The role of semi-open habitats as dispersal corridors for plant species of woodlands and open habitats

Travers, Eliane; Pitz, Witja; Fichtner, Andreas; Matthies, Diethart; Härdtle, Werner

RESEARCH ARTICLE

The role of semi-open habitats as dispersal corridors for plant species of woodlands and open habitats

Eliane Travers[1] | Witja Till Pitz[1] | Andreas Fichtner[1] | Diethart Matthies[2] | Werner Härdtle[1]

[1]Institute of Ecology, Leuphana University Lueneburg, Lueneburg, Germany

[2]Department of Biology, University of Marburg, Marburg, Germany

Correspondence
Eliane Travers, Institute of Ecology, Leuphana University Lueneburg, Universitätsallee 1, 21335 Lueneburg, Germany.
Email: travers@leuphana.de

Abstract

Questions: European pasture landscapes have been shaped by grazing and alternate husbandry. They are structurally characterised by mosaics of open habitat patches, individual trees and groups of trees or shrubs. We investigated whether these semi-open habitats may act as stepping stones and thus as dispersal corridors for both plants from woodlands and open habitats to mitigate habitat fragmentation effects. We (a) contrasted the plant communities in semi-open habitats with those of woodlands and open habitats, and (b) explored which life-history traits or environmental requirements are associated with the presence or absence of species in semi-open habitats.

Location: Swabian Jura, South Germany; Lueneburg Heath, North Germany.

Methods: We selected four study sites in two contrasting landscapes and conducted vegetation surveys and analysed canopy closure and soil chemical properties in four different habitat types: woodlands, semi-open habitats with high and low canopy closure and open habitats. We tested whether habitat type affected species composition, identified habitat-specific indicator species and compared Ellenberg indicator values for light and moisture and species' dispersal and establishment traits across these habitat types.

Results: Plant communities of woodlands were significantly different from those of all other habitat types, whereas open habitats showed some similarities to semi-open habitats. On average, 73% of open habitat and 39% of woodland species were present in semi-open habitats. Habitat requirements as well as dispersal and establishment traits of woodland species were often more specialised and differed from those of species of the other habitat types, making them less capable to disperse into semi-open habitats.

Conclusions: Semi-open corridors have the potential to connect patches of open habitats and to a lesser extent also of woodlands without creating new barriers for either habitat type. Thus, semi-open corridors may counteract habitat fragmentation effects and are a promising tool for biodiversity conservation, particularly in fragmented pasture landscapes.

1 | INTRODUCTION

Changes in land use have resulted in the increasing fragmentation of many habitats (Haddad et al., 2015; Evans et al., 2017). As a consequence, plants of these habitats increasingly occur in isolated and small populations (Matthies, Bräuer, and Maiborn, 2004). Fragmented populations have a higher risk of extinction because of greater sensitivity to demographic, environmental and genetic stochasticity (Honnay and Jacquemyn, 2007). Reduced population size and increased isolation of fragmented populations result in increased inbreeding, reduced gene flow and a loss of genetic variability through genetic drift (Fischer and Matthies, 1998a; Honnay, Jacquemyn, and Bossuyt, 2005; Schlaepfer, Braschler, and Rusterholz, 2018). This in turn can reduce the fitness of plants in these populations (Fischer and Matthies, 1998b; Willi and Van Buskirk, 2006) and their potential to adapt to changing environmental conditions (Kéry et al., 2000; Walisch, Colling, and Poncelet, 2012), further increasing the risk of extinction. The re-colonisation of habitat fragments where a plant species has become extinct is often difficult because of their isolation (Xiao, Xiaohong, and Cao, 2016; Schlaepfer et al., 2018). To counteract the negative effects of fragmentation it has been suggested to create linear dispersal corridors to connect isolated patches of habitats (Rosenberg and Noon, 1997; Damschen et al., 2014), and various forms of corridors to increase dispersal and serve as habitat links have been studied (Kirchner, Ferdy, Andalo, and Colas, 2003; Damschen, Haddad, Orrock, and Tewksbury, 2006; Roy and de Blois, 2006).

Linear corridors are usually designed to connect patches of similar vegetation with each other (Rosenberg et al., 1997). For example, hedgerows have been used to connect isolated woodland patches (Wehling and Diekmann, 2009). However, if corridors intersect other habitat types they can also act as barriers for the dispersal of species of those habitats (Dobson et al., 1999; Eggers, Matern, Drees, Eggers, and Härdtle, 2010; van Dijk, van Ruijven, and Berendse, 2014). Poorly dispersed species in particular may be affected by this barrier effect, and the positive effects of a corridor on species of one type of habitat might be outweighed by barrier effects on species of another habitat.

In many parts of Europe, traditional land-use management such as extensive grazing and alternate husbandry have created pasture landscapes (Finck and Riecken, 2002; Jedicke, 2015). In recent decades, these landscapes have been transformed by the onset of succession due to changes in habitat management (Poschlod and Bakker, 2005). Many of these former pastures are now characterised by a mosaic of open habitat patches and individual trees, groups of trees or shrubs with different degrees of canopy closure (Bergmeier and Petermann, 2010; Popp and Scheibe, 2013). The

high structural diversity results in heterogeneous environmental conditions which can accommodate species with strongly varying habitat requirements (Bergmeier et al., 2010). These so-called semi-open landscapes are among the most species-rich habitats in Europe and host a large proportion of the biodiversity in Europe, including many endangered plant and animal species (Jedicke, 2015). Today, in many parts of Europe, remnants of these landscapes are protected, and management schemes have been designed to preserve their structural and biological diversity (Von Oheimb et al., 2006).

Due to their mosaic character, semi-open habitats may support animal species of both woodlands (e.g. high forests) and open habitats (e.g. grasslands, heathlands; Eggers et al., 2010) by acting as corridors for them and thus providing a link between (separated) habitat patches. Thus, the promotion of semi-open corridors could be a promising approach to mitigate the effects of habitat fragmentation and avoid the barrier effects that are caused by traditional linear corridors when they intersect other habitat types. However, it remains unclear to what extent semi-open corridors might also facilitate the dispersal of plants. The dispersal ability of many plant species is poor, and these species need stepping-stone habitats that allow them to colonise suitable new habitat patches over several generations (Brederveld, Jähnig, Lorenz, and Brunzel, 2011; Saura and Bodin, 2014).

We investigated whether semi-open habitats are suited to act as stepping stones and thus as dispersal corridors for plants of both woodland and open habitats. We contrasted the species composition of four habitat types: woodlands, semi-open habitats with high and low canopy closure and open habitats. We compared life-history traits and realised ecological niches of species growing in those habitat types to identify factors that favour the suitability of semi-open habitats for certain species. Specifically, we asked: (a) whether plant communities of semi-open habitats contain species of both woodlands and open habitats; and (b) which species traits or environmental requirements explain best the differences between species occurring and not occurring in semi-open habitats?

