

Plant diversity in hedgerows and road verges across Europe

Thomas Vanneste¹  | Sanne Govaert¹  | Willem De Kesel¹ | Sanne Van Den Berge¹  | Pieter Vangansbeke¹  | Camille Meeussen¹  | Jörg Brunet²  | Sara A. O. Cousins³ | Guillaume Decocq⁴  | Martin Diekmann⁵ | Bente J. Graae⁶ | Per-Ola Hedwall²  | Thilo Heinken⁷ | Kenny Helsen⁸  | Rozália E. Kapás^{3,6} | Jonathan Lenoir⁴  | Jaan Liira⁹  | Sigrid Lindmo⁶ | Kathrin Litza⁵  | Tobias Naaf¹⁰ | Anna Orczewska¹¹ | Jan Plue³  | Monika Wulf⁹ | Kris Verheyen¹  | Pieter De Frenne¹ 

¹Forest & Nature Lab, Department of Environment, Faculty of Bioscience Engineering, Ghent University, Gontrode-Melle, Belgium; ²Southern Sweden Research Centre, Swedish University of Agricultural Sciences, Alnarp, Sweden; ³Biogeography and Geomatics, Department of Physical Geography, Stockholm University, Stockholm, Sweden; ⁴UR «Ecologie et Dynamique des Systèmes Anthropisés» (EDYSAN, UMR 7058 CNRS-UPJV), Jules Verne University of Picardie, Amiens, France; ⁵Vegetation Ecology and Conservation Biology, Institute of Ecology, FB2, University of Bremen, Bremen, Germany; ⁶Department of Biology, Norwegian University of Science and Technology, Trondheim, Norway; ⁷Institute of Biochemistry and Biology, University of Potsdam, Potsdam, Germany; ⁸Plant Conservation and Population Biology, Biology Department, University of Leuven, Heverlee, Belgium; ⁹Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia; ¹⁰Centre for Agricultural Landscape Research (ZALF), Müncheberg, Germany and ¹¹Faculty of Natural Sciences, Institute of Biology, Biotechnology and Environmental Protection, University of Silesia, Katowice, Poland

Correspondence

Thomas Vanneste
Email: thomas.vanneste@ugent.be

Funding information

Fonds Wetenschappelijk Onderzoek, Grant/Award Number: GOH1517N; H2020 European Research Council, Grant/Award Number: 614839 and 757833; Bijzonder Onderzoeksfonds, Grant/Award Number: 01N02817

Handling Editor: Shekhar Biswas

Abstract

1. Linear landscape elements such as hedgerows and road verges have the potential to mitigate the adverse effects of habitat fragmentation and climate change on species, for instance, by serving as a refuge habitat or by improving functional connectivity across the landscape. However, so far this hypothesis has not been evaluated at large spatial scales, preventing us from making generalized conclusions about their efficacy and implementation in conservation policies.
2. Here, we assessed plant diversity patterns in 336 vegetation plots distributed along hedgerows and road verges, spanning a macro-environmental gradient across temperate Europe. We compared herb-layer species richness and composition in these linear elements with the respective seed-source (core) habitats, that is, semi-natural forests and grasslands. Next, we assessed how these differences related to several environmental drivers acting either locally, at the landscape level or along the studied macro-ecological gradient.
3. Across all regions, about 55% of the plant species were shared between forests and hedgerows, and 52% between grasslands and road verges. Habitat-specialist richness was 11% lower in the linear habitats than in the core habitats, while generalist richness was 14% higher. The difference in floristic composition between both habitat types was mainly due to species turnover, and not nestedness. Most notably, forest-specialist richness in hedgerows responded positively to tree cover, tree height and the proportion of forests in the surrounding landscape, while generalist richness was negatively affected by tree height and buffering effect of trees on subcanopy temperatures. Grassland and road verge diversity was

mainly influenced by soil properties, with positive effects of basic cation levels on the number of specialists and those of bioavailable soil phosphorus on generalist diversity.

