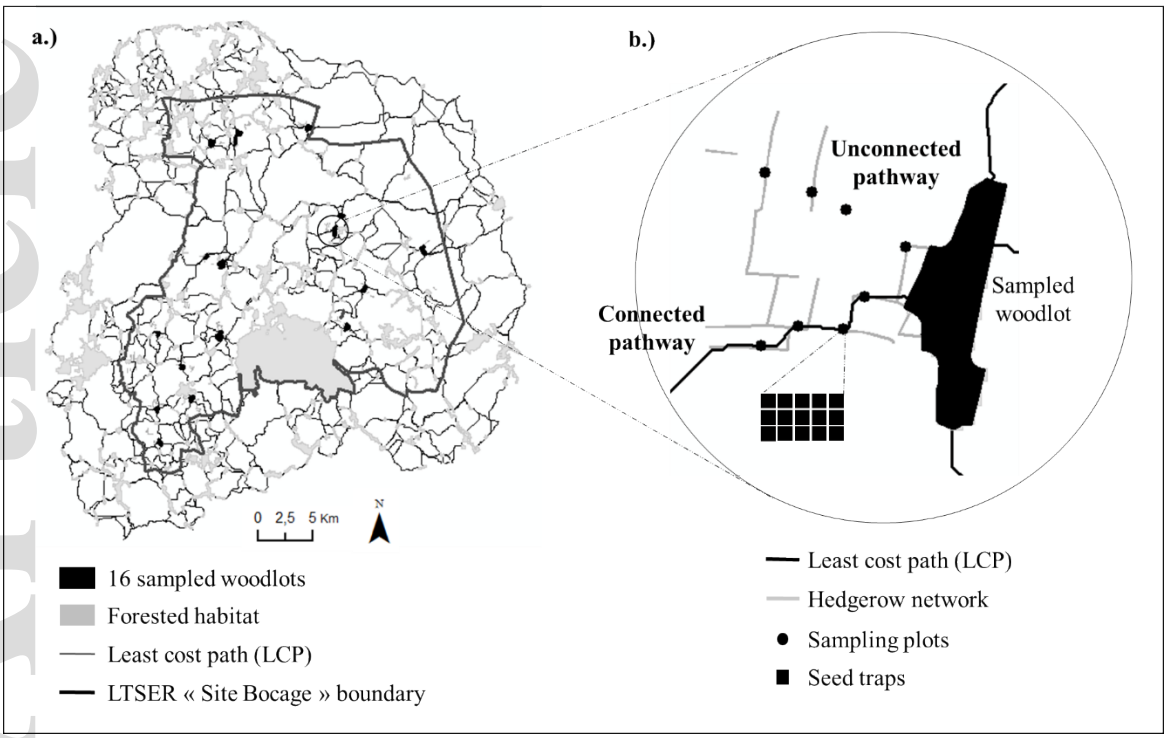


Figure 1 Sampling design. (a) LTSER site area ("agricultural bocage" site) with the 16 sampled woodlots linked with least cost paths. Paths were calculated within the site limit (black line) + a 3km-buffer around (b) Sampling in a given woodlot encompassing two pathways (unconnected and connected). Four sampling plots were delimited for each pathway following a regular distance to the woodlot. They were located in forested habitats. Each sampling plot consisted in 15 seed traps used for studies 1 (Trapping study) and 2 (Seed removal study).

To quantify the distance-dependent colonization of seeds into hedgerows that are either connected or unconnected to a woodlot patch, we analyzed seed flows along each pathway. To this end, we placed seed traps at 75m intervals at four sampling points (at 300-m intervals) along each pathway (32 pathways x 4 points per pathway, i.e. 128 sampling points), starting 75m from the edge of each woodlot. This sampling design was intended to assess the spatial dispersal kernel of plant seeds, under the assumption that dispersed seeds are most abundant closest to the source (Nathan, 2006). We assumed that trapped seeds were produced by plants migrating from the forest patches along the ecological pathways. All four sampling points were located in a hedgerow habitat to standardize local habitat conditions. On some pathways, hedgerow fragments were not available at the defined distances. In 20 of the 128 sampling points, seed plots were then located in the most-natural interface within the pathway at the given distance (e.g., field margin). At 13 of the 128

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sampling points, no possible natural interfaces were available and those points were consequently not sampled.