2 | METHODS

2.1 | Study area

The study was carried out in two contrasting landscapes that differ in soil conditions and prevailing plant communities: the Swabian Jura in South Germany and the Lueneburg Heath in North Germany (Table 1). Both regions have a long history of livestock grazing, which is still continuing today (Beinlich and Plachter,

TABLE 1　Characterisation of the two study regions

Region	Co-ordinates	Altitude range (m a.s.l)	Mean yearly temperature (°C)	Mean yearly precipitation (mm)	Prevailing soil type	Prevailing plant communities
Swabian Jura	48° N/9° E	ca. 600–1,000	ca. 8	850	Leptosols, Cambisols	*Gentiano-Koelerietum* grasslands, *Galio odorati-Fagetum* woodlands
Lueneburg Heath	53° N/9° E	ca. 90–170	ca. 10	700	Podsols	*Genisto-Callunetum* heathlands, *Betulo-Quercetum* woodlands

1995; Cordes, Kaiser, Lancken, and Lütke-Pohl, 1997). However, changes in habitat management have facilitated the onset of succession which produced extensive areas of semi-open habitats (following the definition of Finck et al., 2002). Those are characterised in the Swabian Jura by calcareous grasslands with shrubs and trees of *Juniperus communis*, *Prunus spinosa* and *Quercus robur*, and in the Lueneburg Heath by heathlands with *Juniperus communis*, *Betula pendula*, *Quercus* spp. and *Pinus sylvestris*. The shrubs and trees occur at different densities and ages across the semi-open habitats (Eggers et al., 2010).

2.2 | Study and sampling design

In summer 2013, four study sites of 25 ha each were randomly selected in each region. At each study site, we randomly selected five plots of 5 m × 4 m of each of four types of habitats (i.e. 80 plots overall in each region): woodlands (W), semi-open habitats where canopy closure was high (SOH; Swabian Jura: 66–98%; Lueneburg Heath: 69–96%), semi-open habitats where canopy closure was low (SOL; Swabian Jura: 20–56%; Lueneburg Heath: 36–77%), and open habitats (O). In both regions, woodland with dense canopies (following the definition of Peterken, 1993) and open habitats were located adjacent to the semi-open habitats and transitioned into those. In each plot, we determined all vascular plants and epigaeic bryophytes and estimated their cover and that of shrubs (1–5 m), trees of the lower canopy (5–10 m), and of the upper canopy (>10 m; if these layers were developed; Dierschke, 1994). Nomenclature is based on Jäger (2011) for vascular plants and Frahm and Frey (2004) for bryophytes.

2.3 | Environmental variables of the study sites

A hemispherical photograph was taken 1 m above-ground in the centre of each plot with a fish-eye lens (Nikon, Fisheye Converter FC-E8 0.21×, Tokyo, Japan) to characterise the light conditions (Beckschäfer, Seidel, and Kleinn, 2013). Canopy closure was quantified for each plot using Gap Light Analyzer 2.0 (Frazer, Canham, and Lertzman, 1999).

To study soil conditions, we randomly took five samples of the upper mineral horizon in each plot, pooled them and determined the pH (H_2O) value, the base saturation and the C:N ratio using standard procedures (see Steubing and Fangmeier, 1992). Soil nitrogen and carbon content were determined with a CN-analyser (Elementaranalysator Vario El Cube, Hanau, Germany).

Both in the Swabian Jura and the Lueneburg Heath canopy closure of the semi-open habitats was intermediate between that of the woodlands and open plots (Table 2; Appendix S1). C:N ratios in the different habitat types per region were similar, but open and semi-open habitats with low canopy closure tended to have higher base saturation and pH values. Site conditions between regions were not compared because of entirely different bedrocks, soil types and habitat structures.

2.4 | Analyses of the species composition of habitat types and plant traits

All statistical analyses were conducted in R version 3.5.2 (R Core Team, 2018). We applied generalized linear models for multivariate data (GLM$_{mv}$, using the *manyglm* function of the mvabund R package;

TABLE 2　Canopy closure and soil chemistry in the four studied habitat types in the Swabian Jura and the Lueneburg Heath: W, woodland; SOH, semi-open habitat with high canopy closure; SOL, semi-open habitat with low canopy closure; O, open habitat. Habitat comparisons were conducted using analysis of variance with study site as a block factor, followed by Tukey's multiple comparison procedure ($n = 20$ per habitat type)

	Swabian Jura				Lueneburg Heath			
	W	SOH	SOL	O	W	SOH	SOL	O
Canopy closure (%)	93[a]	86[b]	36[c]	24[d]	86[a]	81[a]	61[b]	27[c]
C:N	13.9[a]	12.9[a]	12.8[a]	11.8[a]	25.3[a]	23.8[a]	23.5[a]	25.4[a]
Base saturation (%)	84.8[a]	89.9[ab]	97.0[b]	98.8[b]	13.9[a]	21.3[a]	34.4[b]	66.4[c]
pH (H2O)	6.5[a]	6.4[a]	7.4[b]	7.6[b]	4.0[a]	4.2[ab]	4.4[b]	4.7[c]

Note: Different letters indicate significant differences ($p_{adj.} < 0.05$) between habitat types within a region.

TABLE 3 Ellenberg indicator values and life-history traits of species used in the comparison of the four habitat types

Ellenberg indicator values	SWA	LH	Dispersal traits	SWA	LH	Establishment traits	SWA	LH
EIV	100	100	*Seed dispersal type*	82	69	*Seedbank type*	79	69
Light			Self-dispersal			Transient seedbank, < 1 year		
Moisture			Wind-dispersal			Short-term seedbank, 1–5 years		
			Short-distance animal-dispersal (by invertebrates)			Long-term seedbank, > 5 years		
			Long-distance animal-dispersal (by vertebrates)					
			Propagation type	56	71	*Age of flowering*	64	50
			Propagation by seeds only			<1 year until flowering		
			Vegetative propagation only			1–5 years until flowering		
			Propagation by seeds & vegetatively			> 5 years until flowering		
			Seed mass	100	100			

Note: Trait types are in italics. Proportion of species (%) for which each trait type was available is given for the Swabian Jura (SWA) and the Lueneburg Heath (LH).

Wang, Naumann, Eddelbuettel, Wilshire and Warton, 2020) to evaluate differences in plant species composition between habitat types. To account for differences between local site conditions, we used study site as block factor. This model-based approach allows to test for location effects by accounting for the mean–variance relationship of untransformed multivariate data (Warton, Wright and Wang, 2012). Models were fitted with a negative binomial distribution and the significance of predictors was assessed by likelihood ratio tests with 1,000 iterations. For pairwise comparisons, we applied a Bonferroni correction. Variation in species composition with habitat type was visualised using non-metric multidimensional scaling (NMDS, using the *metaMDS* function of the vegan R package; Oksanen et al., 2019) with two (Swabian Jura data) and three dimensions (Lueneburg Heath data), respectively. Increasing the number of dimensions for the ordination of the Lueneburg Heath data resulted in a substantial reduction of the ordination stress (two dimensions: 0.18; three dimensions: 0.11). The NMDS was performed on a matrix of Bray–Curtis dissimilarities based on square-root-transformed abundance data (i.e. species cover). Moreover, we included those environmental variables in the ordination plot that showed significant correlations with NMDS axes (using the *envfit* function of the vegan R package).

We applied an Indicator Species Analysis (ISA; Dufrêne and Legendre, 1997) using the package indicspecies (De Cáceres and Legendre, 2009) to test for significant associations of species with specific habitat types. Indicator species for individual habitat types and combinations of habitat types were identified in the community matrix using indicator value indices. These indicator values range from zero (no indication) to one (perfect indication). To test the significance of the indicator value of each species for a certain habitat type or combination of habitats, 999 permutations were run.

In addition, we identified species that were not classified as indicator species (due to low within-habitat type constancy values of ≤15%), but exclusively occurred in one habitat type or a combination of two or three different habitat types. These species are henceforth referred to as "rare species." Moreover, we identified species that were found in all four habitat types. These species showed low between-habitat-type differences in constancy values (≤15%).

