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TITLE

Historical continuity and spatial connectivity ensure hedgerows are effective corridors for forest plants: evidence from the species-time-area relationship

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ABSTRACT

Questions: Are hedgerows efficient corridors for forest-dwelling species within agricultural landscapes? Do time and space interact synergistically to enhance forest plant species accumulation in hedgerows (i.e. the species-time-area relationship)? Does the distribution profile of forest herbs along hedgerows differ between specialist and generalist species?

Location: Agricultural landscapes in northern France.

Methods: We assembled a chronosequence of 99 dated (1725-2008) hedgerows, which were surveyed for forest plant species and a number of local-proximal descriptors. A subset of 29 hedgerows were further sampled for species occurrence data every 5-m segments. We used generalized linear models to test the interaction between time (hedgerow age) and space on species richness. Space was characterized by both habitat size (hedgerow length, width and height) and spatial connectedness: whether a hedgerow is attached to a woodland and how much woodland habitat is available in the surroundings. We used generalized linear mixed-effects models to test whether the probability of occurrence of forest herbs along hedgerows differ between specialists and generalists.

Results: Hedgerow age and length interacted synergistically to increase forest plant species richness. Hedgerows attached to woodlands hosted systematically more species. Taller and wider hedgerows with a lower intensity of adjacent land uses hosted more forest plant species. Increasing the spatial connectedness of hedgerows had a positive effect on the probability of occurrence of dispersal-limited forest specialists in the understorey, which was not the case for generalists.

Conclusion: As predicted by the species-time-area relationship, ancient and long hedgerows attached to woodlands host more species and are more effective corridors. Creating new hedgerows to connect isolated woodlands can be a suitable strategy to restore functional connectivity, but it will be effective only on the long-term. The conservation of the most ancient hedgerows within intensively managed agricultural landscapes, especially those attached to ancient woodlands, should thus be a priority target.

KEYWORDS

Ancient forests, colonization, dispersal limitation, ecological corridor, habitat fragmentation, forest specialists, historical ecology, island biogeography, linear woody habitats, species time-area relationship

INTRODUCTION

The velocity of climate change may limit the capacity of species to redistribute and closely track the shifting isotherms, especially so in agricultural lowlands where isotherms are located further apart than in mountainous regions (Lenoir et al. 2008; Loarie et al. 2009; Bertrand et al. 2011; Lenoir & Svenning 2015). In many rural landscapes worldwide, land-use changes, habitat fragmentation and the intensification of management together concur to further impede this climate-driven redistribution of life, increasing the risk of local extinction (Wilcox & Murphy 1985; Saunders et al. 1991; Warren et al. 2001; Bertrand et al. 2011; Guo et al. 2018). This is especially true for many forest herb species that are slow colonizers of recent woodlands as the result of both high habitat quality requirements and low dispersal capacities (Flinn & Vellend 2005; Honnay et al. 2005; Hermy & Verheyen 2007). Because forest “specialists” (i.e. species strictly associated with woodland habitats) and forest “generalists” (i.e. species that can also establish in more open habitats) differ by their life-history traits, they can respond differently to the same drivers within a given landscape (Jamoneau et al. 2011). Forest herb specialists often exhibit a suite of traits characterizing species growing in a relatively stable environment, such as slow growth rate, long pre-reproductive phase, low reproductive output and short dispersal distances (Matlack 1994; Cain et al. 1998; Hermy et al. 1999; Whigham 2004). As a result, while providing suitable habitat conditions, post-agricultural woodlands often remain species-poor for extended periods of time (De Frenne et al. 2011), with important consequences on ecosystem functioning and the delivery of ecosystem services to society.

Increasing woodland connectivity is expected to mitigate the negative effects of forest fragmentation on biodiversity by promoting species movement among patches (Niemelä 2001; Bennett et al. 2006). This is the rationale behind the use of ecological corridors (i.e. linear landscape elements that facilitate movement of individuals between spatially segregated populations) (Saunders et al. 1991) as a conservation tool (Beier & Noss 1998; Hanski 1999; Davies & Pullin 2007). Hedgerows have been widely advocated to serve as ecological corridors (Pollard et al. 1974; Bailey 2007; Roy & de Blois 2008; Gilbert-Norton et al. 2010), but the question whether it is truly the case for forest plant species remained heavily debated (Fritz & Merriam 1993; French & Cummins 2001; Smart et al. 2001; de Blois et al. 2002; Deckers et al. 2005; Sitzia 2007; Wehling & Diekmann 2009a; Wehling & Diekmann 2009b; Liira & Paal 2013; Paal et al. 2017).