Measuring seed flows in connected and unconnected pathways (Trapping study)

Seed traps (4 sampling points per path) were made from 25 x 25 cm polyethylene artificial turf mats (625 cm2), (Wolters et al., 2005; Sarneel et al., 2014). At each of the four seed-trap points, 15 replicate turf mats were placed on the ground in the hedgerow (inside and at the edges) from mid-November 2013 to mid-January 2014 (10-week-period). This sampling period coincided with peak seed dispersal following summer seed release. In order to minimize potential local effects of seed deposition, we removed all herbaceous vegetation within 2 m of each trap. In addition, we classified the hedgerow at the plot scale using a six-class index (1) no hedgerow, (2) relict hedgerow with a dense cover of *Rubus* spp. and *Pteridium* spp., (3) hedgerow with sparse trees and a short herbaceous layer, (4) hedgerow with sparse trees and a tall herbaceous layer, (5) hedgerow with a dense tree or shrub layer, and (6) hedgerow with both dense tree and shrub layers. At the end of the sampling period, the plastic mats were collected in separate bags and taken to the laboratory for analysis. Each trap was vacuumed to collect the material trapped in the mats. The material collected from the mats was sieved successively at three different mesh sizes (2, 1 and 0.5 cm) to collect the seeds. With this sieving step, we discarded from following analyses seeds coming from *Fagus sylvatica*, *Quercus robur* and *Castanea sativa* that were retained by the first mesh size. These species were planted for constituting the hedgerows. Then, we considered that they were not representative of spontaneous colonization of plants in these landscapes. We counted all the seeds, even those that were obviously not capable of germinating (e.g., those parasitized or partially eaten by predators). These seeds were termed “trapped seeds.”

Characterizing dispersed seed assemblages in connected and unconnected paths (Trapping study)

All the seeds collected in each plot (n = 115) were spread out in a thin layer (< 5 mm thick) on trays filled with sterile potting soil topped with a 4-mm layer of sterile sand, following the method described by ter Heerdt et al. (1996). The samples were moved to a greenhouse maintained at a daytime temperature of 25 °C and nighttime temperature of 15 °C and watered every day. For each batch of 10 trays, a control tray containing no seeds was included to quantify seeds that could have blown onto the trap after it was placed in the greenhouse. Emerging seedlings were identified, counted, and removed as soon as possible. Seedlings that could not be identified were transferred

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to separate pots and allowed to grow until they could be identified. When all germination had ceased, the soil was crumbled by hand and kept for two more weeks to allow any seeds that remained in the soil to germinate. We applied this crumbling procedure to expose seeds buried more deeply in the soil and to reduce the risk of seeds remaining dormant. The germination study ended in December 2014. We termed seeds that had been trapped, counted, and identified after germinating in the greenhouse "emerged seeds". At each sampling point (representing 15 seed traps), we measured species richness and abundance of seedlings at three levels of resolution (1) all plant species (i.e., all forest and non-forest species), (2) forest species [species listed in the French Forest flora of Rameau et al. (1994)], and (3) animal-dispersed forest species [zoochorous species listed in the Baseflor database (Julve, 2015)]. The species composition of the trapped seeds was compared with the flora of the source woodlots using data published in Mony et al. (2018) to check whether both species pools were similar. However, for a given sampling point, we did not specifically relate forest species trapped to those occurring in the corresponding woodlot patch to which the sample point was related. We used the French taxonomic online database TAXREF v12.0 as scientific nomenclature of plant taxa.

Analyzing seeds predated by animals in connected and unconnected pathways (Seed removal study)

As model species, we used two types of seeds belonging to two different taxonomic families, millet (*Panicum miliaceum*; Poaceae) and buckwheat (*Fagopyrum esculentum* ; Polygonaceae). We selected these species because they were included within the size range of the seeds we had trapped in the trapping study (Table S1). Seeds for *P. miliaceum* weigh 4-6.5 mg and measure approximatively 3 x 2 mm. Seeds for *F. esculentum* weigh 25-30 mg and measure approximatively 6 x 3.7 mm. We selected the model species based on their seed size only, as this trait was shown in a recent meta-analysis to be a good proxy of seed removal by predators (Dylewski et al., 2020). We also chose these species because they were not present in the surrounding landscape and could not colonize spontaneously traps through natural seed rain. We performed a seed predation experiment in 15 for buckwheat and 14 for millet out of the 16 woodlots used in the trapping study. We counted the remaining seeds in the seed baits at the same sampling points. We analyzed seed removal during two campaigns, the first in February 2014 and the second in October 2014, which corresponded with the sampling campaign of the prior trapping study. At each sampling point, we placed two sets of 20 millet seeds on two artificial turf seed traps (total 40 seeds) and