To investigate whether dispersal or establishment processes were limiting the presence of species of woodland and open habitats in semi-open habitats, we analysed life-history traits (as community-weighted means) of all herbaceous species and their realised ecological niches in each plot (Garnier et al., 2004). To this end, we evaluated the life-history traits seed mass, dispersal mechanism, seed bank longevity, age at first flowering (as listed by Kleyer et al., 2008) and propagation mode (Fitter and Peat, 1994) for the species for which data were available. If there were several different records for seed mass, we used the mean value. We differentiated between the following modes of dispersal: self-dispersal, dispersal by wind, short-distance dispersal by animals (by invertebrates), and long-distance dispersal by animals (by vertebrates).

For some traits, such as dispersal mode, the database distinguishes several trait classes (cf. Table 3), and a species could be assigned by different authors to a different class. To account for inconsistent literature records for a trait of a species, we calculated "weighted trait values" (i.e. number of literature records per trait class divided by the total number of records for a trait of a given species) and then used these values to calculate community-weighted means for a trait class (obtained by weighting the species' trait values with the species' relative cover in a plot of a respective habitat type; Garnier et al., 2004). We calculated community-weighted means for habitat comparisons including all herbaceous species present in a plot for two reasons. Trait combinations in plant communities have been shown to be predominantly filtered by local-scale factors such as disturbance (incl. management), fine-scale soil conditions, microclimate, or biotic interactions (Bruelheide et al., 2018). Community-weighted traits means

thus can be considered as appropriate indicators for (local-scale) environmental conditions that determine the plant species composition of a focal habitat. Moreover, we wanted to include both specialists and generalists present in a habitat type, because both groups contribute to the species combination and richness typical of a habitat type (particularly in the Lueneburg Heath). In addition to trait analyses, we calculated Ellenberg light and moisture indicator values (EIV) weighted by species' cover (Ellenberg, Weber, Düll, Wirth, and Werner, 1992; Jäger, 2011) to assess between-type differences in realised ecological niches (Table 3). Differences in trait means and weighted EIV between habitat types ($n = 20$) were assessed by analysis of variance followed by Tukey's multiple comparison procedure after accounting for variation between study sites (block factor; type-I sum of squares). Models were fitted for each region separately. This variance modelling framework was preferred, because it allows analysing mean–variance relationships based on untransformed data (Zuur, Ieno, Walker, and Saveliev, 2009; using the packages nlme (Pinheiro, Bates, DebRoy, and Sarkar, 2020) and multcomp (Hothorn and Bretz, 2008)). For all models, residual plots indicated no violation of model assumptions according to Zuur et al. (2009).

3 | RESULTS

3.1 | Species composition among the plant communities of the four habitat types

For both regions, we found significant effects of habitat type (Swabian Jura: L: 3,909, $p < 0.001$; Lueneburg Heath: L: 612, $p < 0.001$) and study site (Swabian Jura: L: 1,728, $p < 0.001$;

Lueneburg Heath: L: 582.6, $p < 0.001$) on species composition. Overall, the effects of habitat type were stronger than those of study site (especially in the Swabian Jura), as indicated by the magnitude of the L-ratio.

The NMDS ordination showed clusters of the plots corresponding to the four habitat types in the Swabian Jura and the Lueneburg Heath (Figure 1a, b). NMDS axes reflected a gradient of light (Swabian Jura: $r^2 = 0.72$, $p < 0.0001$; Lueneburg Heath: $r^2 = 0.74$; $p < 0.0001$) and nutrient availability (Swabian Jura: pH: $r^2 = 0.44$, $p < 0.0001$; base saturation: $r^2 = 0.08$, $p = 0.03$; Lueneburg Heath: pH: $r^2 = 0.45$, $p < 0.0001$; base saturation: $r^2 = 0.62$, $p < 0.0001$; Figure 1). In the NMDS ordination of the vegetation in the Swabian Jura, the W plots formed a distinct cluster and were significantly different from all other habitat types (all comparisons $p_{adj.} < 0.05$; Appendix S2), while plots of the other habitat types were grouped closer together (Figure 1a). SOH plots showed the largest within-habitat-type variation, and species composition differed significantly from that of other habitat types (all comparisons $p_{adj.} < 0.01$; Appendix S2), despite some overlap with SOL plots (Figure 1a). O and SOL plots showed the largest similarity in species composition with loW within-habitat-type variation (Figure 1a and Appendix S3). In the Lueneburg Heath, plant species composition of the four habitat types was more similar than in the Swabian Jura (Figure 1b), but all habitat types differed significantly from each other in their species composition (all comparisons $p_{adj.} < 0.01$: Appendix S2). W plots showed similarities to SOH and SOL in the NMDS. Community composition of O plots showed only some overlap with SOL. Within-habitat-type variation was high in all habitat types, except for open habitats (Figure 1b).
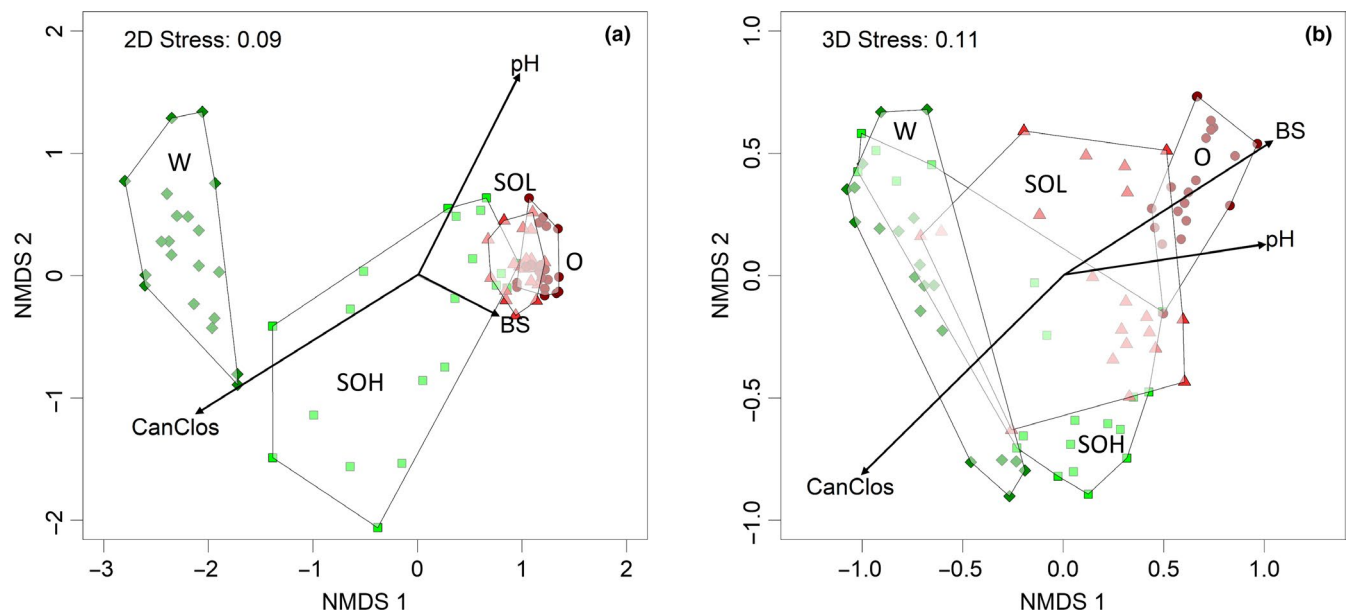
FIGURE 1 Non-metric multidimensional scaling of the plant communities of the four habitat types in (a) the Swabian Jura and (b) the Lueneburg Heath; woodland (W); semi-open habitat with high canopy closure (SOH) and low canopy closure (SOL); open habitat (O). Significant environmental factors are fitted as vectors: pH, base saturation (BS) and canopy closure (CanClos)

3.2 | Indicator species and species richness of the habitat types

We recorded a total of 244 plant species (221 vascular plants, 23 bryophytes) in the Swabian Jura and 53 plant species (43 vascular plants, 10 mosses) in the Lueneburg Heath. About one-third (Swabian Jura: 39%; Lueneburg Heath: 30%) of the plant species proved to be indicator species, i.e. showed a significant affinity either to a habitat type or a combination of habitat types (Table 4a¸ all species with $p \leq 0.05$ are listed in Appendices S4 and S5).