Compared to woodlands, hedgerows exhibit different microclimate conditions, nutrient status and disturbance regimes (McCollin et al. 2000). Higher soil pH and nutrient content have been shown to promote the growth of highly competitive plants, which could exclude forest herbs of smaller stature (Hermy et al. 1999). The drier and less buffered microclimate in hedgerows may further be detrimental to these species (McCollin et al. 2000). Moreover, microhabitat conditions within hedgerows are not only impacted by management practices on the hedgerow itself (e.g. trimming), but also by the surrounding disturbances caused by proximal farming practices such as grazing by domestic animals, tillage, pesticide use and fertilizer misplacement (Kleijn & Snoeiijing 1997; Jobin et al. 1997; Smart et al. 2001; Deckers et al. 2004). Hedgerows thus provide suboptimal habitat conditions to forest herbs, acting as a selective filter rather than as true corridors (Fritz & Merriam 1993; McCollin et al. 2000; French & Cummins 2001; de Blois et al. 2002; Deckers et al. 2005; Sitzia 2007; Wehling & Diekmann 2009a). The longer, wider or higher a hedgerow, the higher the size of suitable shaded habitat for forest herbs to successfully establish (Closset-Kopp et al. 2017). According to the species-area relationship (SAR) (Arrhenius 1921; Rosenzweig 1995) and once the negative effect of proximal farming practices has been cancelled out, forest plant species richness is thus predicted to increase with the size of suitable shaded habitat provided by hedgerows.

Beyond habitat size (i.e. hedgerow length, width and height) and quality (i.e. adjacent land use intensity), two important factors may impact the effectiveness of hedgerows as habitats for forest herbs, namely historical continuity and spatial connectedness (Paal et al. 2017). First, according to the species-time relationship (STR) (Preston 1960; Rosenzweig 1995), the chance for a given hedgerow to be colonized by forest plant species increases with the historical continuity of the land used as hedgerow (Roy & de Blois 2008; Closset-Kopp et al. 2017; Litza & Diekmann 2019) and its historical connectivity to ancient woodlands (Paal et al. 2017). An ancient hedgerow (i.e. a wooded stripe that continuously existed for several centuries, irrespective to the age of constituting woody plants) historically connected to a woodland is thus predicted to host more forest plant species than recent ones. Even the weakest dispersers were retrieved in ancient hedgerows, suggesting that these species are more constrained by dispersal than recruitment limitations (Pollard et al. 1974; Closset-Kopp et al. 2016).

Second, it has been repeatedly shown that the richness and abundance of forest plant species in hedgerows declines with increasing distance to woodlands (Burel & Baudry 1990; Corbit et al.

1999; Sitzia 2007; Roy & de Blois 2008; Wehling & Diekmann 2009b; Litza & Diekmann 2019). Rates of migration for forest herbs in temperate forest range from 0 to 5.5 m.yr⁻¹ (Matlack 1994; Cain et al. 1998; Hermy et al. 1999), with rates often less than 1 m.yr⁻¹, especially in fragmented landscapes (Brunet & von Oheimb 1998). Colonization of hedgerows by forest specialists is thus likely to be more successful as spatial connectedness increases, that is when hedgerows are surrounded by a larger amount of woodland habitat (i.e. the habitat amount hypothesis *sensu* Fahrig 2013) and/or when they are directly attached to ancient woodlands (Peterken & Game 1981; Corbit et al. 1999; McCollin et al. 2000; Paal et al. 2017).

Finally, historical continuity may interact with space through both habitat size (i.e. hedgerow length, width and height), as illustrated by the species-time-area relationship (STAR) (Adler & Lauenroth 2003; Adler et al. 2005; Jamoneau et al. 2011), and spatial connectedness. Indeed, historical continuity and spatial connectedness do not act independently on the colonization of hedgerows by forest species, which are expected to be more abundant in ancient hedgerows attached to woodlands as compared to recent and/or isolated hedgerows. Although the spatiotemporal connectivity between wooded corridors and woodlands has already been tested on species richness, with historically connected hedgerows having significantly more forest specialists than historically isolated hedgerows (Paal et al. 2017), the interaction effect between historical continuity (hedgerow age *per se*) and spatial connectedness has, to our knowledge, never been tested. Here, we aim at evaluating the importance of hedgerow age (i.e. continuity of the habitat through historical times) and its potential interaction with hedgerow size and connectedness to woodland habitats, while accounting for other potential confounding factors (i.e. habitat quality), on the capacity of hedgerows to host forest herb species and hence act as microrefugia for these species across agricultural landscapes. More specifically, we test the following hypotheses:

H1: As the size of shaded habitat depends upon structural features of the hedgerow, we assume that the number of forest plants in the understorey will increase with hedgerow length, width and/or height, according to the SAR.

H2: Hedgerows accumulate forest plant species over time, as predicted by the STR, with the weaker dispersers occurring only in the most ancient hedgerows. If H2 is true and all else being equal, a more ancient hedgerow will host more forest plants in its understorey than a more recent one.

H3: The number of forest plants in the understorey of hedgerows increases with the amount of available woodland habitat in the surroundings and its spatial connectedness to hedgerows. If H3 is true and all else being equal, a hedgerow directly attached to a woodland and/or surrounded by a high density of woodlands will host more forest herbs in its understorey than isolated hedgerows.

H4: Adjacent land uses impact the occurrence of species in a way that the stronger the disturbance, the less abundant the forest plants in the understorey. If H4 is true and all else being equal, the number of forest plants in the understorey will decrease as proximal land-use intensity increases.

H5: Historical continuity, the hedgerow's suitable habitat size and its spatial connectedness to proximal woodlands may interact synergistically (hereafter spatiotemporal connectedness) to enhance forest plant species accumulation by hedgerows. Under H5, all else being equal, the most ancient hedgerows attached to a woodland and/or surrounded by a high density of proximal woodlands and/or providing locally more shaded habitat (i.e. longer, wider and/or higher hedgerows) are predicted to be the most species-rich, according to the STAR.