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two sets of 20 buckwheat seeds on two other traps. At Days 2 and 6 after depositing the seeds, we measured the removal rate, defined as the proportion of the original 40 seeds that were missing. We assumed that the removal rate was an indicator of animal predation, despite the selection of plant species that do not correspond to forest species, and that have gone through the domestication filter.

Statistical analysis

Prior to analyses, we analyzed the independence of the ecological variables through pairwise correlation analysis (Pearson correlations). The species richness of all species at each point was closely correlated with the species richness of forest species (R = 0.91). The abundances of trapped species were closely correlated with the seed abundance of emerged species (R = 0.96) and of the emerged forest species (R = 0.99). We also analyzed the dependence of hedgerow structure at local sampling points based on the type of pathway, with chi-squared tests based on the number of sampling points per index category. Hedgerow structure at sampling points differed significantly between connected and unconnected pathways (Chi-squared = 24.68; $p < 0.001$) (Fig. 2).

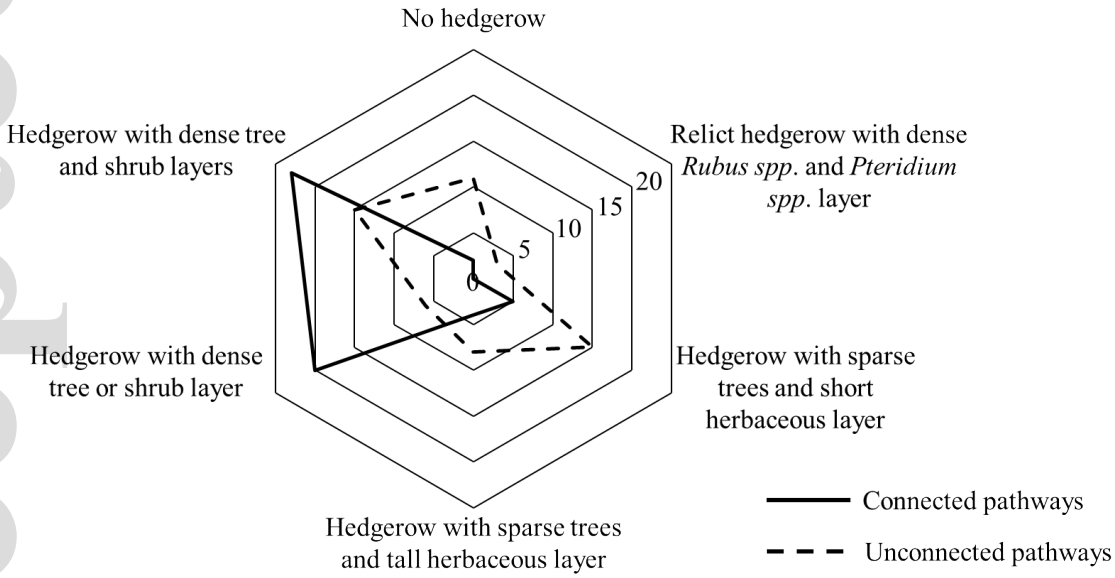


Figure 2 Number of sampling points for connected and unconnected pathways depending on hedgerow structure. Hedgerow structure was characterized using a six-class index.