4. *Synthesis and applications.* We demonstrate that linear landscape elements provide a potential habitat for plant species across Europe, including slow-colonizing specialists. Additionally, our results stress the possibility for land managers to modify local habitat features (e.g. canopy structure, subcanopy microclimate, soil properties, mowing regime) through management practices to enhance the colonization success of specialists in these linear habitats. These findings underpin the management needed to better conserving the biodiversity of agricultural landscapes across broad geographical scales.

KEYWORDS

hedgerows, landscape connectivity, linear landscape elements, macro-environmental gradient, microclimate, multiscale analysis, plant colonization dynamics, road verges

1 | INTRODUCTION

Land-use changes and agricultural intensification have converted complex natural ecosystems across the globe into a patchwork of habitat fragments embedded in a matrix of production systems (Tschardt, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). This fragmentation of habitats may hamper species migrations (Guo, Lenoir, & Bonebrake, 2018), which could lead to a dramatic increase in local extinction risk given that numerous species are currently changing their distribution range towards higher latitudes or elevations in pursuit of the shifting climatic envelopes (Di Marco, Ferrier, Harwood, Hoskins, & Watson, 2019; Matlack, 2005). Habitat-specialist species are particularly sensitive to these global changes (Clavel, Julliard, & Devictor, 2011), and safeguarding their persistence in a changing world constitutes a major challenge for nature conservationists in the coming decades.

Increased connectivity among habitat patches, however, is assumed to mitigate the adverse effects of habitat fragmentation and climate change on biodiversity (Hodgson, Moilanen, Wintle, & Thomas, 2011). This has led to the introduction of landscape corridors as a conservation tool in public policies. These corridors have the potential to facilitate species movements and gene flow by linking suitable habitat patches isolated within an inhospitable matrix, and thus ensure a functioning network of suitable habitats. Besides, they may also serve as suitable habitats themselves and thus as potential refuges for many species, thereby promoting biodiversity conservation in otherwise degraded and species-poor landscapes (McGuire, Lawler, McRae, Nuñez, & Theobald, 2016). Hedgerows and road verges are common landscape elements in many regions, represent key parts of corridor networks and may therefore foster the persistence and migration of specialist species across fragmented landscapes (Baudry, Bunce, & Burel, 2000).

A variety of local-scale studies (e.g. Cousins, 2006; Wehling & Diekmann, 2009) have shown that hedgerows and road verges are

effective secondary habitats for species of conservation concern, and can even serve as dispersal corridors between isolated habitat fragments. For instance, in north-western Germany, Wehling and Diekmann (2009) showed that 77% of all forest plant species occurring in forests were also found in adjacent hedgerows, albeit with a higher representation of forest-dwelling generalists in the hedges. Likewise, Cousins (2006) reported that small remnant habitats such as road verges may provide a refuge habitat for species restricted to semi-natural grasslands in central Sweden, and thus contribute to the conservation of biodiversity in rural landscapes.

Yet, the utility of hedgerows and road verges as a conservation tool is still widely debated. While some studies found no effect of these linear elements on the dispersal probabilities of certain species groups (e.g. butterflies; Öckinger & Smith, 2008), others even advocated that they may be detrimental to biodiversity (Davies & Pullin, 2007), for instance, by acting as population sinks (Henein & Merriam, 1990) or by spreading diseases and pathogens (Hess, 1994). Moreover, research has shown that the effectiveness of linear elements as habitat or migration corridors for plant species varies depending on a wide range of environmental factors acting across different spatial and temporal scales (Cousins, 2006; Paal, Kütt, Löhmus, & Liira, 2017). For example, forest species richness in wooded corridors has been linked to structural canopy characteristics (Wehling & Diekmann, 2009), subcanopy microclimate (Roy & de Blois, 2008), long-term connectivity to forest (Paal et al., 2017) and adjacent forest cover (Van Den Berge et al., 2018). However, so far, studies investigating the drivers of plant distribution patterns in linear landscape elements are almost exclusively restricted to local or regional studies (e.g. Corbit, Marks, & Gardescu, 1999; Cousins, 2006; Liira & Paal, 2013; Litza & Diekmann, 2019). At larger scales, it is still unclear which species will disperse, germinate, establish their populations and successively migrate through these linear structures, and how diversity patterns in these habitats are shaped by multiscale environmental

factors. Consequently, an overall evaluation of linear landscape elements in supporting and preserving diverse plant communities in agricultural regions is still lacking.