H6: The way hedgerows act as corridors for forest species not only depends on spatial connectedness and historical continuity but it also depends upon the species' dispersal capacity. If H6 is true, then bad dispersers (i.e. forest specialists) should hardly colonize isolated and recent hedgerows and their probability of occurrence should decrease with distance to the connecting point in attached and ancient hedgerows. *Per contra*, good dispersers (i.e. generalist species) should colonize hedgerows at random and independently from the distance to woodland sources and irrespective of historical continuity.

To test these hypotheses, we surveyed the forest plant species composition of hedgerows that were either attached or not to a woodland, along a unique chronosequence covering ca. 300 years (1725-2008) between the most ancient and the most recent hedgerow, and we quantified several local-proximal factors potentially explaining this composition.

MATERIALS AND METHODS

Study sites

The study was conducted in northern France (Hauts-de-France region) (Fig. 1a). The climate is temperate oceanic, with mean annual air temperature and total annual rainfall of ca. 8.7-9.8°C and 700-800 mm, respectively. The dominant geological substrate is Cretaceous chalk, usually covered by Quaternary loess. The regional landscape has been patterned by more than two millennia of agricultural activities. It mostly consists of open fields that are intensively cultivated (Fig. 1a) for wheat, sugar beet and rapeseed, but some smaller areas support enclosed grasslands (Fig. 1b) that are grazed by cattle and cows. The woodland cover is highly fragmented, with many small patches (< 4 ha) and few big woodlands. In open field landscapes, hedgerows are usually scattered while they can form dense networks in agricultural landscapes with a mixture of crop fields, pastures and meadows (i.e. “bocage”). Their management depends upon adjacent land use. While they are regularly thinned along cultivated fields to minimize crop shading and allow agriculture vehicles to circulate and manoeuvre as close as possible to the hedgerows, they are typically cantilevered with overhanging branches to provide a shelter for animals along pastures and for people along paths.

Using a range of historical sources available across the study area, we built a chronosequence of hedgerows according to their historical continuity: from one decade to several centuries old (see Closset-Kopp et al. 2017 for more details on the method to date hedgerows from old maps). More specifically, we used: local archives (old maps from the 17th and 18th centuries); the Napoleonic cadastral maps and the associated register of status of the land (1820); historical “Etat-Major” maps (1826); and aerial photographs from 1940 to 2013 (IGN: <http://www.ign.fr/>). For instance, a hedgerow already present on the oldest map available from a local archive dating from 1775 and continuously present on all consecutive maps available for this locality was dated from 1775 (Fig. 1d, lower row). For hedgerows appearing between two consecutive maps, we took the median date between the two maps as the date of first appearance (Fig. 1d, upper row). Using the available historical sources, we were able to date a total of 99 hedgerows, of which 16 were attached to a woodland (Fig. 1c). The date of first appearance of a hedgerow, which is still a hedgerow today (i.e. extent hedgerow), ranged from 1725 to 2008 (mean = 1861; 95% confidence interval = [1842:1880]).

Field surveys

During May-August 2014-2015, we surveyed the 99 selected hedgerows for the occurrence of forest plant species in the understorey herb layer (≤ 1 -m height), by walking along and on both sides of each hedgerow. The understorey was defined as the vegetation that woody species of the hedgerow directly overhung, thus excluding margins of adjacent agricultural lands. Here, we considered forest plant species as the set of vascular plants (mostly perennials) occurring regionally in temperate deciduous forests. It includes both forest specialists, that are restricted to the interior of closed-canopy woodlands, and generalist species that grow in woodland understories as well as in more open habitats such as, e.g., clearings and woodland edges (Oberdorfer 1957; Jamoneau et al. 2011; Valdés et al. 2015; Closset-Kopp et al. 2016) (see Appendix S1 for the full species list). We recorded all vascular plant species in each hedgerow, including herbs, blackberries, lianas creeping on the ground (e.g. *Hedera helix*), seedlings and small saplings (≤ 1 -m height) of shrubs and trees. Species that did not belong to the regional species pool of forest plants (e.g. grassland species) were excluded. Species from the shrub and tree vegetation layers (> 1 -m height) were recorded separately. During field surveys, we also recorded the following features for each hedgerow: total length (m); maximum height (m); minimum height (m); maximum width (m); and adjacent land uses (i.e. cropland, grassland, path and road). In open field landscapes, almost all the dated hedgerows that we sampled, either attached or not to a woodland, were standalone linear elements. Some of these linear elements underwent size reduction over time due to land consolidation but none did develop into denser networks. Hence, the total length of hedgerows in open field landscapes was measured as the length extending from one end to the other. In the bocage landscape, some of the dated linear elements that we sampled were part of a network of linear elements, sometimes more recent, connected by nodes. In that particular case, hedgerow length was measured as the length extending from one node to the next, but making sure that the entire segment was of the same age (using archives; see above). To quantify adjacent land use intensity, we affected an index to each land use type (from the least to the most intensive: foot path = 1; road = 2; meadow = 4; and crop field = 5) and then added the two indices corresponding to the land use type on each side of the hedgerow (e.g. for a hedgerow between a meadow and a cultivated field: $4 + 5 = 9$) (Closset-Kopp et al. 2016).