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To test for the effect of connectivity on dispersed plant assemblage indices (number of seeds, plant species richness, and abundance) (Trapping study), and on seed removal rate (Seed removal study), we used mixed models. Models tested for the effect of the type of pathway (connected vs. unconnected, qualitative variable), position along the pathway (from one to four, qualitative variable), and their interaction as fixed effects, and pathway type nested within the woodlot source patch as random effects (Explained variable~pathway type * position + 1|source patch/pathway type). For most explained variable tested, data showed a strong overdispersion. Especially in the seed removal study, seeds were absent at many of the sampling points (especially buckwheat). We therefore used generalized linear mixed-effects models with a log link function and a negative binomial distribution, which are adapted to count data and yielded GLMs without overdispersion (Zuur et al., 2009). In the seed removal study, lack of convergence was detected for one model for buckwheat (seed remaining at Day 6 in February). For all models used in both studies, we tested the model including all variables. We analyzed the significance of each variable within the model through ANOVA type II sums of squares. We calculated the proportion of variance explained by the fixed effect (marginal R^2) and by random effects (conditional R^2) (*sensu* Nakagawa & Schielzeth, 2013). We graphically checked for homoscedasticity, independence and normality of residuals for the tested models. We performed all statistical analyses using the following software packages in R: *lme4*, *nmle*, *car*, *glmmTMB, piecewiseSEM*.

Results

Trapping study: Seed flows in connected and unconnected pathways

Dispersed species assemblages were characterized by a large number of trapped seeds (Fig. 3), with high variability among sampled points, ranging from zero to 14,475 seeds/m². After the greenhouse emergence study, the germination rate of the trapped seeds was low, ranging from 0 to 57% (mean germination rate: 9.2% ± 10.6%). We recorded 91 plant species in the emergence study with 42 species that are also present in the flora of the woodlots. Seed fluxes were dominated mostly by *Populus tremula*, *Galium aparine*, *Alnus glutinosus* (5-37% of the total number of emerged seeds), and to a lesser extent by *Dactylis glomerata*, *Chenopodium album*, *Rumex crispus*, *Holcus lanatus*, *Poa pratensis*, *Urtica dioica*, *Epilobium tetragonum* and *Persicaria lathifolium* (1-5% of the total number of emerged seeds, Appendix S1). Within these 91 plant species, forest species represented 78.6% ± 27.4% of species richness and 83.9% ± 26.4 of

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seedling abundance. Within forest species, animal-dispersed species represented 60.9% ± 36.6% of species number and 62.9% ± 39.6 of seedling abundance.