Here we surveyed plant populations in 336 vegetation plots distributed along hedgerows and graminoid-dominated road verges, spanning a macro-environmental gradient across the European temperate biome. We assessed differences in herb-layer diversity and community composition between these linear elements and their respective seed-source (core) habitats, that is forests and semi-natural grasslands. Next, we linked the observed patterns in species diversity to several environmental variables varying either locally (canopy structure and composition, soil variables and microclimate buffering), at a landscape level (proportion of surrounding core habitat) or along a wide and continental-scale environmental gradient (nitrogen [N] deposition, macroclimate temperature and precipitation; see also Valdés et al., 2015; Vanneste et al., 2018).

Specifically, we sought to test the following hypotheses:

- a. Herb-layer plant diversity and composition differs between the linear landscape elements (hedgerows and road verges) and respective seed-source habitats (forests and semi-natural grasslands). In line with the preceding local-scale studies, we expect a lower proportion of habitat specialists and higher proportion of generalists in the linear elements.
- b. Potential differences in species diversity and composition between both habitat types are driven by a range of environmental factors, acting across multiple spatial scales. At the continental level, we expect that increased N deposition and higher ambient temperatures negatively affect plant diversity in linear habitats, particularly by inducing competitive exclusion of stress-tolerant habitat specialists by generalists. At the landscape level, we hypothesize that a larger amount of surrounding seed-source habitats contributes to a higher overall species richness (both specialists and generalists) in the linear structures. At the local scale, we expected to find a strong relationship between habitat quality (related to edaphic properties, canopy structure and microclimatic buffering) and species diversity of the linear elements, particularly the balance between specialists and generalists.

This knowledge is imperative to better understand and predict plant species distribution and colonization dynamics in agricultural regions across temperate Europe, and will have important implications for biodiversity conservation and landscape planning. The latter includes, for instance, developing guidelines for the preservation, management and establishment of linear landscape elements to improve habitat connectivity and promote species colonization across fragmented landscapes. This may apply to many legislative levels, from the local (e.g. hedgerow management), regional (e.g. management of road verges) to the (inter) national (e.g. environmental protection at national and EU level; Bonebrake et al., 2018).

2 | MATERIALS AND METHODS

2.1 | Study area and site selection

This study was conducted in agricultural landscapes of nine different regions spanning a continental-scale environmental gradient in climatic conditions (temperature and precipitation) as well as atmospheric N deposition across the European temperate biome (Olson et al., 2001; Figure 1A). The mean annual temperature (MAT) between 1970 and 2000 ranged from 5.5°C (Central Norway) to 10.3°C (Belgium), mean annual precipitation (MAP) from 583 (Central Sweden) to 1,057 mm (Central Norway) and N deposition in 2000 from 1.6 (Central Norway) to 23.8 kg N ha⁻¹ year⁻¹ (Belgium).

Within each region, four wooded habitat and/or four grassland sites were selected, according to a predefined set of criteria (see Materials and Methods in Supporting Information; Table S1). Each site

