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RESEARCH ARTICLE

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Immigration credit of temperate forest herbs in fragmented landscapes–Implications for restoration of habitat connectivity

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Abstract

- 1. In many agricultural landscapes, it is important to restore networks of forests to provide habitat and stepping stones for forest specialist taxa. More knowledge is, however, needed on how to facilitate the immigration of such taxa in restored forest patches. Here, we present the first chronosequence study to quantify the dynamics of immigration credits of forest specialist plants in post-arable forest patches.
- 2. We studied the distribution of herbaceous forest specialist plant species in 54 post-arable broadleaved forest patches along gradients of age (20-140 years since forest establishment), distance from ancient forest (0-2,600 m) and patch area (0.5-9.6 ha). With linear mixed models, we estimated the effects of these factors on species richness, patch means of four dispersal-related plant traits and with generalized linear models on the occurrence of 20 individual species.
- 3. Post-arable forest patch age and spatial isolation from ancient forest, but not patch size, were important predictors for species richness of forest specialists, suggesting that also small patches are valuable for habitat connectivity. Compared to species richness in ancient forest stands, the immigration credit was reduced by more than 90% after 80 years in post-arable forest patches contiguous to ancient forest compared to 40% after 80 years and 60% after 140 years in isolated patches (at least 100 m to next forest). Tall-growing species with adaptations to long-distance dispersal were faster colonizers, whereas species with heavy diaspores and clonal growth were slower to colonize.
- 4. Synthesis and applications. We show that post-arable oak plantations have a high potential for restoration of forest herb vegetation. Dispersal-related plant traits play a key role in explaining interspecific differences among forest specialists. To facilitate forest herb immigration across all functional groups in agricultural landscapes, we suggest to create clusters of relatively small new forest patches nearby older forest with source populations.

KEYWORDS

colonization credit, dispersal traits, forest restoration, fragmentation, habitat network, herbaceous understorey, post-agricultural forest, temperate deciduous forest

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1 | INTRODUCTION

There is a long history of anthropogenic forest fragmentation and land-use change in temperate biomes, often driven by forest clearance for agriculture and wood supply and later followed by spontaneous regrowth or plantation of secondary forests on abandoned agricultural land (Flinn & Vellend, 2005; Hermy & Verheyen, 2007). These processes have resulted in current landscapes forming a mosaic of agricultural land, remnant ancient forests and postagricultural recent forest patches (Jamoneau et al., 2012; Peterken & Game, 1984).

In such dynamic and fragmented landscapes, local species extinction and immigration are the main processes explaining longterm changes in species diversity (Jackson & Sax, 2010). After habitat fragmentation, ancient forests may carry an extinction debt due to delayed extinction (Rogers et al., 2009; Vellend et al., 2006). In post-agricultural forests, on the other hand, delayed colonization will result in immigration credits, defined as the number of species committed to eventual immigration following forest establishment (Jackson & Sax, 2010; Naaf & Kolk, 2015).

Forest habitat restoration and the development of new habitat networks in agricultural landscapes are becoming increasingly important for conservation policies globally (Humphrey et al., 2015). A habitat network is a number of areas of habitat connected by corridors and/or smaller stepping stones facilitating movement of species or their propagules (Saura et al., 2014). Developing these networks for forest species in agricultural landscapes requires a good understanding on how immigration credits in new forests depend on, for example, isolation from older forests (Humphrey et al., 2015). In this context, ancient forests harbouring the local pool of forest specialists are crucial as source habitat for seeds and other diaspores (Hermy & Verheyen, 2007).

Although the colonization of post-agricultural forests by forest plants has been intensively studied (De Frenne et al., 2011; Flinn & Vellend, 2005; Humphrey et al., 2015), the reduction of immigration credit with time has so far only been analysed and quantified in two re-survey studies (Kolk et al., 2017; Naaf & Kolk, 2015). Empirical assessment of immigration credits is difficult because of the long time-scale of immigration processes, and the difficulty of attributing species immigrations to specific previous events (Jackson & Sax, 2010). Long-term data may be preferable for these assessments, but such data are not available in most cases. Alternatively, space-for-time substitutions, such as chronosequence studies, can advance our understanding on the dynamics of immigration credits as long as certain critical assumptions are met, such as comparability of initial soil and vegetation conditions (Jackson & Sax, 2010; Johnson & Miyanishi, 2008; Kimberley et al., 2019). In this approach, accurate historical records of land-use are needed to establish a baseline for change, as well as ancient forests as reference sites (Watts et al., 2016).