Most species (about two-thirds) proved to be "rare species," and some species occurred across all habitat types (Table 4b; for constancy tables see Appendices S6 and S7 and for complete species lists of habitat types see Appendices S8 and S9).

In the Swabian Jura, 93 species were found in W plots, of which 23 proved to be indicator species for the W habitat type. In addition, a further 34 rare species appeared only in W plots. Thus,

57 species (61%) were restricted to woodlands, but W plots also shared a total of 27 (indicator and rare) species (29%) with semi-open corridors. In the Lueneburg Heath, the number of indicator and rare species restricted to W was much lower (three and six out of 27 species, respectively, i.e. 33% in total). In addition, W plots had a total of 13 species (48%) in common with semi-open corridors.

In the Swabian Jura, 110 species were found in O plots, but only 11 (indicator and rare) species were restricted to this habitat type (10%). A total of 89 species (81%) in O plots also occurred in semi-open corridors (including the species which occurred across all habitat types). In the Lueneburg Heath, overall species richness of O plots was lower than in the Swabian Jura (36 species), and only four (indicator and rare) species were restricted to this habitat type (11%). O plots, in turn, had a total of 23 species (64%) in common with semi-open corridors (including the species which occurred across all habitat types).

TABLE 4 Total species richness and number of (a) indicator species and (b) "rare species" for the four individual habitat types and for combinations of these habitats in the Swabian Jura and the Lueneburg Heath

(a)	Swabian Jura				Lueneburg Heath			
Habitat type	**W**	**SOH**	**SOL**	**O**	**W**	**SOH**	**SOL**	**O**
Total species richness	93	162	120	110	27	33	34	36
	23				3			
		12						
			2				3	
				1				1
	3				2			
		5						
		17						
			31				4	

(b)	Swabian Jura				Lueneburg Heath			
Habitat type	**W**	**SOH**	**SOL**	**O**	**W**	**SOH**	**SOL**	**O**
Total species richness	93	162	120	110	27	33	34	36
	34				6			
		34				3			
			6				3	
				10				3
	7				8			
	13				1			
	4				2			
		8						
		27				9		
			7				2	

Abbreviations: W, woodland; SOH, semi-open habitat with high canopy closure; SOL, semi-open habitat with low canopy closure; O, open habitat (for the sake of clarity, the table only considers habitat combinations that are characterised by more than one species). In addition, the number of species is given that appeared in all habitat types.

In the Swabian Jura, SOH and SOL plots were characterised by the highest species richness (162 and 120, respectively) of all habitat types. A total of 46 (indicator and rare) species were restricted to SOH, and eight to SOL plots. In contrast, overall species richness of SOH and SOL plots in the Lueneburg Heath was lower than in O plots. Three indicator species were typical of SOL plots, and three rare species each were found in SOL and SOH plots.

3.3 | Community-weighted trait means and mean Ellenberg indicator values of habitat types

In the Swabian Jura seeds of species growing in SOL and O plots were much smaller than those of species in SOH and W plots. At least two-thirds of the species found in the SOH, SOL and O plots were dispersed by vertebrates over long distances (Table 5; Appendix S1), while self-dispersal, dispersal by wind and short-distance dispersal by invertebrates was much less common among the species. In contrast, W plots had a significantly lower proportion of species with long-distance dispersal by animals but also a significantly higher proportion of species that were self-dispersed and dispersed by invertebrates over short distances. In SOH, SOL and O plots a higher

proportion of species exclusively propagated by seeds, whereas species in W plots were more likely to propagate vegetatively (Table 5).

In the Lueneburg Heath we found patterns of seed mass similar to those in the Swabian Jura (Table 5; Appendix S1). However, the proportion of long-distance animal-dispersed species was very high across all habitat types, including W plots (Table 5). While species of SOH, SOL and O plots were more likely to also disperse via wind dispersal, W plots contained more species which were short-distance animal-dispersed. Self-dispersal played a minor role for species of all habitat types in the Lueneburg Heath. Species with vegetative propagation tended to be more frequent in W and SOH plots, whereas the proportion of species which are able to propagate by both seeds and vegetatively was higher across SOH, SOL and O plots (Table 5).

In the Swabian Jura, the proportion of species with a transient seed bank was very high and that of species with a persistent seed bank was low across habitat types (Table 5; Appendix S1). SOH, SOL and O plots, however, contained a higher proportion of species with short-term seed banks than W plots. In the Lueneburg Heath, W plots contained the highest proportion of species with a transient seed bank, whereas the proportion of species with short- and long-term seed banks was higher in SOH, SOL and O plots.

TABLE 5 Community-weighted means of dispersal and establishment traits and mean Ellenberg indicator values (EIV) for the different habitat types in the Swabian Jura and the Lueneburg Heath (W, woodland; SOH, semi-open habitat with high canopy closure; SOL, semi-open habitat with low canopy closure; O, open habitat; $n = 20$ per habitat type)

Trait	Swabian Jura				Lueneburg Heath			
	W	SOH	SOL	O	W	SOH	SOL	O
Seed mass (mg)	9.3[a]	4.2[b]	2.4[c]	2.2[c]	20.2[a]	10.9[ab]	6.1[bc]	0.3[c]
Seed dispersal type								
% self-dispersed	24[a]	9[bc]	8[b]	11[c]	0.2[a]	2[ab]	1[b]	1[ab]
% wind-dispersed	11[a]	16[a]	15[a]	15[a]	3[a]	9[b]	9[b]	14[c]
% dispersed by invertebrates	18[a]	5[bc]	4[b]	6[c]	6[a]	5[ab]	3[b]	1[c]
% dispersed by vertebrates	48[a]	70[bc]	73[b]	68[c]	90[a]	84[ab]	85[ab]	85[b]
Propagation type								
% propagated by seeds	22[a]	58[b]	77[c]	78[c]	9[a]	8[a]	3[a]	2[a]
% propagated vegetatively	49[a]	9[b]	1[b]	2[b]	55[a]	32[ab]	16[bc]	1[c]
% propagated by both types	29[ab]	33[b]	22[ab]	20[a]	36[a]	60[ab]	81[bc]	97[c]
Seed bank type								
% with transient seedbank	87[a]	84[a]	84[a]	83[a]	77[a]	57[b]	49[b]	28[c]
% with short-term seedbank	5[a]	12[b]	11[b]	12[b]	15[a]	28[b]	29[b]	38[c]
% with long-term seedbank	8[a]	4[a]	5[a]	5[a]	8[a]	15[b]	22[b]	34[c]
Age of flowering								
% flowering within a year	6[a]	26[b]	35[b]	32[b]	43[a]	23[b]	25[b]	7[c]
% flowering after 1–5 years	88[a]	73[b]	65[b]	68[b]	55[a]	62[ab]	75[b]	90[c]
% flowering after > 5 years	6[a]	1[a]	0.3[a]	0.1[a]	2[a]	15[b]	0.3[a]	3[ab]
Ellenberg Indicator Values (EIV)								
Mean EIV for light	3.3[a]	6.5[b]	7.3[c]	7.4[c]	5.6[a]	5.6[ab]	6.4[b]	7.5[b]
Mean EIV for moisture	5.1[a]	4.4[b]	3.9[c]	3.7[c]	4.9[ac]	4.5[b]	4.7[ab]	5.0[c]

Note: Different letters indicate significant differences ($p_{adj.} < 0.05$) between habitat types within a region.