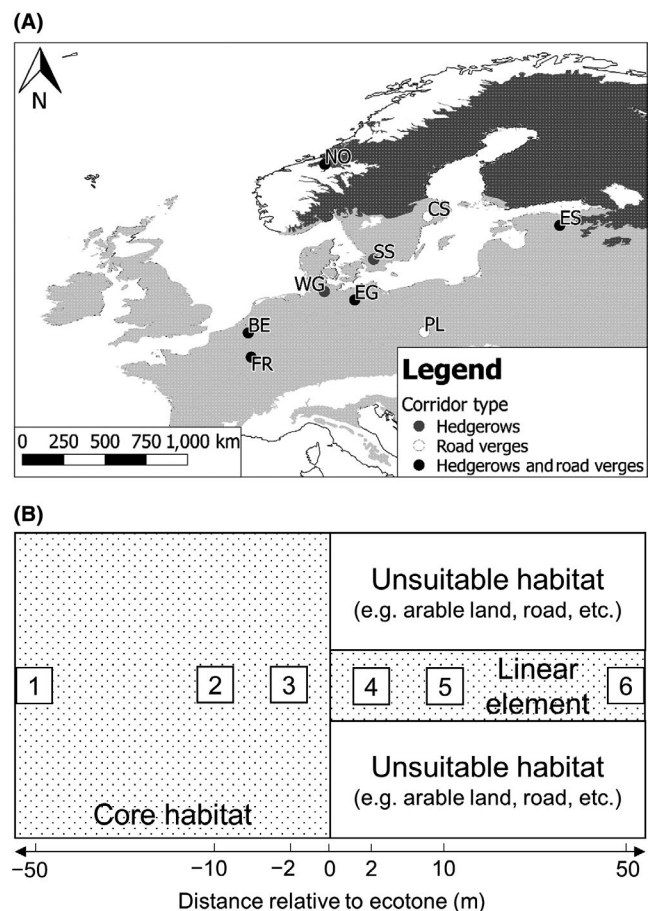


FIGURE 1 (A) Map showing the distribution of the nine study regions (FR = France, BE = Belgium, WG = Western Germany, EG = Eastern Germany, PL = Poland, SS = Southern Sweden, CS = Central Sweden, ES = Estonia and NO = Norway). The light grey area represents the temperate forest biome, while the dark grey area denotes the boreal forest biome (Olson et al., 2001). (B) In each study site, six vegetation plots were installed at fixed distances along a 100-m transect, that is three plots in the core habitat (at 2, 10 and 50 m relative to the ecotone between both habitat types) and three plots in the linear landscape element (again at 2, 10 and 50 m)

was composed of a linear element (hedgerow or graminoid-dominated road verge) and a corresponding core habitat (forest and semi-natural grassland respectively). Each selected hedgerow was connected to an ancient forest (i.e. always forest and no land-cover change according to the oldest available sources), whereof the canopy was mainly composed of broadleaf species. The selected road verges were connected to a species-rich, semi-natural grassland of the class Molinio-Arrhenatheretea (Mucina et al., 2016).

2.2 | Floristic surveys

The herb-layer flora in the linear elements and adjacent core habitat patches (forests and grasslands) was surveyed in July–August 2017 and April–May 2018 to include both summer and vernal species. Surveys of spring and summer species were pooled for the analyses. When a species was recorded in both surveys, only the highest of the two cover values was used. Plots with a size of 2 m × 2 m for the forest-hedgerow transects and 1 m × 1 m for the grassland-road verge transects were positioned at 2, 10 and 50 m away from the ecotone in both directions, resulting in six plots per transect (Figure 1B). In the hedgerows, the plots were located in the centre of the corridor, while in the road verges, the plots were positioned as far from the roads as possible to avoid the effects of run-off pollutants and salts.

In each plot, we collected species-specific data on both occurrence (presence/absence) and abundance (percentage ground cover) of all vascular plants. In the forest-hedgerow transects, the floristic survey was performed for the different vertical layers of vegetation, that is herb layer (<1 m), shrub layer (1–7 m) and tree layer (>7 m). The recordings from the shrub and tree layer were used to describe the canopy (see Section 2.3.3). Tree canopies in forests mainly consisted of *Fraxinus excelsior* (occurring in 31.0% of all plots), *Fagus sylvatica* (23.8%) and *Carpinus betulus* (17.9%), while in hedgerows mostly *F. excelsior* (29.6%), *C. betulus* (21.4%) and *Quercus robur* (21.4%) were found. The most common shrub species in the forests were *Corylus avellana* (38.1%), *Sorbus aucuparia* (14.3%) and *Sambucus nigra* (11.9%), and in the hedgerows *C. avellana* (23.8%), *S. nigra* (22.6%) and *Crataegus monogyna* (19.0%).