Here, we present the first chronosequence study to quantify the dynamics of immigration credits of forest specialist plants. We analyse oak-dominated post-arable forests in a temperate mixed-history cultural landscape in southern Sweden. We hypothesize that the immigration credit of post-arable forests is gradually reduced with time, and that it is reduced faster in post-arable forest patches that are larger and less isolated from ancient forests (Naaf & Kolk, 2015). We further hypothesize that dispersal-related plant traits play a key role in explaining spatiotemporal changes in species richness and species-specific distribution patterns (Kolb & Diekmann, 2005; Lõhmus et al., 2014; Verheyen et al., 2003).

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted in the forests of Skabersjö and Torup (55°32'N 13°11'E) in southernmost Sweden (Figure 1). The studied landscape has a size of approximately 5,000 ha (8.5×6 km) and is dominated by agriculture but also contains a large number of recent (including both post-arable and post-grassland) forest patches and several areas of ancient forest. There are no other ancient forests outside the study area which are closer to any recent forest patches than the ancient forest in the study area, implying that the latter are the main dispersal sources of forest species. The ancient forest is dominated by European beech Fagus sylvatica and, to a lesser extent, pedunculate oak Quercus robur. The soils are generally dystric cambisols derived from glacial till (Weichselian glaciation). Altitude ranges from 25 to 75 m a.s.l. in a gently undulating landscape. The climate is temperate and the annual mean temperature is 7.5°C (0.5°C in January and 16.5°C in July) during the latest standard reference period (1961-1990). Mean annual precipitation during the same period was 650 mm (Germundsson & Schlyter, 1999).

Between 1800 and 1995, a large number of forest patches were established on arable fields in the study area (Brunet, Felton, et al., 2012). Historical sources at the Swedish national archives, the Swedish land survey office, the Skabersjö estate office and the Malmö city archive (Table S1) provided information on forest age, in many cases the exact year of stand establishment, while in a few of the oldest recent patches, establishment could only be dated with a decade's precision. Based on this dating, we determined the time between the year of initial forest patch establishment and the floristic survey. For each patch, we measured size (ha) for the forest area established at the same point in time, including both discrete patches surrounded by other land uses and patches adjacent to ancient or previously established forest (Figure 1). We measured the distance between post-arable forest patches and nearest ancient forest border (Distance ancient) to account for the nearest primary source populations of forest plant species. We also measured the distance between post-arable forest patches and the nearest border of any other recent forest patch of higher age (Distance older) to account for the distance to the nearest secondary source populations. Ancient forests were defined as being wooded continuously at least since the oldest



FIGURE 1 Map over the study landscape and its location in southernmost Sweden. The overall distribution of ancient and recent forest is shown. In addition, the recent post-arable forest patches and ancient forest reference stands included in the study are indicated. There are no other ancient forests outside the study area which are closer to any post-arable forest patches than the ancient forest in the study area

survey maps (240-320 years, Table S1), but they have probably a much longer continuity as wooded land (Brunet, Felton, et al., 2012).

2.2 | Study sites and species

Based on the historical data, 54 broadleaved forest patches were selected for further studies of forest plant colonization patterns. A predefined list of forest specialist plants was used for field mapping, including herbaceous species with a predominant occurrence in closed forest according to Schmidt et al. (2002, species class B1.1), nomenclature follows Mossberg and Stenberg (2018). Additionally, *Ficaria verna* and *Scrophularia nodosa* were also included as they are shade-tolerant forbs typical for forests in the study landscape (Table S4).

To ensure that there were no forest plant species present when forest patches were established, only recent forest patches on former arable fields were included in this study, as some forest specialist plants occasionally occur in semi-natural grassland (Tyler et al., 2021). Post-arable patches were not allowed to be adjacent to another selected post-arable patch. An exception was made for two patches which were established 116 years later than their adjacent older patch (patch pairs 8c–8h and 14c–14i, see Table S2a).

Median post-arable patch area was 2.2 ha (range: 0.5-9.6 ha), median forest age was 40 years (range 21–140 years), median distance to the nearest ancient forest border was 155 m (range 0-2,625 m) and the median distance to the nearest older recent forest was 10 m (range 0-1,000 m, see Table S2a).