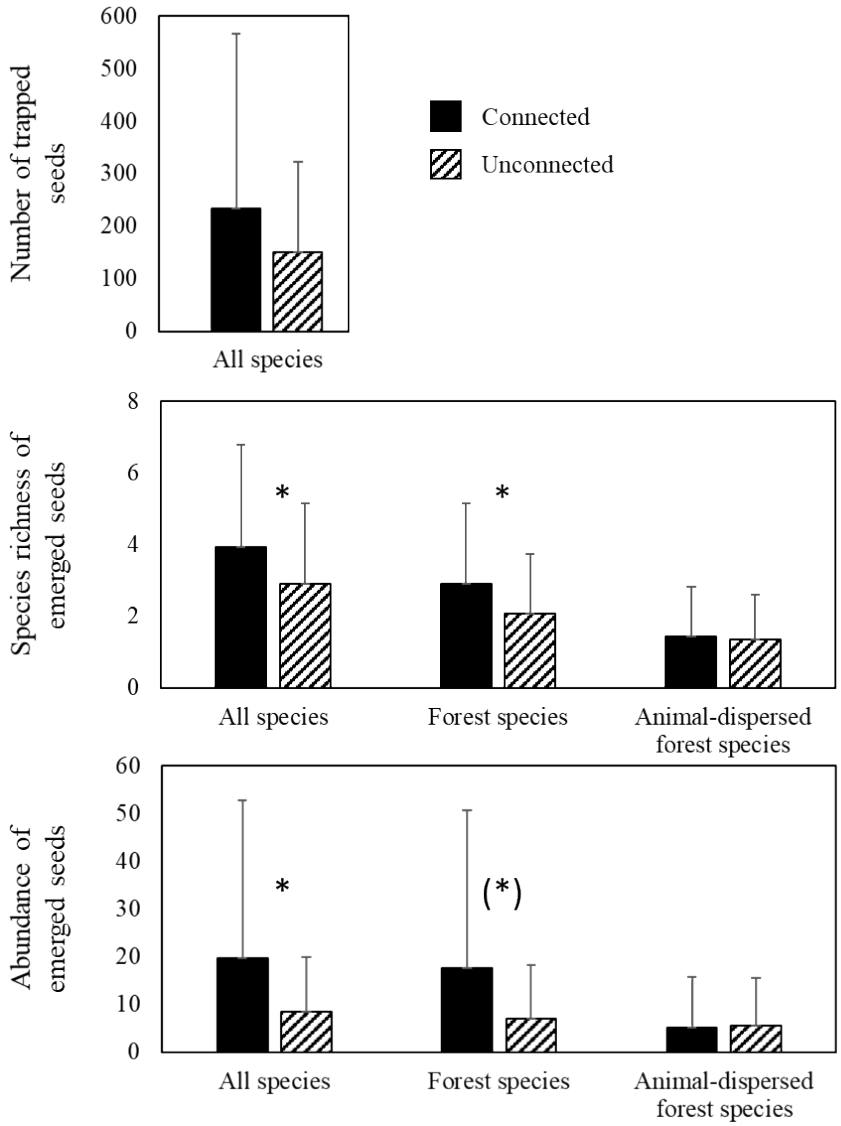


Figure 3 Number of trapped seeds, species richness of emerged seeds and abundance of emerged seeds (Mean and Standard Deviation) for connected and unconnected pathways. Significant differences are indicated with asterisks (Detailed statistics in table 1).

The total abundance of trapped seeds was independent of the type of pathway and distance from the woodlot. However, abundance varied widely, especially in the connected pathway. One sampling point (Corridor pathway type) displayed especially a very high density in seeds (14, 475 seed/m²) due to a high number of *P. tremula* seeds. *P. tremula* belonged to the category of non-animal dispersed forest species. Because statistical models did not converge for the seed number

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of emerged seeds of all and forest species owing to this atypical value, we tested the relationships discarding this point (Fig. 3 did not include this atypical value). Relationships were kept identical (Table 1).

Species richness and the number of emerged seeds of all species and of forest species were significantly higher in the connected than in the unconnected pathway (statistical tendency for seed abundance of forest species), whereas no effect was found for animal-dispersed forest species (Fig. 3; Table 1). The distance to the woodlot and its interactive effect with pathway type were not related to any of the measured variables (Table 1).

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Table 1 Effect of type of pathway and distance from woodlot source (16 woodlots) on seed flows and species richness of dispersed seed assemblages. "Trapped seeds" are those intercepted by seed traps; "emerged seeds" are seeds that were trapped and subsequently germinated in the greenhouse. The number of seeds is expressed per m². . Given model parameters are the Chi-square statistic (Chisq) and p-values from ANOVA II, the marginal and complete R^2 (R^2m; R^2c) and the AIC. Variables in bold and in bold-italics are statistically significant ($p < 0.05$) and tend to be significant ($p<0.1$) respectively

	$R^2m(R^2c)$	**AIC**	**Pathway type**		**Distance from source**		**Interaction effect**	
			Chisq-test	p-value	Chisq-test	p-value	Chisq-test	p-value
N° of trapped seeds (N°/m²)	**0.05 (0.20)**	**1431.4**	2.24	0.13	0.30	0.96	4.98	0.17
Species richness of emerged seeds								
N° of species	0.04 (0.08)	522.2	**5.15**	**0.02**	0.61	0.89	0.70	0.87
N° of forest species	0.06 (0.11)	458.3	**6.17**	**0.01**	2.25	0.52	0.65	0.89
N° of animal-dispersed forest species	0.03 (0.13)	364.7	0.07	0.79	5.56	0.14	0.23	0.97
Abundance of emerged seeds (N°/m²)								
N° of seeds	0.06 (0.16)	813.8	**5.01**	**0.03**	3.54	0.32	1.04	0.79
N° of forest species seeds	0.07 (0.24)	759	***3.52***	***0.06***	**8.58**	**0.04**	1.11	0.77

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N° of animal-dispersed forest species seeds	0.05 (0.19)	606.6	0.75	0.39	***7.70***	***0.05***	1.36	0.71

Seed removal study: Seed removal by animals in connected and unconnected pathways

Fewer buckwheat seeds (mean = 7.0 +/- 12.3 seeds/point) than millet seeds (mean = 16.5 +/- 11.3 seeds/point) remained after six days in both survey periods. More millet seeds remained in the unconnected pathway than in the connected pathway, independent of the distance from woodlot (Fig. 4; Table 2).