For a subset of 29 hedgerows (15 attached and 14 not attached to a woodland), we recorded the occurrence of each forest plant species in both the herbaceous and tree layers within each 5-m consecutive segment we could fit along the midline of the focal hedgerow (Corbit et al. 1999; Sitzia 2007) (Figs. 1b and 1c). Both forest specialists and generalists were sampled for presence-absence along each hedgerow. For hedgerows attached to a woodland, sampling began at the connection point between the woodland and the hedgerow. For isolated hedgerows not attached to a woodland, sampling began at any open end, as there was no clear starting point relative to woodlands.

Data analysis

Drivers of species richness within hedgerows (H1-H5)

We ran generalized linear models (GLMs) with a Poisson family distribution for count data. We used the total number of forest plant species occurring within the herbaceous layer of each hedgerows ($n = 99$) as the response variable. Indeed, species occurring in the herbaceous layer better reflect local habitat conditions within hedgerows, in contrast with species from the tree and shrub layers that are usually planted and thus less likely to reflect the impact of local habitat conditions on species richness. To explain the observed variation in the total number of forest plant species occurring within the herbaceous layer and test our first five research hypotheses (H1-H5), we prepared a set of ten local-proximal descriptors: (1) total length (m); (2) maximum width (m); (3) mean height (m), as the average between the maximum and minimum height value measured in the field; (4) height range (m) (maximum – minimum); (5) total number of species occurring in the shrub and tree layers; (6) date (year) of first appearance of a hedgerow in the historical archives; (7) attachment (yes/no) to a forest fragment; (8) cumulated forest cover within a buffer area of 500 m around each hedgerow (m^2), computed in a geographic information system (ArcGis Pro ©ESRI inc.); (9) distance to the nearest woodland (m), also computed in ArcGis Pro; and (10) adjacent land use intensity. Explanatory variables number 1-5, 6, 7-9, 10 refer to hypotheses H1 (i.e. SAR), H2 (i.e. STR), H3 (i.e. spatial connectedness) and H4 (i.e. habitat quality), respectively. Distance to the nearest woodland was highly correlated to the cumulated forest cover around the hedgerow (Pearson's correlation coefficient = 0.87, $P < 0.001$) while the range of height values of a given hedgerow was highly correlated to its putative year of first appearance in the historical archives (Pearson's correlation coefficient = 0.43; $P < 0.001$). Hence, to avoid multi-collinearity issues, we excluded the distance to the nearest woodland and the range

of height values from the set of predictor variables. All other predictor variables had relatively low (< 0.38) pairwise correlation values (Appendix S2).

To test for space-time interactions on forest species richness (STAR; cf. H5), we also included the two-way interaction term between the year of first appearance of a hedgerow in the historical archives and hedgerow length. We also tested for four alternative candidate models (i.e. alternative spatiotemporal-continuity hypotheses) by replacing hedgerow length in the two-way interaction term by one of the four other variables accounting for hedgerow size or spatial connectedness, namely width, height, attachment to a woodland and cumulated woodland cover around the hedgerow. These five candidate models (Appendix S3) were ranked according to the Akaike information criterion (AIC) (Burnham & Anderson 2002), with the best candidate model being the one with the lowest AIC value. Once the best candidate model was selected, we reran it but rescaling all predictor variables for comparison purposes, except attachment to a forest fragment which was a binary predictor. We used the “gscale” function from the “jtools” package in R (R Core Team 2019) which standardizes each value of a given variable by subtracting it from the mean and dividing it by 2 times the standard deviation of the focal variable. This rescaling formula is recommended over the traditional formula of dividing by one time the standard deviation because it allows direct comparisons of model coefficients with untransformed binary predictors (Gelman 2008). To assess the goodness of fit of the best candidate model, albeit there is no commonly accepted agreement on how to measure it for GLMs, we ran the “PseudoR2” function from the “DecsTools” package in R, which computes the McFadden (1977) as well as the Cox & Snell (1989) pseudo R^2 values.

Species distribution along the hedgerow (H6)

Finally, to test whether the species distribution profile along the hedgerow differed between forest specialists and generalists (H6), we used the subset of 29 hedgerows divided into 5-m consecutive segments. We built a generalized linear mixed-effects model (GLMM) with a binomial family distribution for binary data (i.e. logistic models). The response variable was the presence-absence, coded as 1-0, of all forest herb species occurring at least 25 times in the 29 hedgerows (i.e. 30 out of 111 species). Distance between the centroid of each 5-m segment and the closest edge of a woodland was computed in ArcGis Pro. For hedgerows attached to a woodland, the distance of the first 5-m segment connected to the woodland is ca. 2.5 m and gradually increases for all the subsequent and consecutive 5-m segments sampled along the hedgerow as one moves away from

the attached woodland. For isolated hedgerows (i.e. not attached to a woodland) and without clear starting point relative to a focal woodland, the distance of a given 5-m segment to the closest woodland edge does not necessarily increase linearly along the hedgerow length as each end of a given hedgerow may be assigned to two different woodlands in terms of proximity.