As reference for forest herb species richness, 42 ancient forest stands were surveyed in a large unfragmented forest (Figure 1; Table S2b), following the approach of Jamoneau et al. (2012). For these reference stands, we chose those with soil conditions as similar as possible to the post-arable patches. This means stands on cambisols (Asperulo-Fagetum or Stellario-Carpinetum forests) as post-arable patches were all are located on cambisols. As all ancient stands are part of a large continuous forest, the connectivity between these non-isolated 'patches' was assumed to be sufficient regarding forest specialists (Jamoneau et al., 2012). We thus also assume that their forest species numbers generally are in equilibrium, without significant extinction debts or immigration credits.

The validity of the chronosequence approach depends on the similarity of the study sites in terms of initial soil conditions and site history (Johnson & Miyanishi, 2008). In addition to the detailed information on patch history described above, we also analysed spatial variation in top soil pH for 28 of the post-arable forest patches to exclude that trends in soil conditions cause the effects of distance to ancient forest in our analyses (see below). The results of these analyses show that soil pH was not correlated with patch area and longitudinal or latitudinal gradients in the study landscape, nor with distance to the nearest ancient or older post-agricultural forest. Soil pH decreased, however, as post-arable patches became older (Table S3).

2.3 | Field survey and data sampling

Floristic surveys of forest specialist plants were carried out twice in each patch. Vernal species were recorded in April and May; summer species were surveyed between June and August (Table S2). To be able to survey the entire patch area for occurrence of forest plants in the herbaceous layer, walks along parallel transects located *c*. 10 m apart from each other were made through the entire patch. This implies that the overall sampling effort per patch was proportional to patch area, and thus allows analysis of species-area relationships. Occurrence of all species included in the list of herbaceous forest specialist plants was noted within 5 m on both sides along the transects.

The main diaspore dispersal mode was classified according to a review by Hermy et al. (1999), but modified for some species based on more recent field studies on adhesive and ingested dispersal (see Table S4 for references). Data on diaspore mass were taken from the BiolFlor database (Klotz et al., 2002) and the BioPop database (Poschlod et al., 2003). Data on annual clonal spread were taken from Brunet and von Oheimb (1998) and Brunet, De Frenne, et al. (2012). Data on maximum plant height were based on Mossberg and Stenberg (2018, see Table S4). Diaspore dispersal types were ranked with regard to dispersal distance according to a six-degree scale developed by Vittoz and Engler (2007). Additionally, diaspore mass and potential annual clonal spread were ranked in five classes (Table S4). Presence-/absence-based mean values for each post-arable forest patch and ancient reference stand were calculated for dispersal distance class, diaspore mass class, clonal spread class and maximum plant height (Table S5).

2.4 | Data analysis

2.4.1 | Analyses of forest species richness and traits

All statistical analyses were done in R version 3.6.1 (R Core Team, 2019). We used linear mixed models (LMM) to model the effects of explanatory variables on overall forest specialist species richness as well as on patch trait means in post-arable forest patches (excluding the ancient forest reference stands). Explanatory variables included patch area, post-arable patch age as a factor with two levels (see below), and distances to the nearest ancient forest and nearest older recent forest, as well as the two-way interactions between age group and the two distance measures. These models were fitted with the restricted maximum likelihood approach by the Ime function in the 'NLME' package (Pinheiro et al., 2020) and an exponential covariance structure of the patches' centre coordinates was included in these models to account for potential spatial autocorrelation. Tests of effect of age group as well as comparisons of regression slopes of the distance measures between age groups were done by estimated marginal means extracted by the emmeans and emtrends functions, respectively, in the 'EMMEANS' package (Lenth et al., 2020). The two different levels of patch age consisted of patches younger and patches older than 30 years. When a temperate forest ecosystem establishes on a former arable field, it forms a closed tree canopy and a layer of leaf litter during the first 20-30 years, while changes in light and soil conditions are slowing down after this establishment phase (Honnay et al., 2002). Distance to the closest older recent forest patch was introduced in the models to account for dependency between adjacent young and older patches and for dispersal between recent patches. Importantly, the distance to the nearest ancient forest border was measured using all ancient forest in the study landscape, not only the 42 ancient forest reference stands (see Figure 1). To facilitate comparison of effect sizes, the continuous predictors were standardized prior to analyses by subtracting the mean of all values from the individual value and dividing the differences by the standard deviation of all values. Prior to this standardization, the variables were log transformed to account for an expected nonlinear response (Hermy & Verheyen, 2007). All statistical models were evaluated by plotting the residuals against predicted values and predictors. Patch trait means in ancient forest reference stands, older and younger post-arable forest patches were compared with ANOVA and Tukey-test after normality testing.