In both regions, the species from different habitats varied in the length of their vegetative phase. While in the Swabian Jura the proportion of species with a short vegetative phase increased with the openness of the habitats (i.e. from W to O; Table 5, Appendix S1) and that of species flowering only after a prolonged time of growth decreased, in the Lueneburg Heath the proportion of species with a short vegetative phase (<1 year) was highest in W plots and that of species with a longer vegetative phase was higher in SOH, SOL and O plots (Table 5).

In both regions, the mean Ellenberg indicator values for light increased with the openness of the habitats (i.e. from W to O; Table 5; Appendix S1). Conversely, in the Swabian Jura the mean indicator value for moisture decreased with habitat openness, but we found no clear pattern for the indicator values for soil moisture in the Lueneburg Heath. While in the Swabian Jura, only the SOL plots were very similar to the O plots in their light and moisture conditions as indicated by the mean indicator values, in the Lueneburg Heath, SOH plots also showed similarities to the light conditions of SOL and O plots.

4 | DISCUSSION

4.1 | Plant communities and species composition in semi-open habitats

Our results demonstrate that the composition of the plant community of semi-open habitats shows a great overlap with that of open habitats and to a lesser extent with that of woodlands. Furthermore, several species showed a clear preference for semi-open habitats, particularly in the Swabian Jura. This explains the extraordinary phytodiversity of semi-open habitats found in this region.

Overall, the plant species composition of semi-open habitats was more similar to that of open habitats than to that of woodlands. This was reflected by both the results of the analysis of species composition and the analyses of indicator/rare species, according to which only a small proportion of plant species (Swabian Jura: 10%; Lueneburg Heath: 11%) was restricted to O plots. In contrast, many species occurred in both SO and O plots, indicating that species of open habitats successfully disperse into semi-open habitats and cope well with the environmental conditions there. This corroborates that semi-open habitats can provide appropriate stepping stones for many open habitat species, and that this function was realised both in the limestone landscape of the Swabian Jura and in the Lueneburg Heath region with its acidic soils.

In contrast to the situation in open habitats, a higher proportion of species in the W plots (61% in the Swabian Jura and 33% in the Lueneburg Heath) was restricted to that type of habitat. This suggests that woodland species are either more stenoecious or have a lower dispersal ability than species of open habitats (Dzwonko, 2001; Härdtle and Von Oheimb, 2003; Schmidt and Kriebitzsch, 2011). In fact, many of the species only found in W

plots could be characterised as "ancient woodland species" (e.g. *Helleborus viridis* and *Cephalanthera damasonium* in the Swabian Jura), whose populations are mostly restricted to sites with a continuous forest cover for more than 200 years (Hermy, Honnay, Firbank, and Grasdorf-Bokdam, 1999). However, ca. 29% (Swabian Jura) and 48% (Lueneburg Heath) of all species in the W plots were also found in the SO plots, suggesting that semi-open habitats can serve as stepping stones for at least some woodland species. Remarkably, at least some SOH plots in the Swabian Jura contained the ancient woodland species *Helleborus viridis* and *Cephalanthera damasonium* and species that are less habitat-specific and hence appeared in woodlands and open habitats (e.g. *Viola hirta* and *Potentilla erecta*; Schmidt et al., 2011). The presence of both stenoecious and euryoecious species in SO plots suggests that a range of species with different environmental requirements can inhabit semi-open habitats, likely attributable to spatially heterogeneous conditions with regard to light, temperature, air humidity or soil moisture (Dierschke, 1974). This interpretation is supported by a study of Eggers et al. (2010) of the composition of the carabid beetle community of semi-open corridors in the Lueneburg Heath, in which both stenoecious woodland and open-landscape species were found in the same pitfall traps established in SO plots.

A number of indicator and rare species were specific to semi-open habitats in both regions (particularly in the Swabian Jura). Many of these species are typical of fringe and ruderal communities (e.g. of the *Trifolio-Geranietea* or *Geo-Alliarion*; Leuschner and Ellenberg, 2018), which occur neither in forests with closed canopies nor in completely open habitats.

4.2 | Occurrence of species in semi-open habitats in relation to their traits andenvironmental requirements

An understanding of the mechanisms that drive the occurrence of species in semi-open habitats is important for an assessment of the potential of that habitat type to connect other habitats. The successful establishment of a population at a site depends on several processes: seed dispersal, plant establishment upon arrival and reproduction (Hampe, 2011). Seed dispersal is only successful if the dispersed seed is able to establish and produce a new generation. For semi-open habitats to function as a stepping-stone habitat, these processes must be repeated in them by several generations until a target habitat is reached. A species' potential to establish itself in semi-open habitats may therefore be limited by the ability to produce descendants either by seed or vegetatively, by dispersal, or by low-density establishment.

Our trait analyses suggest that the sparse occurrence of woodland species in semi-open habitats could be related to both limited dispersal and establishment. Although a high proportion of woodland species may be dispersed by vertebrates and thus potentially over long distances, the species are also dispersed by invertebrates such as ants (Brunet and Von Oheimb, 1999), and are self-dispersed or spread by vegetative propagation. However, these modes of

dispersal are very inefficient (in terms of long-distance dispersal; Brunet and Von Oheimb, 1999; Von Oheimb, Kriebitzsch, Schmidt, and Heinken, 2009). As a consequence, ancient woodland species in particular are dispersal-limited. For example, the ant-dispersed *Anemone nemorosa* shows migration rates of 0.2 m/year (Wulf, 1997; Brunet and Von Oheimb, 1999) and *Melampyrum pratense* of 0.91 m/ year (Heinken, 2004).

In contrast, more than three-quarters of the species of semi-open and open habitats were adapted to long-distance animal dispersal. Historically, these man-made landscapes have been shaped by transhumance (Poschlod and Bonn, 1998), and even today livestock grazing is an important conservation measure to preserve these landscapes (e.g. to prevent shrub encroachment and to support seed dispersal). Seed dispersal by large animals such as cattle and sheep through adhesion (and endozoochory) may even result in long-distance transports, for instance over several hundred kilometres (Couvreur, Christiaen, and Verheyen, 2004; Manzano and Malo, 2006). On top of that, semi-open and open habitats contained also a higher proportion of wind-dispersed species than woodlands. Adaptations to wind dispersal and low seed mass may facilitate long-distance dispersal of species of semi-open and open habitats (Damschen et al., 2014). As a result, the general ability to disperse is higher for O than for W species, which also facilitates their dispersal into semi-open habitats.

A significant proportion of species of semi-open and open habitats of both the Swabian Jura and the Lueneburg Heath were more likely to have either a short- or long-term seed bank than woodland species. While the seeds of many O species can persist up to five years in the soil, the longevity of the seeds of many W species is less than one year (Hopfensperger, 2007; Bossuyt and Honnay, 2008). Persistent seed banks provide species with the capability to survive unfavourable environmental conditions and allow them to germinate once environmental conditions have improved (Bazzaz, 1979; Bossuyt and Honnay, 2008). For example, species which preferably grow in the darker conditions of SOH may germinate once semi-open habitats have developed a denser shrub or tree layer. W species with transient seed banks have to germinate within a year in semi-open habitats; otherwise, their seeds become non-viable and dispersal fails. Flowering age also showed habitat-specific differences. Most W species of the Swabian Jura, for example, need several years to reach flowering and produce seeds, which in turn might delay establishment in SO plots. In contrast, about one-third of SO and O species are able to flower within the first year after germination, which in turn might facilitate early propagation.