As fixed-effect explanatory variables, we included: (1) the distance of the 5-m segment to the closest woodland (m); (2) the date (year) of first appearance of the hedgerow in the historical archives, ranging from 1725 to 2002 for this subset of 29 hedgerows; (3) whether or not the hedgerow was attached to a woodland; and (4) whether the species is a forest specialist or a generalist. To test for different distribution patterns along the hedgerow between forest specialists and generalists, we also included the two-way interaction term between the affinity of plant species for closed-canopy forests and distance to the closest woodland. As we expect different patterns between forest specialists and generalists depending upon hedgerow age, we added a two-way interaction term between the affinity of plant species for closed-canopy forests and the year of first appearance of the hedgerow. Finally, we included the two-way interaction term between attachment and distance to the closest woodland to account for different species distribution patterns between attached and isolated hedgerows. We included the hedgerow identity as well as the species name as random intercept terms in our GLMM. By doing so, we pooled information from all hedgerows and all species together to increase statistical power when testing differences in the distribution profile of forest specialists *vs.* generalists while keeping the possibility to generate estimates of the distribution profile for each individual species along each individual hedgerow (i.e. partial pooling). We ran this model twice: first with the raw values of the explanatory variables to be able to predict species response curves along the hedgerow based on our set of predictor variables in their natural scales and then with all quantitative predictor variables rescaled according to the “gscale” function in R in order to make direct comparisons of the relative importance of each predictor variable in the model. For illustrative purposes, we also ran species-specific GLMMs to display the response curve of several example species along the hedgerow. The same set of fixed-effect explanatory variables were used in each of the species-specific GLMMs, except that the affinity of plant species for closed-canopy forests and its two-way interaction terms with other covariates were not used as predictors since we focused on species-specific responses. Additionally, and for the same reason, the variable “species name” was removed from the list of random intercept terms when running species-specific GLMMs. We used

the “glmer” function from the “lme4” package in R to run our GLMMs. To assess the goodness of fit of our GLMMs, we ran the “r.squaredGLMM” function from the “MuMIn” package in R, which computes both the marginal and conditional R^2 values (Nakagawa & Schielzeth 2013).

RESULTS

We found a total of 111 forest herb species occurring in the understorey (≤ 1 -m height) of the 99 sampled hedgerows, of which 43 and 68 were forest specialists and generalists, respectively (Appendix S1). The average ($\pm$ SD: standard deviation) number of forest plant species occurring in the understorey of a single hedgerow was 18 ± 10 . Among the five candidate models we tested to explain species richness in the understorey of hedgerows, the best one, with the lowest AIC value, included the two-way interaction term between the year of first appearance of the hedgerow in the historical archives (i.e. historical continuity) and hedgerow length (Appendix S3 and Table 1). Note that the candidate model ranked second according to AIC values (i.e. the one including the two-way interaction term between historical continuity and hedgerow width) had a delta AIC value of 13 compared to the best candidate model (Appendix S3). Hence, we reported only the outcomes of the best candidate model here (Table 1) (McFadden pseudo $R^2 = 0.36$; Cox and Snell pseudo $R^2 = 0.98$). As hedgerow length increases, the most ancient hedgerow (ca. 290-yr old at the time of the survey) showed an exponential increase in the number of forest plant species occurring in the understorey, while more recent hedgerows (from 20-yr to 40-yr old at the time of the survey) showed a flat trend switching towards a decreasing trend for the most recent one (ca. 8-yr old at the time of the survey) (Fig. 2). In addition to this strong interaction effect ($P < 0.001$) (Table 1), we found that whether a hedgerow is attached or not to a woodland is the most important variable explaining forest plant species richness in the understorey, with hedgerows attached to a woodland being the most species-rich (Fig. 2 and Appendix S4). Other relevant explanatory variables were (Table 1 and Appendix S4): hedgerow width ($P = 0.016$; Appendix S4a); hedgerow height ($P = 0.002$; Appendix S4b); adjacent land-use intensity ($P < 0.001$; Appendix S4c); and the number of tree and shrub species occurring in the overstorey ($P = 0.014$; Appendix S4d). Hedgerow width, hedgerow height as well as the richness of woody species in the overstorey had a positive effect on the number of forest plant species occurring in the herbaceous layer, while adjacent land-use intensity had a negative effect. The cumulated amount of forest habitat surrounding hedgerows within a buffer area of 500 m had no effect on species richness ($P = 0.705$).

A total of 30 forest herbs (Appendix S5), including 11 forest specialists and 19 generalists, were frequent enough in the subset of 29 hedgerows to allow examination of species distribution response curves along the distance to the closest woodland (Figs. 3 and 4). Based on the single

model we fitted using distribution data from all species together (marginal $R^2 = 0.16$; conditional $R^2 = 0.41$), we found contrasted responses between forest specialists and generalists (Table 2), with the probability of occurrence of forest specialists consistently decreasing as the distance from woodlands increases ($P < 0.001$; Fig. 3). This pattern was especially pronounced along ancient hedgerows attached to a woodland (Fig. 3a). In general, the probability to find forest specialists was the highest within ancient hedgerows attached to a woodland. For instance, the species-specific models we ran for the two forest specialists *Stellaria holostea* (marginal $R^2 = 0.39$; conditional $R^2 = 0.75$) and *Viola reichenbachiana* (marginal $R^2 = 0.32$; conditional $R^2 = 0.75$) showed a much higher probability of occurrence within ancient hedgerows, as opposed to recent hedgerows, with a steep decline in occupancy as the distance to the woodland attached to the focal ancient hedgerow increases (Fig. 4). Yet, the positive effect of hedgerow age on forest plant species richness was more pronounced for generalists than for forest specialists ($P < 0.001$; Fig. 3). For isolated and recent hedgerows, the probability to find forest specialists was close to zero (Fig. 3d). *Per contra*, we found that the probability of occurrence of generalist species along isolated hedgerows, be they recent or ancient, was increasing along with the distance from woodlands (Figs. 3c and 3d), while it tended to decrease along hedgerows attached to woodlands (Figs. 3a and 3b).