2.4.2 | Analyses of individual forest species

Additionally, we also modelled the effect of patch area, post-arable patch age (as above), and distances to the nearest ancient forest and nearest older recent forest on the occurrence of all individual forest specialist plant species with a frequency >20% and <90% in post-arable patches (20 species). This was done by applying Generalized Linear Models with binomial error distribution and logit-link as implemented in the *glmmTMB* function in the package with the same

name (Brooks et al., 2017). The percentage of correct predictions (PCP) was calculated by the *performance_pcp* function in the 'PERFORMANCE' package (Lüdecke et al., 2020) for the null (intercept-only) and full models. The difference between these in percentages of correct predictions is presented as an indication of model performance.

2.4.3 | Analysis of immigration credit

The linear regression line of species richness versus patch area of the 42 ancient forest reference stands was calculated (Figure S1) and used to extract area-specific benchmark values (100%) along this line to estimate the remaining immigration credit of post-arable patches. This value was calculated by dividing the species richness (i.e. not accounting for species identity) of a post-arable patch with the benchmark value of an ancient forest stand of the same size. The change of the immigration credit in relation to post-arable forest patch age was then compared between patches contiguous with (n = 28) and isolated from ancient forest (n = 26), respectively, again using linear regression analyses.

3 | RESULTS

3.1 | Forest species richness and traits

We found 48 specialist forest species during our survey, all of which occurred in ancient forests, with frequencies varying from 5% to 100% (Table S4). Species richness in ancient forest reference stands varied between 19 and 32 and slightly increased with patch area (p < 0.001, Figure S1). In all, 41 of the 48 species were found at least once in post-arable forest patches (Table S4 for species-wise frequency values).

There were significant effects of forest age (according to LMMs) on both the total richness of forest specialist species in post-arable patches and all four mean plant traits (Table 1, see also Figure S2 for species richness). The number of species, means of diaspore mass and clonal spread classes were all higher in older stands than in younger, whereas means of dispersal distance class and maximum height were higher in the young stands. There was significant spatial autocorrelation in the case of dispersal distance, diaspore mass and max height, but not concerning clonal spread or the total richness of forest species. Distance to ancient forest significantly affected the number of forest species as well as the dispersal distance and maximum height. The number of forest species decreased with increasing distance to ancient forest while both trait means increased. There were no significant interactions between distance to ancient forest and age group indicating that the effects of this distance were independent of the age of the forest patch (Table 1, Figure 2a,c,e,g,i). In contrast, there were clear distinctions between young and older post-arable patches in their response to the distance to older recent forest patches. While there were no significant effects of this distance in older post-arable patches, in the younger post-arable

patches both diaspore mass and clonal spread decreased with increasing distance to older recent patches while the maximum height increased (Table 1, Figure 2b,d,f,h,j). There were no significant effects of the patch area on any of these response variables (see also Figure S3 for forest species richness vs. patch area).

Patch-based mean values of all four plant traits differed between ancient reference forest stands and young post-arable forest patches. Means of older post-arable patches were intermediate but generally closer to those of ancient forests (Table S6).

3.2 | Individual forest species

Out of the individually tested forest specialist species, a majority (15 of 20) showed a higher probability of occurrence in the older patches than in the young ones while no species were more common in the young patches than in the older (Table 2). Increasing distance to ancient forest affected seven species negatively, and distance to older patches four species (Table 2). Only *Athyrium filix-femina* was negatively affected by distance to both ancient and older patches (Table 2).

3.3 | Immigration credit over time

In post-arable forest patches contiguous with ancient forest, the mean immigration credit of forest species had already been reduced by 50% in the young patches at the time of the survey (patch age 21–28 years) and had almost disappeared at a patch age of 80 years (Figure 3). In isolated patches, however, the reduction of the immigration credit in young patches varied from 41% to only 3% (mean 20%). With increasing patch age, the reduction reached *c*. 60% in the oldest isolated patches (age 140 years, Figure 3).