For forests and hedgerows, understorey species were classified as forest specialists or generalists according to Heinken (2019). For road verges and grasslands, species were categorized as semi-natural grassland specialists or generalists based on Ellenberg et al. (1991). More specifically, species classified as grassland specialists are the indicator species of the classes Nardo-Callunetea, Sedo-Scleranthetea, Festuco-Brometea and Molinio-Arrhenatheretea (see also Leuschner & Ellenberg, 2017; Mucina et al., 2016; see Table S2 for a complete species list).

2.3 | Explanatory variables

2.3.1 | Nitrogen deposition and climate data

Standardized N deposition data were obtained from the European Monitoring and Evaluation Program (EMEP; <http://www.emep.int>),

while macroclimatic conditions were extracted from WorldClim 2.0 (<https://www.worldclim.org>). We focused on MAT and MAP, which are generally considered as standard variables for describing global patterns of species diversity (Fick & Hijmans, 2017; see Materials and Methods in Supporting Information for more details on the calculation of these variables; Tables S3–S4).

2.3.2 | Habitat amount at landscape level

For each forest-hedgerow transect, we digitized all forests in a 500-m radius using digital aerial images obtained from Google Earth in QGIS 2.18.25 (QGIS Development Team, 2018), and calculated the proportion of forest cover in this buffer zone. For the grassland-road verge transect, we digitized all grassland types (including semi-natural grasslands, improved grasslands, pastures, hay meadows, etc.) in a 500-m radius, and computed the proportion of grassland cover.

2.3.3 | Canopy structure and composition

For each plot inside the forests and hedgerows, we measured four variables related to the canopy structure: the height of the shrub and tree layers, and the total cover of the shrub and tree layers (quantified as the sum of the cover percentages of all species in these respective layers). To characterize the composition of the canopy, we focused on two variables: shade-casting ability (SCA) and litter quality (LQ; sensu Verheyen et al., 2012; see Materials and Methods in Supporting Information; Tables S3–S5; Figure S1).

2.3.4 | Soil properties

In each plot, three soil samples were collected to a depth of 10 cm and merged into one soil sample. The mixed samples were dried to constant weight and subsequently analysed for pH-H₂O, exchangeable K⁺, Ca²⁺ and Mg²⁺ concentrations, total carbon (C) and N content and bioavailable phosphorus (P; see Materials and Methods in Supporting Information). The set of soil variables was subjected to a principal component analysis (PCA), and the loadings of the first two PCA axes were used as explanatory variables in the models. For hedgerows and forests, the first and second PCA axes explained 51.3% and 25.1% of the variation in soil variables respectively (Figure S2). For road verges and grasslands, the first and second PCA axes explained 41.4% and 34.6% of the variation in soil variables respectively (Figure S3).

2.3.5 | Microclimate

To quantify the microclimate in each site, the air temperature was recorded at a two-hourly interval between 1 September 2017 and 1 September 2018 using miniature temperature sensors (HOBO Pendant Data logger). For each sensor, we computed daily mean,

minimum and maximum temperature values. Corresponding 'free-air' (macroclimate) temperature data were obtained for each study site from nearby weather stations (using the sources listed in Table S6). For each station, we extracted the daily mean, minimum and maximum statistics for the same period as the in situ recordings. The magnitude of the temperature offset for daily mean, maximum and minimum temperature values was then calculated as microclimate temperatures minus macroclimate temperatures. We mainly focused on the effect of minimum and maximum temperature offsets during summer (June, July and August) and winter (December, January and February; see Materials and Methods in Supporting Information; Tables S3 and S4).