DISCUSSION

Beyond their own respective positive effect, hedgerow age and length interact synergistically to increase forest plant species richness in the understorey. This increase was disproportionately pronounced in hedgerows that were attached to woodlands or tall and wide enough to provide a sufficient amount of shaded habitat for forest herbs. Yet, the benefit of these structural conditions were reduced as management intensity of adjacent lands increased. Moreover, we evidenced a proximal and directional colonization of ancient hedgerows from attached woodlands by forest specialists, whilst generalist species were more likely to randomly colonize isolated hedgerows away from woodlands. This suggests that ancient hedgerows can act as effective corridors for forest specialists to migrate among woodlands while generalists tend to use hedgerows as stepping stones rather than as corridors because their dispersal capacity is higher. Altogether, these findings highlight the relevance of maintaining a high spatiotemporal connectedness among wooded elements of agricultural landscapes to enhance forest plant biodiversity, especially so for forest specialists. Hereafter we discuss these main results.

The species-time-area relationship applies to hedgerows

As expected from theoretical and empirical work on the species-time-area relationship (STAR) (Rosenzweig 1995; Adler & Lauenroth 2003; Adler et al. 2005; Song et al. 2018), we found that the combined effect of time (i.e. the historical continuity of hedgerows) and space (the total length of hedgerows) on forest plant species richness in the understorey of hedgerows is greater than the sum of its parts (H5). Although several studies have already highlighted the positive effect of hedgerow age on forest herb species richness (Roy & de Blois 2008; Closset-Kopp et al. 2017; Litza & Diekmann 2019), following the species-time relationship (H2) (Preston 1960; Rosenzweig 1995), as well as the combined positive effect of hedgerow age and spatial connectedness on forest herb species richness (Paal et al. 2017), we here provide the first quantitative evidence for a STAR in forest plant assemblages of hedgerows. More precisely, we report an island type of STAR (ISTAR: Type IV *sensu* Scheiner 2003; Song et al. 2018) since we tallied total forest plant richness of entire hedgerows varying in size and historical continuity, similar to studies focusing on island-like systems. So far, the ISTAR model has been reported for zooplankton assemblages monitored during 21 years in a set of lakes in Wisconsin (Adler et al. 2005), as well as for bird assemblages monitored during 9 years in a set of Chinese islands (Song et al. 2018). Building on a

unique long-term chronosequence (1725-2008), we propose to thus extend the ISTAR model to forest plant assemblages in hedgerows.

It should be noted that when seeking a STAR in forest plant assemblages of hedgerows, only hedgerow length interacted synergistically with hedgerow age, in contrast with width and height. This is likely because length has a greater contribution than width or height in increasing the surface area and volume by which hedgerows can intercept diaspores and thus accumulate species over time. The longer the hedgerow, the higher the probability that it acts as a windbreak for wind-dispersed species or as a conduit for vectors, such as birds and mammals (Hinsley & Bellamy 2000; Haddad et al. 2003) thereby facilitating the colonization of hedgerows by vertebrate-dispersed herbs. This is consistent with a recent review, which revealed that surface area and volume were key structural features for hedgerows to form suitable habitats for mammals, birds and invertebrates in agricultural landscapes (Graham et al. 2018). Diaspore interception along hedgerows is less likely for forest specialists, which are mostly ant-dispersed species and species with no specific dispersal mode (Flinn & Vellend 2005; Roy & de Blois 2006). Here, the interaction between space and time increases the probability of rare long-distance dispersal events and successful colonization of long hedgerows by forest specialists.

Interestingly, we found that the accumulation of forest plant species over time and along hedgerows was disproportionately high in hedgerows that were attached to woodlands compared to hedgerows that were not (H3). This component of spatial connectedness even had the highest effect size among all the predictor variables that were included in our best candidate model of forest plant species richness in the understorey of hedgerows (see Table 1), suggesting a proximal and directional mass effect from the woodland (source) towards the attached hedgerow. This supports earlier findings from Sitzia (2007) and Paal et al. (2017) who have collectively shown that historically connected hedgerows harbour more forest plant species than historically isolated hedgerows. Surprisingly, we found no effect of the cumulated amount of woodland habitat surrounding the hedgerows on forest plant species richness, providing little support to the habitat amount hypothesis (Fahrig 2013) (H3). Because most forest herbs, especially forest specialists, are bad dispersers, they are unlikely to colonize distant, isolated woody habitats such as hedgerows (Brunet & von Oheimb 1998; Corbit et al. 1999; Roy & de Blois 2008). The proximal colonization of hedgerows from attached woodlands is thus the dominant mechanism behind the accumulation of forest plant species in hedgerows.