4 | DISCUSSION

4.1 | Effects of age, isolation and area

The results confirmed our hypotheses that the immigration credit of post-arable forests is gradually reduced when forests grow older, and that it is reduced faster in forest patches that are contiguous to ancient forests compared to isolated patches. Already early during forest succession, many forest specialists colonized non-isolated patches (mean of 12 species at patch age 23–28 years). Nonisolated post-arable forest patches can approach a species richness of forest specialist plants comparable to ancient forest stands after only 80 years while it takes more than at least 140 years for isolated patches. However, our results revealed a steady reduction of immigration credits with time also in isolated patches. The negative effect of spatial isolation from ancient forest is in accordance to previous studies (e.g. Honnay et al., 2002; Matlack, 1994). However re-survey studies from post-agricultural forests (Baeten **TABLE 1** Results from linear mixed models of the effects of patch area, patch age (factor: young, older), distance to nearest ancient forest patch and distance to nearest older recent patch as well as the two-way interactions between the age factor and the two distance measures on five response variables including richness of forest specialist species and four mean trait values. The continuous variables were log-transformed, centred and standardized prior to the analyses

	Factor test F-value (df: 1, 47)	p-value (F-test)	Factor level	Parameter estimate (±SE)	p-value (t-test, mean or slope ≠ 0)
Forest species					
Intercept	77.86	<0.0001		15.42 + 1.75	
Area (log)	1.24	0.2717		0.70 ± 0.63	
Age group	38.31	<0.0001			
			Older	15.42 ± 1.75	<0.00001
			Young	7.35 ± 1.82	0.0004
Distance Ancient (log)	7.75	0.0077			
Age group × Distance Ancient	0.52	0.4730			
			Older	-3.16 ± 1.14	0.0077
			Young	-2.12 ± 1.03	0.0448
Distance Older (log)	0.14	0.7107			
Age group \times Distance Older	2.50	0.1206			
			Older	0.38 ± 1.02	0.7107
			Young	-1.92 ± 1.01	0.0623
Spatial autocorrelation		0.0948	$\Delta AIC = -0.79$		
Dispersal distance					
Intercept	616.70	<0.0001		4.31 ± 0.17	
Area (log)	0.01	0.9246		0.01 ± 0.06	
Age group	36.08	<0.0001			
			Older	4.31 ± 0.17	<0.0001
			Young	5.10 ± 0.18	<0.0001
Distance Ancient (log)	5.46	0.0238			
Age group × Distance Ancient	0.16	0.6921			
			Older	0.26 ± 0.11	0.0238
			Young	0.32 ± 0.10	0.0029
Distance Older (log)	0.09	0.7702			
Age group \times Distance Older	0.08	0.7818			
			Older	-0.03 ± 0.10	0.7702
			Young	-0.07 ± 0.10	0.4873
Spatial autocorrelation		0.0437	$\Delta AIC = -2.07$		
Diaspore mass		0.0004			
Intercept	226.31	<0.0001		2.95 ± 0.20	
Area (log)	1.86	0.1796		-0.07 ± 0.05	
Age group	25.00	<0.0001		0.05	0.0001
			Older	2.95 ± 0.20	<0.0001
	1 / 0	0.0010	roung	2.41 ± 0.20	<0.0001
	1.00	0.2018			
Ancient	<0.01	0.7/33			
			Older	-0.14 ± 0.11	0.2018
			Young	-0.14 ± 0.10	0.1507

TABLE 1 (Continued)

	Factor test F-value (df: 1, 47)	p-value (F-test)	Factor level	Parameter estimate (±SE)	p-value (t-test, mean or slope ≠ 0)
Distance Older (log)	2.23	0.1423			
Age group \times Distance Older	21.25	< 0.0001			
			Older	0.13 ± 0.09	0.1423
			Young	-0.43 ± 0.08	<0.0001
Spatial autocorrelation		0.0225	$\Delta AIC = -3.21$		
Clonal spread					
Intercept	307.77	<0.0001		2.38 ± 0.14	
Area (log)	0.03	0.8696		-0.01 ± 0.05	
Age group	41.71	<0.0001			
			Older	2.38 ± 0.14	<0.0001
			Young	1.75 ± 0.14	<0.0001
Distance Ancient (log)	0.20	0.6563			
Age group × Distance Ancient	0.77	0.3846			
			Older	-0.04 ± 0.09	0.6563
			Young	0.06 ± 0.08	0.4841
Distance Older (log)	0.38	0.5381			
Age group \times Distance Older	10.33	0.0024			
			Older	-0.05 ± 0.08	0.5381
			Young	-0.40 ± 0.08	<0.0001
Spatial autocorrelation		0.0701	∆AIC = −1.28		
Max height					
Intercept	208.25	< 0.0001		75.25 ± 5.22	
Area (log)	3.99	0.0516		2.96 ± 1.48	
Age group	41.15	< 0.0001			
			Older	75.30 ± 5.21	<0.0001
			Young	96.00 ± 5.36	<0.0001
Distance Ancient (log)	5.06	0.0292			
Age group × Distance Ancient	0.27	0.6075			
			Older	6.92 ± 3.08	0.0292
			Young	5.09 ± 2.81	0.0763
Distance Older (log)	0.82	0.37			
Age group \times Distance Older	5.08	0.0289			
			Older	-2.35 ± 2.60	0.37
			Young	5.87 ± 2.52	0.024
Spatial autocorrelation		0.004	∆AIC = −6.26		