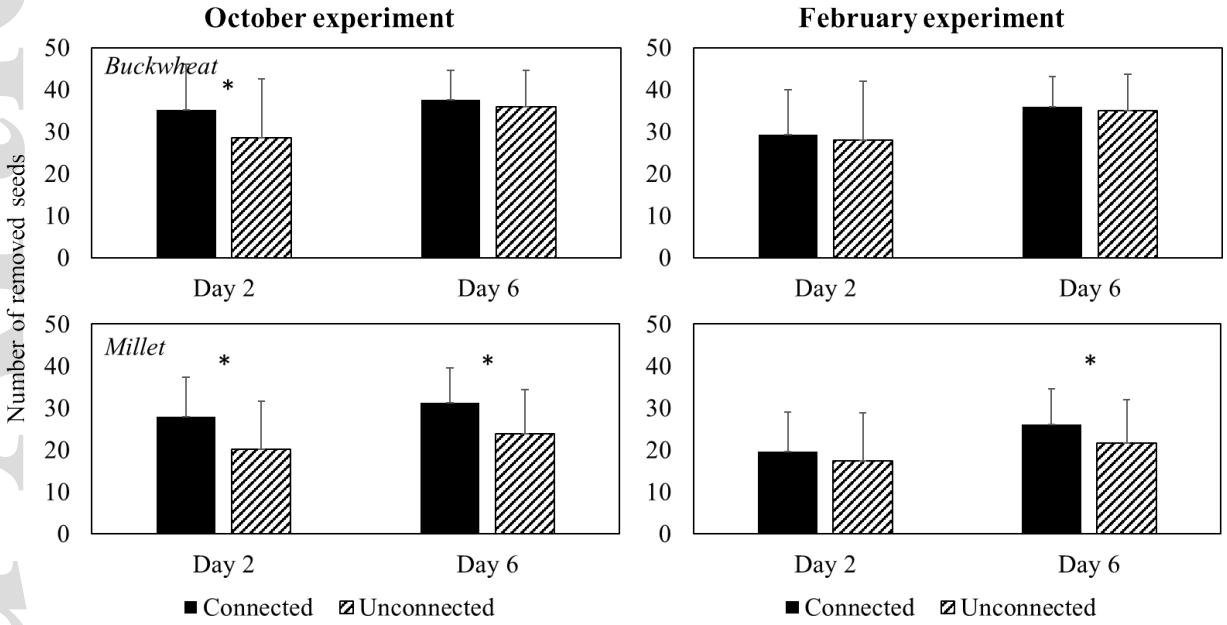


Figure 4 Number of seeds (buckwheat and millet) removed from the 40 seeds originally placed at sampling points, according to the sampling period (October and February 2014) and date of survey (Day 2 and Day 6), for connected and unconnected pathways. Significant differences in seed removal rates per species are indicated with asterisks.

Seed predation was higher in the connected pathways than in the unconnected pathways. This effect occurred on Day 2 and on Day 6 in the October samples and only on Day 6 in the February samples. We found no effect of the type of pathway or distance from the woodlot for buckwheat seeds except for Day 2 in the October samples (Table 2, Fig. 3).

Table 2 Effect of type of pathway and distance from woodlot source (15 woodlots for Buckwheat and 14 for millet) on remaining millet and buckwheat seeds. February and October experiments were performed in 2014. Given model parameters are the Chi-square statistic (Chisq) and p-values

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from ANOVA II, the marginal and complete R^2 (R^2m; R^2c) and the AIC. Variables in bold and in bold-italics are statistically significant ($p < 0.05$) and tend to be significant ($p<0.1$) respectively

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			Pathway type		**Source distance**		**Interaction**	
	R^2m (R^2c)	AIC	Chisq-test	p-value	Chisq-test	p-value	Chisq-test	p-value
Millet								
October								
Seeds remaining (Day 2)	0.16 (0.30)	742.6	**18.82**	**1.4×10^{-5}**	0.81	0.85	3.60	0.30
Seeds remaining (Day 6)	0.16 (0.32)	709.1	**15.83**	**7.0×10^{-5}**	0.60	0.90	3.96	0.26
February								
Seeds remaining (Day 2)	0.06 (0.07)	824.1	1.09	0.30	2.03	0.57	3.65	0.30
Seeds remaining (Day 6)	0.11 (0.18)	802.4	**4.57**	**0.03**	2.57	0.46	***6.63***	***0.08***
Buckwheat								
October								
Seeds remaining (Day 2)	0.19 (0.98)	1511.6	**14.44**	**1.4×10^{-4}**	**37.13**	**4.3×10^{-8}**	**9.52**	**0.02**
Seeds remaining (Day 6)	0.01 (0.02)	362.9	1.22	0.27	3.56	0.31	0.92	0.82
February								
Seeds remaining (Day 2)	0.01 (0.01)	711.9	0.001	0.97	2.61	0.45	3.17	0.36
Seeds remaining (Day 6)	-	-	-	-	-	-	-	-