According to the species-area relationship and the high habitat quality requirements characterizing forest plant species (Flinn & Vellend 2005; Honnay et al. 2005; Hermy & Verheyen 2007), all structural features of hedgerows, namely length, width and height, had a positive effect on forest herb species richness (H1). This is consistent with former reports demonstrating that larger (Sitzia 2007; Roy & de Blois 2008; Litza & Diekmann 2019) or taller (Closset-Kopp et al. 2017) hedgerows harbour more forest plant species than narrower or smaller ones. It also confirms that a minimum height, width and cross-sectional area is required to ensure the establishment and the sustainability of healthy populations of forest herbs (Burel & Baudry 1990). For instance, based on our findings (see Fig. S3), we can recommend a minimum height and width of 10 m and 3 m, respectively. As hedgerow width or height increases, the volume and the quality of shaded habitats in the hedgerow increases, providing protection from wind and direct solar radiations, reducing air-mixing near the ground and ultimately generating a more stable and forest-like microclimate (i.e. temperature and humidity conditions are buffered). Over time, the combined effect of these microclimatic factors will help developing forest soil conditions and increase the chances for forest plant species to establish in the understorey of hedgerows (Roy & de Blois 2006; Closset-Kopp et al. 2016). It should be noted that wider and taller hedgerows are associated with more species-rich overstories, which in turn may increase habitat heterogeneity in the understorey of hedgerows and hence increase species richness within the herb layer (i.e. the habitat heterogeneity hypothesis). However, as we controlled for that potential confounding effect in our analyses (see Table 1 and Appendix S3), it is unlikely that the positive effects of height and width we found was due to greater habitat heterogeneity. Importantly, the size and quality of shaded habitats provided by hedgerows may be mitigated by the combined effect of local management-associated disturbances (e.g. trimming, thinning, pollarding, grazing) and proximal disturbances (e.g. drift of pesticides and fertilizers). Consistently, we found that increased land use intensity adjacent to hedgerows decreased forest plant species richness in the understorey of hedgerows (H4). Farming practices are known to alter habitat quality along woodland edges (e.g. increased light and nutrient levels) and foster the replacement of forest herbs by a few competitive nitrophilous non-forest forbs and grasses (Chabrierie et al. 2013). Based on these findings, in addition to ensuring a minimum height and width to hedgerows, we recommend to keep overhanging branches as well as a buffer zone between the hedgerow and the tilled or grazed area so that hedgerows can provide suitable habitat conditions for forest herbs, which is a prerequisite for corridors to be effective.

Hedgerows as effective corridors for forest specialists

If hedgerows are effective corridors for the movement of forest plant species, the probability of occurrence of forest species should decrease with distance from the source, especially so for forest specialists being bad dispersers and requiring high habitat quality conditions to establish (H6). Accordingly, we found a negative effect of the distance from the source for forest specialists, a pattern which was even more pronounced for ancient hedgerows attached to a woodland (Fig. 4c). This is consistent with former studies showing a decrease in either forest plant species richness, forest plant abundance, forest plant species probability of occurrence or similarity in species composition along hedgerows as the distance from the attached woodland increases (Burel & Baudry 1990; Corbit et al. 1999; Sitzia 2007; Roy & de Blois 2008; Wehling & Diekmann 2009b; Liira & Paal 2013). Whether this pattern is due to dispersal limitation, recruitment limitation or both remains unclear. It could be argued that the decreasing probability to find a forest specialist along hedgerows attached to woodlands is not due to dispersal limitations but to poor habitat quality further away from the woodland-hedgerow connection point (Corbit et al. 1999; Wehling & Diekmann 2009b). For instance, Wehling & Diekmann (2009b) reported that hedgerow segments close to the woodland-hedgerow connection point showed better forest-like environmental conditions than segments further away from this point. However, we found a similar pattern with distance to woodland for forest specialists in isolated hedgerow, even if the probability of occurrence is much lower in that case. This suggests that dispersal limitation matters more than habitat quality for forest specialists, and that woodlands are sources of and hedgerows are effective corridors for forest specialists, especially so whenever hedgerows are attached to woodlands and are ancient enough to provide forest-like habitat conditions.

For generalist species, we found contrasting patterns with distance to woodland between isolated and attached hedgerows. In the former, the probability to find generalist species increased with the distance to woodland, reaching very high values at very far distances from woodlands (> 1 km) (Figs. 4c and 4d). This is consistent with the findings of Wehling & Diekmann (2009b) who reported that non-forest species more easily outcompeted forest specialists in hedgerow segments located further away from woodlands, due to the higher availability of light and nutrient in comparison with hedgerow segments located closer to woodlands. Consistently, it has been shown that generalist species depend more on landscape composition and management practices than on the spatial connectedness of woodlands (Jamoneau et al. 2011). Within hedgerows attached to

woodlands, generalist species follow the same pattern with distance to woodland as forest specialists (Figs. 4a and 4b). Our findings thus indicate that generalist species may find suitable habitat conditions anywhere along hedgerows, while forest specialists may be limited as much by habitat quality as by dispersal.

As a result, forest specialists are more likely to proximally colonize an hedgerow attached to a woodland and subsequently migrate along this hedgerow through successive generations (Brunet & von Oheimb 1998). To ensure the migration of forest plant species among forest fragments in agricultural landscapes, it is thus crucial to maintain ancient hedgerows, especially those attached to ancient woodlands (Paal et al. 2017). Planting new hedgerows for conservation purpose will be effective only on the (very) long term and mostly if they are attached to extent woodlands. In conclusion, the conservation of the most ancient hedgerows within intensively managed agricultural landscapes should be a priority target.