et al., 2010; Kolk et al., 2017) as well as chronosequence studies with accurate information on patch age are very rare (Brunet, 2007; Flinn & Marks, 2004; Jacquemyn et al., 2001). Therefore, our chronosequence adds new valuable knowledge about the spatiotemporal dynamics of immigration credit in forest plants in new forests.

The hypothesized positive effect of patch area on species recruitment, observed in re-survey studies of ancient forest patches (e.g. Rogers et al., 2009), was absent in our study landscape, and instead confirming results reported by Naaf and Kolk from postagricultural forest (2015). This suggests that habitat variability may increase with area in ancient forests, whereas in post-arable forests site conditions have been homogenized by previous agricultural use (Foster et al., 1998) and habitat variability is less pronounced (Jacquemyn et al., 2001) Most post-arable patches in our study are located on even ground and planted with a single tree species, which additionally delays development of site heterogeneity.



FIGURE 2 Interaction diagrams showing model predictions (95% CI) from linear mixed models (Table 1). Left panels show the interactions between patch age and distance to nearest ancient forest while the right panels show the interactions between patch age class and distance to nearest older recent forest patch. Solid regression lines indicate a significant effect of the distance (p < 0.05) while dotted have a $p \ge 0.05$. Effects are shown on species richness (a, b), dispersal distance (c, d), diaspore mass (e, f), clonal spread (g, h), and maximum height (i, j)

4.2 | Trait-related interspecific differences

Our data enabled us to unravel large interspecific differences on how forest age and isolation affect species immigration to new forest. Here, the results support our hypothesis that plant species colonization to a large extent can be predicted by life-history traits related to dispersal. We show that dispersal-related plant traits play a key role in explaining interspecific differences also within the group of forest specialists, not only between forest specialists and habitat generalists (Brunet, De Frenne, et al., 2012; Graae & Sunde, 2000; Lõhmus et al., 2014; Verheyen et al., 2003). With increasing post-arable patch age, not only species richness but also mean values of the four plant traits approached those of the ancient reference forest stands. However, mean trait values in young post-arable forest patches differed much from ancient stands, indicating the influence of strong dispersal filters during early succession. According to our results, all four plant traits studied were closely related to the colonization process of young post-arable forest patches, implying that a combination of adaptation to longdistance dispersal, low diaspore mass, non-clonal growth habit and tall growth characterizes a successful early-successional colonizer. In our study, the tall fern *Dryopteris filix-mas* possesses all these **TABLE 2** Results from binomial generalized linear models of the effects of patch area, patch age (factor: young, older), distance to nearest ancient forest patch and distance to nearest older recent patch on the occurrence of forest species with 20%–90% patch occupancy. Δ PCP is the difference in percentage correct predictions of the null (intercept only) and full models. **p < 0.01, *p < 0.05, ns $p \ge 0.05$. The continuous variables were log-transformed, centred and standardized prior to the analyses