2.4 | Data analysis

First, we adopted a multilevel modelling approach using generalized linear mixed-effect models (GLMM; Bolker et al., 2009) with Poisson distribution to test whether the total, generalist and specialist herb-layer species richness differed between core habitats and linear elements. In these models, 'herb-layer species richness' (total, generalist or specialist) was used as response variable, while 'habitat' (core habitat vs. linear habitat) was included as fixed effect. In addition, 'region' and 'site' (nested within 'region') were included as random intercept terms in the models to account for the hierarchical structure of the dataset and spatial autocorrelation between populations of the same geographical region or study site. GLMMs were constructed in R 3.5.1 (R Core Team, 2019) using the 'glmer' function in the 'lme4' package (Bates, Mächler, Bolker, & Walker, 2015).

To quantify the dissimilarity in species composition (i.e. β -diversity) within each site, we constructed distance matrices using the abundance-based Bray–Curtis dissimilarity index (Bray & Curtis, 1957). Next, we calculated the compositional differentiation of each plot by averaging the pairwise dissimilarities against all other plots of that particular site (i.e. plot-level dissimilarity; sensu Baeten et al., 2012). Differences in plot-level dissimilarity within each site were then analysed with linear mixed-effect models (LMM) using the 'lmer' function. These models contained 'plot-level dissimilarity' as response variable, 'plot' as fixed effect, and 'region' and 'site' (nested within 'region') as random intercept terms. A Tukey's post hoc test was applied for pairwise comparisons using the 'glht' function of the 'MULTCOMP' package (Hothorn, Bretz, & Westfall, 2008). The average site-level dissimilarity was calculated as the mean of the six plot-level dissimilarities. Following Baselga (2013), we subsequently decomposed the Bray–Curtis dissimilarity into its turnover (balanced variation in species abundances) and nestedness (abundance gradient) components. All β -diversity measures were computed using the 'beta.pair.abund' function of the 'BETAPART' package (Baselga et al., 2018). In addition, nonmetric multidimensional scaling (NMDS) was adopted to visualize differences in herb-layer species composition between core habitats and linear elements with the 'metaMDS' function of the 'VEGAN' package (Oksanen et al., 2018; Figure S4).

Finally, we assessed how the different environmental variables (Table S7; Figures S5–S6) affected the variation in herb-layer species richness in core habitats and linear habitats, and whether the effect differed between both habitat types. We ran a series of separate univariate GLMMs, one per environmental variable as fixed effect. These models contained 'herb-layer species richness' (total, generalist or specialist) as response variable, the interaction between an environmental variable and 'habitat' (core habitat vs. linear habitat) as fixed effect, and 'region' and 'site' (nested within 'region') as random intercept terms.

3 | RESULTS

3.1 | Species richness

In the understorey layer of the hedgerows, we recorded 224 vascular plant species across all surveyed sites with an average of 16.6 (± 6.7 SE) species per plot, including 131 generalists and 61 forest specialists. In the forest understorey, we found 195 species with an average of 14.0 (± 6.6 SE) species per plot, including 98 generalists and 72 forest specialists (Table S8). About 54.6% of the total species pool occurring in forests was also found in hedgerows, but the percentage of shared species among forest and hedgerow plots of the same site (i.e. paired combinations of both habitat types) was, on average, only 4.8% (Tables S9 and S10). Furthermore, we recorded a significantly higher total number of species in the hedgerows than in the adjacent forests ($\chi^2 = 19.4$, $p < 0.001$). The number of generalists was significantly higher in the hedgerow than in the forest ($\chi^2 = 64.1$, $p < 0.001$), while the number of forest specialists was lower ($\chi^2 = 17.1$, $p < 0.001$; Figure 2; Figure S7).