Analyses of the realised ecological niches suggest that abiotic site conditions can act as a filter for the establishment of species in semi-open habitats. The requirements of species in woodlands in terms of light and soil moisture differed clearly from that of species of semi-open and open habitats, supporting the conclusion that environmental conditions limit the suitability of semi-open habitats for woodland species. Species of SOL habitats in the Swabian Jura showed the same light and soil moisture requirements as open-habitat species and the establishment of species from open habitats was less likely to be inhibited in SOL habitats due to site conditions.

In the Lueneburg Heath, patterns were less clear, which also corresponds to the patterns of life-history traits recorded. Although species in woodlands had significantly lower light requirements, the differences to species of semi-open and open habitats were small. Therefore, W, SOH, SOL and O species in the Lueneburg Heath had similar light demands.

The differences in traits and site requirements of the species of the Swabian Jura and the Lueneburg Heath may be explained by differences in site management history, vegetation structure, phenology or soil conditions (e.g. calcareous vs acidic sites, *Fagion* vs *Quercion* forest communities, and *Mesobromion* vs *Genistion* communities in the Swabian Jura and the Lueneburg Heath, respectively; cf. Leuschner and Ellenberg, 2018). Between-region differences in traits (e.g. seed propagation, seedbank type, and flowering age) — particularly with regard to open habitats (i.e. *Bromion* vs *Genistion* communities) — are strongly shaped by differences in land-use management and history. In the Swabian Jura, *Bromion* communities are shaped by a long history of grazing (Leuschner and Ellenberg, 2018). As a consequence, plant species have been favoured that are adapted to and depend on (epi-)zoochory, i.e. dispersal of seeds by grazing animals such as sheep (Bonn and Poschlod, 1998; Bonn, 2004). In contrast, open landscapes in the Lueneburg Heath (i.e. *Genistion* communities) have been subject to a long-lasting mixture of different management regimes (i.e. mowing, prescribed burning, sod-cutting, grazing; Härdtle, Niemeyer, Niemeyer, and Assmann, 2006), which in turn favours plants that are propagated by both seeds and vegetatively, and whose re-establishment (after a total removal of the aboveground biomass due to sod-cutting or prescribed burning) benefits from the formation of long-term seedbanks. In addition, open landscapes in the Lueneburg Heath often are characterised by the dominance of dwarf shrubs (e.g. *Calluna vulgaris*) that are well adapted to these management measures. This in turn explains the low proportion of species with low flowering age (i.e. within the first year).

5 | CONCLUSIONS

Our findings suggest that semi-open habitats have the potential to mitigate the effects of habitat fragmentation by serving as stepping stones and thus as dispersal corridors — at least in the two cultural landscapes investigated. We found that on average 73% of open habitat species (81% in the Swabian Jura and 64% in the Lueneburg Heath) and 39% of woodland species (29% in the Swabian Jura and 48% in the Lueneburg Heath) were also present in semi-open habitats (i.e. SOL and/or SOH). This indicates that semi-open habitats can potentially act as stepping stones for species of open habitats and, to a lesser degree, of woodlands on their way to reach another target habitat and thus

contribute to preserve the phytodiversity of woodland and open habitats in fragmented landscapes (Benayas and Bullock, 2008). Furthermore, semi-open corridors were very heterogeneous between study sites and characterised by a high phytodiversity, in part attributable to species that were only found in these habitats. Semi-open habitats are both hotspots of phytodiversity and potential species pools for the colonisation of adjacent habitats. However, there are limits to the suitability of semi-open habitats as corridors and they do not function for all species. About two-thirds of woodland species were not recorded in semi-open habitats, likely attributable to the stenoecious behaviour and dispersal limitation of woodland species. This suggests that semi-open corridors do not work for the majority of woodland species. Moreover, it remains unclear to what extent this concept may work for regions with different environmental settings (e.g. other types of bedrock, soil or climatic conditions) and species assemblages.

In summary, our results show the potential of semi-open habitats for species conservation by providing suitable interim habitats for species, in particular for those of open habitats and to a lesser extent for those of woodlands. Restoration strategies should therefore consider the development of semi-open corridors to alleviate barrier effects and to mitigate the effects of habitat fragmentation.

ACKNOWLEDGEMENTS

AUTHOR CONTRIBUTIONS

WH, DM and ET conceived the research idea and designed the methodology; ET and WTP collected the data; ET and AF performed statistical analyses; ET wrote the paper with significant contributions from all other co-authors.

DATA AVAILABILITY STATEMENT

The primary data used in this study are available in Appendices S8 and S9.

ORCID

Eliane Travers https://orcid.org/0000-0002-3582-411X
Andreas Fichtner https://orcid.org/0000-0003-0499-4893
Diethart Matthies https://orcid.org/0000-0003-2439-0501
Werner Härdtle https://orcid.org/0000-0002-5599-5792

REFERENCES

Bazzaz, F.A. (1979) The physiological ecology of plant succession. *Annual Review of Ecology and Systematics*, 10, 351–371. https://doi.org/10.1146/annurev.es.10.110179.002031

Beckschäfer, P., Seidel, D., Kleinn, C. and Xu, J. (2013) On the exposure of hemispherical photographs in forests. *iForest*, 6, 228–237. https://doi.org/10.3832/ifor0957-006

Beinlich, B. and Plachter, H. (1995) *A nature conservation concept for the calcareous grasslands of the central Swabian Jura (Baden-Württemberg): Protection, use and development (German)*. Karlsruhe: Landesanstalt für Umweltschutz Baden-Württemberg.

Benayas, J.M.R., Bullock, J.M. and Newton, A.C. (2008) Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. *Frontiers in Ecology and the Environment*, 6, 329–336. https://doi.org/10.1890/070057

Bergmeier, E., Petermann, J. and Schröder, E. (2010) Geobotanical survey of wood-pasture habitats in Europe: Diversity, threats and conservation. *Biodiversity Conservation*, 19, 2995–3014. https://doi.org/10.1007/s10531-010-9872-3

Bonn, S. (2004) *Dispersal of plants in the Central European landscape – dispersal processes and assessment of dispersal potential exemplified for endozoochory*. PhD thesis. Regensburg: Regensburg University.

Bonn, S. and Poschlod, P. (1998) *Propagation biology of plants of Central Europe. Basics and cultural historical aspects (German)*. Wiesbaden: Quelle & Meyer.

Bossuyt, B. and Honnay, O. (2008) Can the seed bank be used for ecological restoration? An overview of seed bank characteristics in European communities. *Journal of Vegetation Science*, 19, 875–884. https://doi.org/10.3170/2008-8-18462

Brederveld, R.J., Jähnig, S.C., Lorenz, A.W., Brunzel, S. and Soons, M.B. (2011) Dispersal as a limiting factor in the colonization of restored mountain streams by plants and macroinvertebrates. *Journal of Applied Ecology*, 48, 1241–1250. https://doi.org/10.1111/j.1365-2664.2011.02026.x

Bruelheide, H., Dengler, J., Purschke, O., Lenoir, J., Jimenez-Alfaro, B., Hennekens, S.M. et al (2018) Global trait-environment relationships of plant communities. *Nature Ecology and Evolution*, 2, 1906–1917. https://doi.org/10.1038/s41559-018-0699-8

Brunet, J. and Von Oheimb, G. (1999) Migration of vascular plants to secondary woodlands in southern Sweden. *Journal of Ecology*, 86, 429–438. https://doi.org/10.1046/j.1365-2745.1998.00269.x

Cordes, H., Kaiser, T., Lancken, H., Lütke-Pohl, V. and Prüter, J. (1997) *Lüneburger Heide nature reserve: History, ecology, nature conservation (German)*. Bremen: Hauschild.