Species	p-value	ΔΡCΡ	Intercept	Area	Distance ancient	Distance older	Age
Adoxa moschatellina	0.0039	13.00	-0.23 ^{ns}	-0.39 ^{ns}	-0.20 ^{ns}	-0.33 ^{ns}	1.09**
Anemone nemorosa	< 0.0001	39.61	-2.41 ^{ns}	-1.67 ^{ns}	-7.30*	2.00 ^{ns}	5.92*
Athyrium filix femina	<0.0001	22.67	0.67 ^{ns}	1.11*	-1.01*	-1.35*	2.15**
Brachypodium sylvaticum	0.1762	4.09					
Circaea lutetiana	0.0071	9.82	1.58**	-0.34 ^{ns}	0.80 ^{ns}	-1.75**	0.53 ^{ns}
Dryopteris carthusiana	0.0011	14.44	0.65 ^{ns}	1.12**	0.71 ^{ns}	-0.80 ^{ns}	1.40**
Elymus caninus	0.0003	15.18	-1.39**	0.52 ^{ns}	-1.96**	0.22 ^{ns}	-0.39 ^{ns}
Ficaria verna	<0.0001	28.89	0.50 ^{ns}	-0.34 ^{ns}	-1.23*	-0.67 ^{ns}	2.28**
Lamiastrum galeobdolon	0.0021	12.66	-0.99**	-0.71 ^{ns}	-0.95 ^{ns}	0.010 ^{ns}	0.52 ^{ns}
Melica uniflora	< 0.0001	21.59	-2.14**	0.43 ^{ns}	-1.73*	-1.29 ^{ns}	2.02**
Mercurialis perennis	< 0.0001	19.73	-0.73 ^{ns}	-0.20 ^{ns}	-1.02*	-0.77 ^{ns}	1.49**
Milium effusum	0.0022	11.75	1.29**	0.57 ^{ns}	-0.35 ^{ns}	-0.91 ^{ns}	1.36**
Oxalis acetosella	< 0.0001	21.45	-0.89*	-1.05*	-0.27 ^{ns}	-1.32*	1.46**
Poa nemoralis	0.0001	12.66	3.95**	0.70 ^{ns}	2.82 ^{ns}	-2.66 ^{ns}	3.36*
Schedonorus giganteus	0.0058	8.70	2.45**	0.11 ^{ns}	0.51 ^{ns}	-1.26*	1.91*
Scrophularia nodosa	0.0746	7.27					
Stachys sylvatica	0.0014	11.90	-1.50**	-0.67 ^{ns}	-0.40 ^{ns}	-0.70 ^{ns}	1.25*
Stellaria holostea	< 0.0001	25.98	0.19 ^{ns}	-0.58 ^{ns}	-1.58**	-0.48 ^{ns}	1.66**
Stellaria nemorum	<0.0001	26.10	-0.25 ^{ns}	-0.16 ^{ns}	-0.35 ^{ns}	-1.25 ^{ns}	2.44**
Viola reichenbachiana	< 0.0001	26.28	-0.15 ^{ns}	-0.56 ^{ns}	-0.41 ^{ns}	-0.72 ^{ns}	2.09**

traits and was first to colonize all seven completely isolated young patches. Other species found in these patches included the ferns Athyrium filix-femina and Dryopteris carthusiana, the grasses Milium effusum, Poa nemoralis and Schedonorus giganteus and the herbs Circaea lutetiana and Scrophularia nodosa, all sharing several or all of the traits mentioned above (see Table S4).

Only adaptations to long-distance dispersal and tall growth were beneficial for colonization of forest patches isolated from ancient forest. This is in accordance with results from a metaanalysis where maximum plant height had stronger explanatory power than did diaspore mass (Thomson et al., 2011). Within dispersal syndromes, and independently of diaspore mass, tall stature may generally increase the chance of diaspores being dispersed to new forest by ingestion (herbivory) or attachment to mammal fur (Thomson et al., 2011). In our study, some species with heavy diaspores had adaptations for long-distance dispersal (cf. Table S4), possibly weakening the positive effects of low diaspore mass on colonization of isolated forests.

Older post-arable patches were only affected by distance to ancient forests (cf. Vellend, 2003) but in the younger patches, both diaspore mass and clonal spread of forest specialists decreased with increasing distance to older recent patches while the maximum height increased, indicating a dominance of species with good seed dispersal in isolated younger patches. Initial colonization of young isolated patches may be additionally affected by remaining immigration credits in older recent patches (Jacquemyn et al., 2003).

Medium-sized mammals such as fox, badger, hare, wild boar and roe deer have increased during recent decades (Germundsson & Schlyter, 1999) and may play a more important role as seed dispersers than previously. Tall plant species have a higher chance to attach their seeds to these animals or to become ingested. In five relatively tall species that frequently colonize post-arable forest patches (Brachypodium sylvaticum, Circaea lutetiana, Milium effusum, Poa nemoralis and Schedonorus giganteus), adhesive and/ or ingested seed dispersal has been shown (see Table S4 and references therein). Most slow colonizers are either mainly dispersed by ants or have fleshy fruits. Ants may be able to disperse seeds across ecotones between ancient and recent forest, but for longdistance dispersal, these plant species have to rely on rare events of adhesive or ingested dispersal although evidence for such dispersal is scarce (see references in Table S4). The low relative frequency of species with berries in post-arable forests is less expected (Convallaria majalis, Maianthemum bifolium and Polygonatum multiflorum). It seems that birds or larger mammals do not consume and disperse these berries to any larger extent, at least not to post-arable forests (Ehrlén & Eriksson, 1993; Schaumann & Heinken, 2002).