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Discussion

Effect of corridors on seed dispersal patterns

Contrary to our expectations, we found no difference in the quantity of dispersed seeds between connected and unconnected pathways, but the number of germinating seeds (i.e. viable seeds) did differ, as the connected pathways contained more seeds than the unconnected pathways. The quantity of trapped seeds was surprisingly high (mean ~ 300 seeds/m²) and highly variable, especially in the connected pathways. This variability was due in some sampling points to seeds produced by a few tree species (e.g., *Populus tremula*). *P. tremula* is common in the woodlots of our study area and produces many small seeds that are efficiently dispersed by the wind. For this species and other wind-dispersed species, hedgerows likely affect wind dynamics by redirecting airflow and increasing the likelihood of wind-blown seed being intercepted by hedgerows (Damschen et al., 2014). Such effects may depend on local hedgerow characteristics and connectivity patterns leading to the high variability we observed in the number of trapped seeds. Despite the high seed flows we recorded, most seeds did not germinate (the mean germination rate was only 10%), i.e. lower than the mean germination rate recorded for these plant species in optimal conditions (TRY database; Kattge et al., 2011). This difference in germination success suggests that parasitism or partial predation has a strong impact on dispersed seeds and may impede effective dispersal along corridors.

Forest species (e.g. species listed in the French forest flora of Rameau et al., 1994) represented the majority of the germinating seeds in our study. Our results showed that the type of pathway had a positive influence on seed abundance and species richness for whole assemblages and particularly for forest species assemblages (statistical tendency for seed abundance). This effect of connectivity supports our hypotheses that continuous hedgerow corridors promote the dispersal of forest species by enhancing their migration. Connectivity is however not totally independent from the hedgerow local habitat conditions as we demonstrated that hedgerows sampled in the connected pathways had a more complex structure (with multiple layers of trees, shrubs, and herbaceous species) than hedgerows in the unconnected pathways. This might affect the effective dispersal of species that use corridors as alternative habitats along their dispersal path among forest patches. Surprisingly however, animal-dispersed plants were not favoured by corridors but rather tended to depend on the distance to source-patch. This absence of connectivity effect on animal-dispersed forest plant species may be related an overall low density of animal-vectors in this landscape, especially those dispersing forest plants, which would have to be

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investigated in a further work. This could be also related to predation pressure during the sampling period that might differ between connected and unconnected hedgerows (see results from seed removal study).

Effect of corridors on seed predation

Our results showed that the removal rate especially of small seeds was higher in connected pathways than in unconnected pathways. These results suggest that connectivity favors the movement of granivorous animals, and primarily those that feed on small seeds (i.e., small animals such as carabids, rodents, or birds). In this landscape, woodlots are small and have limited carrying capacity (Gil-Tena et al., 2014). Therefore, the animals that frequent them tend to be small and have restricted ranges. These species might predate seeds and partly offset the higher number of seeds dispersed along corridors; but they can also disperse some of the seeds. Such dispersal has been demonstrated at short distances: for instance, rodents disperse small seeds less than 30 m (Cain et al., 1998; Xiao et al., 2004), by means of seeds attached to their fur (Kiviniemi and Telenius, 1998) or for scatter hoarding seeds (Wang and Corlett, 2017). Bird disperse seeds while feeding and by hiding fruits and nuts for winter. Dispersal distances are difficult to assess in both cases but are likely to range from a few dozen meters when the birds are feeding to a few hundred meters when food is being stockpiled (Vittoz and Engler, 2007). Analyzing the proportion of predated seeds that are still viable and hence play an active role in dispersal would therefore advance our understanding of actual dispersal along corridors. However, our results have to be interpreted within the limitations of the experimental design where we studied seed predation of only two species, *P. miliaceum* and *F. esculentum*. These species represent two seed sizes within the whole range of seed size of forest species, while seed size has been demonstrated to be an important predictor of seed removal and plant recruitment after dispersal (Dylewski et al., 2020). In addition *P. miliaceum* and *F. esculentum* are not forest-species and do not develop locally. We preferred to select these species instead of artificial seeds such as in Wang & Corlett (2017) or species occurring naturally in the woodlands, in order to avoid trap colonization by natural seed rain coming from local populations of these plants. However, we cannot exclude a possible bias linked to particular seed traits that might differ from seeds dispersing naturally in this landscape. Due to domestication, seeds might not be totally representative of forest-plant seed traits in terms of nutrient content and secondary compounds, whereas those traits are known to influence predation rate (Gong et al., 2015) and predator behavior (Wang & Corlett, 2017) in wooded