R Core Team. (2018) *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available at https://www.R-project.org/

Couvreur, M., Christiaen, B., Verheyen, K. and Hermy, M. (2004) Large herbivores as mobile link between isolated nature reserves through adhesive seed dispersal. *Applied Vegetation Science*, 7, 229–236. https://doi.org/10.1111/j.1654-109X.2004.tb00614.x

Damschen, E.I., Baker, D.V., Bohrer, G., Nathan, R., Orrock, J.L., Turner, J.R. et al (2014) How fragmentation and corridors affect wind dynamics and seed dispersal in open habitats. *Proceedings of the National Academy of Sciences USA*, 111, 3484–3489. https://doi.org/10.1073/pnas.1308968111

Damschen, E.I., Haddad, N.M., Orrock, J.L., Tewksbury, J.J. and Levey, D.J. (2006) Corridors increase plant species richness at large scales. *Science*, 313, 1284–1286. https://doi.org/10.1126/science.1130098

De Cáceres, M. and Legendre, P. (2009) Associations between species and groups of sites: Indices and statistical inference. *Ecology*, 90, 3566–3574. https://doi.org/10.1890/08-1823.1

Dierschke, H. (1974) *Fringe communities in the vegetation and site gradient at forest edges (German), Scripta Geobotanica 6*. Göttingen: Verlag Erich Goltze KG.

Dierschke, H. (1994) *Plant sociology: Principles and methods (German)*. Stuttgart: Eugen Ulmer.

Dobson, A., Ralls, K., Foster, M., Soulé, M.E., Simberloff, D., Doak, D. et al (1999) Corridors: Reconnecting fragmented landscapes. In: Soulé, M.E. and Terborgh, J. (Eds.) *Continental Conservation: Scientific Foundations of Regional Reserve Networks*. Washington, D.C.: Island Press, pp. 129–170.

Dufrêne, M. and Legendre, P. (1997) Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs*, 67, 345–366. https://doi.org/10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2

Dzwonko, Z. (2001) Assessment of light and soil conditions in ancient and recent woodlands by Ellenberg indicator values. *Journal of Applied Ecology*, 38, 942–951. https://doi.org/10.1046/j.1365-2664.2001.00649.x

Eggers, B., Matern, A., Drees, C., Eggers, J., Härdtle, W. and Assmann, T. (2010) Value of semi-open corridors for simultaneously connecting open and wooded habitats: A case study with ground beetles. *Conservation Biology*, 24, 256–266. https://doi.org/10.1111/j.1523-1739.2009.01295.x

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. and Paulissen, D. (Eds) (1992) *Indicator values of plants in Central Europe (German)*, *Scripta Geobotanica 18*, 2nd edition. Göttingen, DE: Verlag Erich Goltze KG.

Evans, M.J., Banks, S.C., Driscoll, D.A., Hicks, A.J., Melbourne, B.A. and Davies, K.F. (2017) Short- and long-term effects of habitat fragmentation differ but are predicted by response to the matrix. *Ecology*, 98, 807–819. https://doi.org/10.1002/ecy.1704

Finck, P., Riecken, U. and Schröder, E. (2002) Pasture landscapes and nature conservation – New strategies for the preservation of open landscapes in Europe. In: Redecker, B., Finck, P., Härdtle, W., Riecken, U. and Schröder, E. (Eds.) *Pasture Landscapes and Nature Conservation*. Berlin, Heidelberg: Springer Verlag, pp. 1–13.

Fischer, M. and Matthies, D. (1998a) RAPD variation in relation to population size and plant performance in the rare *Gentianella germanica*. *American Journal of Botany*, 85, 811–819.

Fischer, M. and Matthies, D. (1998b) Effects of population size on performance in the rare plant *Gentianella germanica*. *Journal of Ecology*, 86, 195–204. https://doi.org/10.1046/j.1365-2745.1998.00246.x

Fitter, A.H. and Peat, H.J. (1994) The ecological flora database. *Journal of Ecology*, 82, 415–425. https://doi.org/10.2307/2261309

Frahm, J.P. and Frey, W. (2004) *Mossflora (German)*, 4th edition. Stuttgart: UTB.

Frazer, G., Canham, C., & Lertzman, K. (1999). *Gap Light Analyzer (GLA): Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation*. Burnaby, British Columbia and Millbrook, New York: Simon Fraser University and Institute of Ecosystem Studies.

Garnier, E., Cortez, J., Billès, G., Navas, M.L., Roumet, C., Debussche, M. et al (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, 85, 2630–2637. https://doi.org/10.1890/03-0799

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D. et al (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, 1, e1500052. https://doi.org/10.1126/sciadv.1500052

Hampe, A. (2011) Plants on the move: The role of seed dispersal and initial population establishment for climate-driven range expansions. *Acta Oecologica*, 37, 666–673. https://doi.org/10.1016/j.actao.2011.05.001

Härdtle, W., Niemeyer, M., Niemeyer, T., Assmann, T. and Fottner, S. (2006) Can management compensate for atmospheric nutrient deposition in heathland ecosystems? *Journal of Applied Ecology*, 43, 759–769. https://doi.org/10.1111/j.1365-2664.2006.01195.x

Härdtle, W., Von Oheimb, G. and Westphal, C. (2003) The effects of light and soil conditions on the species richness of the ground vegetation of deciduous forests in northern Germany (Schleswig-Holstein). *Forest Ecology and Management*, 182, 327–338. https://doi.org/10.1016/S0378-1127(03)00091-4

Heinken, T. (2004) Migration of an annual myrmecochore: A four year experiment with *Melampyrum pratense* L. *Plant Ecology*, 170, 55–72. https://doi.org/10.1023/B:VEGE.0000019020.90968.0b

Hermy, M., Honnay, O., Firbank, L., Grasdorf-Bokdam, C. and Lawesson, J.E. (1999) An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biological Conservation*, 91, 9–22. https://doi.org/10.1016/S0006-3207(99)00045-2

Honnay, O. and Jacquemyn, H. (2007) Susceptibility of common and rare plant species to the genetic consequences of habitat fragmentation. *Conservation Biology*, 21, 823–831. https://doi.org/10.1111/j.1523-1739.2006.00646.x

Honnay, O., Jacquemyn, H., Bossuyt, B. and Hermy, M. (2005) Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. *New Phytologist*, 166, 723–736. https://doi.org/10.1111/j.1469-8137.2005.01352.x

Hopfensperger, K.N. (2007) A review of similarity between seed bank and standing vegetation across ecosystems. *Oikos*, 116, 1438–1448. https://doi.org/10.1111/j.0030-1299.2007.15818.x

Hothorn, T., Bretz, F. and Westfall, P. (2008) Simultaneous inference in general parametric models. *Biometrical Journal*, 50, 346–363. https://doi.org/10.1002/bimj.200810425

Jäger, E.J. (2011) *Rothmaler. Excursion flora of Germany. Vascular plants. Critical volume (German)*, 20th edition. Heidelberg: Spektrum Akademischer Verlag.

Jedicke, E. (2015) "Living biotope network" in pasture landscapes - grazing animals as triggers of dynamic processes and as vectors - an overview (German). *Naturschutz Und Landschaftsplanung*, 47, 257–262.