FIGURE 3 Relation of area-corrected immigration credits with patch age for post-arable forest patches isolated from (n = 26) and contiguous with ancient forest (n = 28), respectively. Values below zero are from post-arable patches with higher species richness than ancient reference patches of corresponding size. The regression equation for contiguous patches is: Immigration credit = 0.7099 - 0.008221 × patch age ($R^2 = 63.1\%$, F = 44.50, p < 0.001). The regression equation for isolated patches is: Immigration credit = 0.8942 - 0.003605 × patch age ($R^2 = 65.8\%$, F = 46.18, p < 0.001)

4.3 | Recruitment limitation

Tall-growing species have also been found to have higher colonization rates in other recent forest across Europe (De Frenne et al., 2011). This is probably related to their capacity to compete with other tallgrowing species such as *Urtica dioica* or *Rubus idaeus* under nutrient rich conditions (Brunet et al., 2011). Especially in combination with open tree canopies, competition from tall light- and nutrientdemanding grassland and generalist species may limit recruitment of small forest specialists in eutrophic young post-agricultural forests (Baeten & Verheyen, 2017).

The difference to ancient forest concerning tall-growing species gradually decreases with increasing post-arable forest age in our study, as soil pH and nutrient levels decrease and species with lower competitive ability can establish, but differences can persist longer in isolated patches. Recruitment limitation due to unfavourable soil chemistry is probably not crucial for differences in colonization patterns, as the young post-arable forest patches in our study area generally have mildly acidic soils suitable for most forest herbs (Valtinat et al., 2008). However, plant recruitment is also limited by lack of sites with suitable micro-climate and soil moisture. As an example in our study, the occurrence of the tall fern Athyrium filix-femina was limited by low forest age and high distance to both older and ancient forest. This species is probably more dependent on high air humidity than the two Dryopteris species in our study, and suitable humid sites may be more frequent in older and less isolated forest patches (Flinn, 2007).

Forest herbs started to colonize the post-arable patches in our study area soon after stand establishment while colonization showed a longer time lag in the study by Flinn and Marks (2004). The faster initial colonization in our study may partly be explained by preplanting herbicide treatment (in stands established after 1950) and subsequent rapid canopy closure due to high tree planting densities, both limiting the establishment of competitive weeds, grassland species and generalists, when compared to the spontaneous old-field succession in the study by Flinn and Marks (2004). Although immigration credits in terms of species richness are reduced relatively quickly in our post-arable forest plantations, an earlier study indicates, however, that compositional differences may persist longer (Brunet, 2007). This is probably related to species-specific effects of long-term legacies of agricultural use concerning soil chemistry and topography (Falkengren-Grerup et al., 2006; Flinn, 2007), and low dispersal capacity of certain forest specialists (De Frenne et al., 2011).

4.4 | Implications for restoration of forest habitat connectivity

Despite their often small size and isolation, forest patches have a crucial role for plant biodiversity in agricultural landscapes (Valdés et al., 2020; Wintle et al., 2019). By providing habitat for forest species, such forest patches also increase the connectivity of larger forest areas by providing stepping stones (Saura et al., 2014). Species with adhesive and ingested diaspores in particular may benefit from such small patches if these patches attract their animal dispersal vectors as food resource or shelter. Wind-dispersed species often produce high diaspore numbers, but dispersal still decreases with distance making small patches valuable as stepping stones (Fischer et al., 2006).

Our results show that even small new forest patches (no larger than 0.5–2 ha, Figure S3) can be spontaneously colonized by a high number of forest herbs within a few decades as long as they are linked to ancient forest by other recent forest. Under such conditions, the immigration credit of forest herbs will be reduced much faster than in strongly isolated patches.

To optimize the gain for forest biodiversity across all functional groups of forest herbs and across a landscape gradient from mainly agricultural to forested, we therefore suggest to create clusters of many small new forest patches, with relatively low betweenpatch distances and including new patches adjacent to ancient forest. Emphasis should also be put on maintenance of favourable growing conditions for source populations of forest herbs in these ancient forests. Such measures will also provide new habitat for antdispersed forest herbs close to ancient forest.

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CONFLICT OF INTEREST

The authors have declared no conflicts of interest.

AUTHORS' CONTRIBUTIONS

J.B. and S.A.O.C. conceived the ideas; J.B. and P.-O.H. designed the methodology; J.B. collected the data; P.-O.H., J.B. and J.L. analysed the data; J.B. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via Dryad Digital Repository https://doi.org/10.5061/ dryad.wm37pvmnm (Brunet et al., 2021).

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