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habitats. Predator familiarity with the species can also be an important driver of seed removal. Next steps would be then to validate these results using a large set of small-seeded forest species, encompassing a large range of seed nutrient content and quality.

Dispersal of woodlot plants: corridors are used as both a dispersal pathways and habitat

Distance to the woodlot had low effect on the abundance or richness of seed assemblages (but see significant effect for seed abundance of forest species and tendency for animal-dispersed plants) trapped or on the seed removal rate. Old hedgerows may provide viable corridors for forest species because of the local quality of habitat they provide to plants and contribute to the species displacement along the corridor. Local management of hedgerows is thus of particular importance in sustaining the dispersal of forest plants. Connectivity models could be perhaps improved by taking the fine-scale heterogeneity of corridors into account. Such an approach was applied successfully by Betbeder et al. (2015), who derived an index of structure entropy from radar images to characterize the heterogeneity of the cover structure. Abundance of carabids was better predicted using this entropy index than only hedgerow density at both at local and landscape scale. Extending these approaches to plants would be an interesting research direction.

Because in our study only half of the species were also found in the species pool occurring in woodlots, trapped species may mostly be generalist species rather than specialist forest species (See Table S1 for species list). The latter species are mostly long-lived perennials with a low reproduction capacity (Hermy et al., 1999; Whigham, 2004) with rare long-distance dispersal (Cain et al., 1998; Vellend et al., 2003). Most of these specialist forest species rely on local clonal multiplication (Kolb and Diekmann, 2005). Thus for these species, actual dispersal is still difficult to assess and may require more focused methods.

Conclusion

Our study is the first to examine along corridors the actual dispersal of plant species at the community scale. Using two complementary methods, a seed trapping and a seed removal experiment, we demonstrated the positive effect of habitat corridors on the actual dispersal of forest plant species in a fragmented agricultural landscape but highlighted the potential effect of corridors on the predation pressure. The increase of the predation pressure in corridors may partly counterbalance the positive effect of corridors on seed fluxes, or alternatively play a role in seed dispersal. This result has to be confirmed using a larger set of species, growing in forest habitats,

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and encompassing a larger range of seed traits. In addition our results suggest that what enhances seed dispersal in agricultural landscapes is also the quality of the corridor in addition to the presence of a corridor *per se*, Indeed the corridor structure, especially its three-dimensional morphology, could determine the movement of seeds and/or provide a suitable habitat corridor for the step-by-step migration of woodland plants from one woodlot patch to another. Overall the present study emphasizes the role of hedgerows as a supplementary habitat for plants and the importance of hedgerows in biodiversity conservation in fragmented agricultural landscapes through their additional role in plant dispersal. This particular case study on woodland species assemblages underlines therefore the importance of disentangling the effect of corridors on dispersal from the conditions prevailing in the patch where the seeds finally establish. Assessing actual dispersal along corridors should advance our understanding and analysis of the functional connectivity of forest patches.

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Author contributions

A.E., C.M., A.B. and F.B. conceived the research idea and all authors contributed to the methodology of the study. All authors collected the data. C.M. and A.E. performed the statistical analyses; C.M. and A.E. wrote the first draft of the paper. All authors contributed critically to interpretations of results and to the drafts and gave final approval for publication.

Data availability statement

Data are available on the figshare platform at the following private link https://figshare.com/s/a10e93dc3288f23361d3 (open access will be granted after article acceptance)

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Appendix S1. List of species recorded

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