Kéry, M., Matthies, D. and Spillmann, H.H. (2000) Reduced fecundity and offspring performance in small populations of the declining grassland plants *Primula veris* and *Gentiana lutea*. *Journal of Ecology*, 88, 17–30. https://doi.org/10.1046/j.1365-2745.2000.00422.x

Kirchner, F., Ferdy, J.B., Andalo, C., Colas, B. and Moret, J. (2003) Role of corridors in plant dispersal: An example with the endangered *Ranunculus nodiflorus*. *Conservation Biology*, 17, 401–410. https://doi.org/10.1046/j.1523-1739.2003.01392.x

Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M. et al (2008) The LEDA traitbase: A database of life-history traits of the Northwest European flora. *Journal of Ecology*, 96, 1266–1274. https://doi.org/10.1111/j.1365-2745.2008.01430.x

Leuschner, C. and Ellenberg, H. (2018) *Ecology of European non-forest vegetation: Coastal to alpine, natural to man-made habitats*. Vol. II, Cham: Springer.

Manzano, P. and Malo, J.E. (2006) Extreme long-distance seed dispersal via sheep. *Frontiers in Ecology and the Environment*, 4, 244–248. https://doi.org/10.1890/1540-9295(2006)004[0244:ELSDVS]2.0.CO;2

Matthies, D., Bräuer, I., Maiborn, W. and Tscharntke, T. (2004) Population size and the risk of local extinction: Empirical evidence from rare plants. *Oikos*, 105, 481–488. https://doi.org/10.1111/j.0030-1299.2004.12800.x

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D. et al. (2019). Vegan: Community ecology package. R package version 2.5-6. Available at: https://CRAN.R-project.org/package-vegan

Peterken, G.F. (1993) *Woodland conservation and management*. Boston, MA: Springer. https://doi.org/10.1007/978-1-4899-2857-3

Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D. (2020). Nlme: Linear and nonlinear mixed effects models. R package version 3.1-145. Available at: https://CRAN.R-project.org/package=nlme

Popp, A. and Scheibe, K.M. (2013) The importance of groves for cattle in semi-open pastures. *Agriculture*, 3, 147–156. https://doi.org/10.3390/agriculture3010147

Poschlod, P., Bakker, J.P. and Kahmen, S. (2005) Changing land use and its impact on biodiversity. *Basic and Applied Ecology*, 6, 93–98. https://doi.org/10.1016/j.baae.2004.12.001

Poschlod, P. and Bonn, S. (1998) Changing dispersal processes in the central European landscape since the last ice age: An explanation for the actual decrease of plant species richness in different habitats. *Acta Botanica Neerlandica*, 47, 27–44.

Rosenberg, D.K., Noon, B.R. and Meslow, E.C. (1997) Biological corridors: Form, function, and efficacy. *BioScience*, 47, 677–687. https://doi.org/10.2307/1313208

Roy, V. and de Blois, S. (2006) Using functional traits to assess the role of hedgerow corridors as environmental filters for forest herbs. *Biological Conservation*, 130, 592–603. https://doi.org/10.1016/j.biocon.2006.01.022

Saura, S., Bodin, Ö. and Fortin, M.J. (2014) Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. *Journal of Applied Ecology*, 51, 171–182. https://doi.org/10.1111/1365-2664.12179

Schlaepfer, D.R., Braschler, B., Rusterholz, H.-P. and Baur, B. (2018) Genetic effects of anthropogenic habitat fragmentation on remnant animal and plant populations: A meta-analysis. *Ecosphere*, 9, e02488. https://doi.org/10.1002/ecs2.2488

Schmidt, M., Kriebitzsch, W.U. and Ewald, J. (2011) *List of forest species of ferns and allies, flowering plants, mosses and lichens of Germany (German)*. Bonn: Bundesamt für Naturschutz.

Steubing, L. and Fangmeier, A. (1992) *Practical in plant ecology (German)*. Berlin: Parey Verlag.

van Dijk, W.F.A., van Ruijven, J., Berendse, F. and de Snoo, G.R. (2014) The effectiveness of ditch banks as dispersal corridors for plants in agricultural landscapes depends on species' dispersal traits. *Biological Conservation*, 171, 91–98. https://doi.org/10.1016/j.biocon.2014.01.006

Von Oheimb, G., Eischeid, I., Finck, P., Grell, H., Härdtle, W., Mierwald, U. et al (2006) *Semi-open pasture landscape Höltigbaum: Perspectives for the conservation and nature-compatible use of open land habitats (German)*. Bonn: Bundesamt für Naturschutz.

Von Oheimb, G., Kriebitzsch, W.U., Schmidt, M., Heinken, T. and Ellenberg, H. (2009) Why are so few forest plant species spread by hoofed game? (German). *Forstarchiv*, 80, 215–221.

Walisch, T.J., Colling, G., Poncelet, M. and Matthies, D. (2012) Effects of inbreeding and interpopulation crosses on performance and plasticity of two generations of offspring of a declining grassland plant. *American Journal of Botany*, 99, 1300–1313. https://doi.org/10.3732/ajb.1100479

Wang, Y., Naumann, U., Eddelbuettel, D., Wilshire, J., & Warton, D. (2020) Mvabund: Statistical methods for analysing multivariate abundance data. R package version 4.1.3. Available at: https://CRAN.R-project.org/package=mvabund

Warton, D.I., Wright, S.T. and Wang, Y. (2012) Distance-based multivariate analyses confound location and dispersion effects. *Methods in Ecology and Evolution*, 3, 89–101. https://doi.org/10.1111/j.2041-210X.2011.00127.x

Wehling, S. and Diekmann, M. (2009) Importance of hedgerows as habitat corridors for forest plants in agricultural landscapes. *Biological Conservation*, 142, 2522–2530. https://doi.org/10.1016/j.biocon.2009.05.023

Willi, Y., Van Buskirk, J. and Hoffmann, A.A. (2006) Limits to the adaptive potential of small populations. *Annual Review of Ecology Evolution and Systematics*, 37, 433–458. https://doi.org/10.1146/annurev.ecolsys.37.091305.110145

Wulf, M. (1997) Plant species as indicators of ancient woodland in northwest Germany. *Journal of Vegetation Science*, 8, 635–642. https://doi.org/10.2307/3237367

Xiao, Y., Xiaohong, L., Cao, Y. and Dong, M. (2016) The diverse effects of habitat fragmentation on plant-pollinator interactions. *Plant Ecology*, 217, 857–868. https://doi.org/10.1007/s11258-016-0608-7

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. and Smith, G.M. (2009) *Mixed effects models and extensions in ecology with R*. New York, NY: Springer.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1 Results of ANOVA tests for the comparison of the light and soil characteristics and species traits

Appendix S2 Results of generalized linear models for the effects of habitat type on plant species composition fitted for each region separately

Appendix S3 Bray–Curtis dissimilarities of the square-root-transformed abundance data of the different habitat types of (a) the Swabian Jura and (b) the Lueneburg Heath

Appendix S4 Significant and non-significant indicator species of single habitat types in the Lueneburg Heath and the Swabian Jura

Appendix S5 Significant and non-significant indicator species of habitat type combinations in the Lueneburg Heath and the Swabian Jura

Appendix S6 Constancy table of the plant communities of the Swabian Jura

Appendix S7 Constancy table of the plant communities of the Lueneburg Heath

Appendix S8 Plant species list of vegetation surveys in all plots of the Swabian Jura

Appendix S9 Plant species list of vegetation surveys in all plots of the Lueneburg Heath