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AUTHOR CONTRIBUTIONS

JL, GD and DCK conceived the study and the analytical framework; JL, GD, FS and DCK collected the field data; JL ran the statistical analyses; EGM conducted all GIS analyses; EGM and JB dated all hedgerows based on historical maps and archives. JL led the writing with contributions from GD; all co-authors discussed the results, provided feedback and commented on the manuscript.

DATA ACCESSIBILITY

The data and the R scripts used to run the analyses and generate figures are available at <https://figshare.com/s/fe9fbe75888aae25183>

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SUPPORTING INFORMATION

Appendix S1: List of forest plant species occurring within the studied hedgerows

Appendix S2: Correlation matrix of the variables used in the analyses

Appendix S3: List of candidate models used to test the six research hypotheses

Appendix S4: Predictions of the best model of forest plant species richness

Appendix S5: List of species used to test patterns with distance from woodlands

TABLES AND FIGURES

Table 1: Coefficient estimates of the best candidate model (cf. M1 in Table S2) providing insights on the main drivers of species richness within the herb layer of hedgerows. All continuous variables were standardised so that coefficient estimates can be compared among each other's and interpreted as effect sizes (see the materials and methods section for more information). The intercept gives the effect size with all other continuous variables set to zero and the attached factor variable set to "no".

Variable	Coefficient	Standard error	Z-value	P-value
Intercept	2.695	0.031	87.193	<0.001
Attached	0.562	0.086	6.492	<0.001
gscale(Year)	-0.329	0.060	-5.432	<0.001
gscale(Length)	0.124	0.067	1.836	0.066
gscale(Width)	0.128	0.053	2.403	0.016
gscale(Height)	0.161	0.052	3.066	0.002
gscale(Forest cover)	0.025	0.067	0.379	0.705
gscale(Adjacent land-use)	-0.307	0.050	-6.193	<0.001
gscale(Richness shrub and tree layers)	0.137	0.056	2.451	0.014
gscale(Year) : gscale(Length)	-0.470	0.117	-4.030	<0.001

Table 2: Coefficient estimates of the model testing patterns with distance from woodland habitats for both forest specialist and generalist species. All continuous variables were standardised so that coefficient estimates can be compared among each other's and interpreted as effect sizes (see the materials and methods section for more information). The intercept gives the effect size with all other continuous variables set to zero, the species status factor variable set to “generalists” and the attached factor variable set to “no”.

Variable	Coefficient	Standard error	Z-value	P-value
Intercept	-2.600	0.289	-8.999	<0.001
Specialists	-0.535	0.402	-1.330	0.183
Attached	0.579	0.286	2.026	0.043
gscale(Distance)	0.671	0.242	2.776	0.005
gscale(Year)	-1.435	0.223	-6.449	<0.001
gscale(Year) : Specialists	0.346	0.137	2.516	0.012
gscale(Distance) : Specialists	-0.771	0.176	-4.376	<0.001
gscale(Distance) : Attached	-2.214	0.733	-3.018	0.002

Figure 1: Distribution of the 99 hedgerows sampled across the study area **(a)** and sampling design used for a subset of 29 hedgerows **(b, c)**. All studied hedgerows were dated according to local maps from historical archives and aerial photographs **(d)**. Both isolated hedgerows (non-attached) **(b)** and hedgerows attached to a woodland **(c)** were surveyed. The size of dots on the map **(a)** are proportional to hedgerow age with large dots depicting the most ancient hedgerows. A total of 29 hedgerows were divided into 5-m segments **(b, c)**. For hedgerows attached to a woodland, we

systematically started each transect (segment #1) at the connection point between the forest fragment and the hedgerow (c). A timeline provides examples of hedgerow datation using available archives (d). The row above the timeline shows a recent hedgerow appearing between 2001 and 2013 (median year = 2008) whereas the row below the timeline shows as ancient hedgerow already present on the oldest map (1775).

Figure 2: Space-time interaction between the year of first appearance of a hedgerow in the historical archives (**a**, **b**), as a proxy for hedgerow age, and the total length of the hedgerow (**c**, **d**) on the total number of forest plant species occurring in the understorey of hedgerows non-attached (isolated) (**a**, **c**) or attached to a woodland (**b**, **d**). Predictions are based on the best candidate model (see Table 1 for standardized coefficients). All other covariates not displayed on a given plot are set to their median values.

Figure 3: Effect of distance to woodland (m) on the distribution of both forest specialists and generalists along hedgerows that are either attached (a, b) or not (isolated) (c, d) to a woodland. For illustrative purposes, we set the year of first appearance of the hedgerow in the historical archives to 1700 (a, c) and 2000 (b, d) for ancient and recent hedgerows, respectively. Shaded ribbons show the 95% confidence interval around each response curve.

Figure 4: Effect of distance to woodland (m) on the probability of occurrence of *Viola reichenbachiana* (a) and *Stellaria holostea* (b) along both recent (year of first appearance of the hedgerow in the historical archives set to 2000) and ancient (year of first appearance of the hedgerow in the historical archives set to 1700) hedgerows that are attached to a woodland. Shaded ribbons show the 95% confidence interval around each response curve.