In the road verges, we found 152 species with an average of 11.8 (± 3.6 SE) species per plot, including 47 grassland specialists and 104 generalists. In the semi-natural grasslands, 143 species were recorded, with an average of 10.9 (± 4.2 SE) species per plot, including 47 grassland specialists and 96 generalists (Table S11). About 51.5% of all species occurring in grasslands was also recorded in road verges, but the paired combinations of both habitat types shared, on average, only 9.79% of their species (Tables S12 and S13). Besides, we detected a marginally significant difference in total species richness between the road verges and the grasslands ($\chi^2 = 2.79$, $p = 0.094$). The number of generalists was higher in the road verges than in the grasslands ($\chi^2 = 13.3$, $p = 0.0003$), while the number of specialists did not differ between both habitat types ($\chi^2 = 1.93$, $p = 0.165$; Figure 2; Figure S8).

3.2 | Community composition

Across all regions, the average site-level Bray–Curtis dissimilarity (total β -diversity) along the forest-hedgerow transects was 0.573 (± 0.071 SE), whereas the turnover and nestedness components of dissimilarity were 0.482 (± 0.096 SE) and 0.091 (± 0.054 SE)

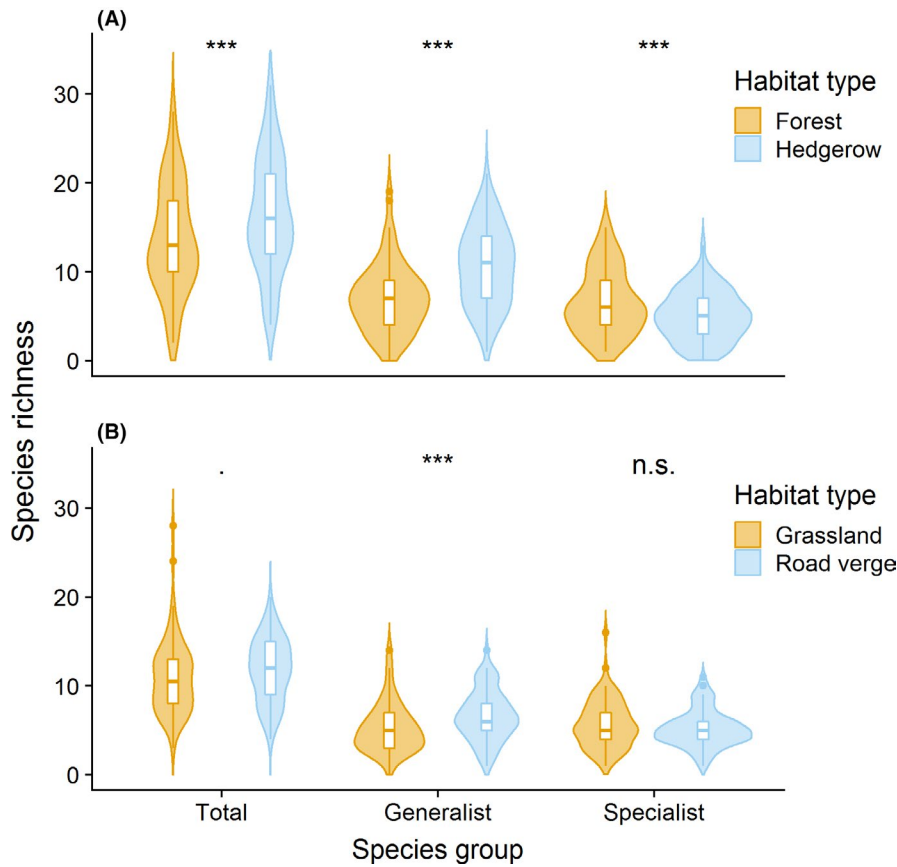


FIGURE 2 (A) Violin plots showing the total, generalist and specialist understorey plant species richness in forests and hedgerows. (B) Violin plots showing the total, generalist and specialist plant species richness in grasslands and road verges. The difference in species richness between both habitat types (core habitat vs. linear habitat) was tested with a generalized linear mixed-effect model with Poisson distribution (*Species richness* ~ *Habitat*). Significant differences are indicated as: '***' for $p < 0.001$, '**' for $p < 0.01$, '*' for $p < 0.05$, '^' for $p < 0.1$ and 'n.s.' for $p > 0.1$

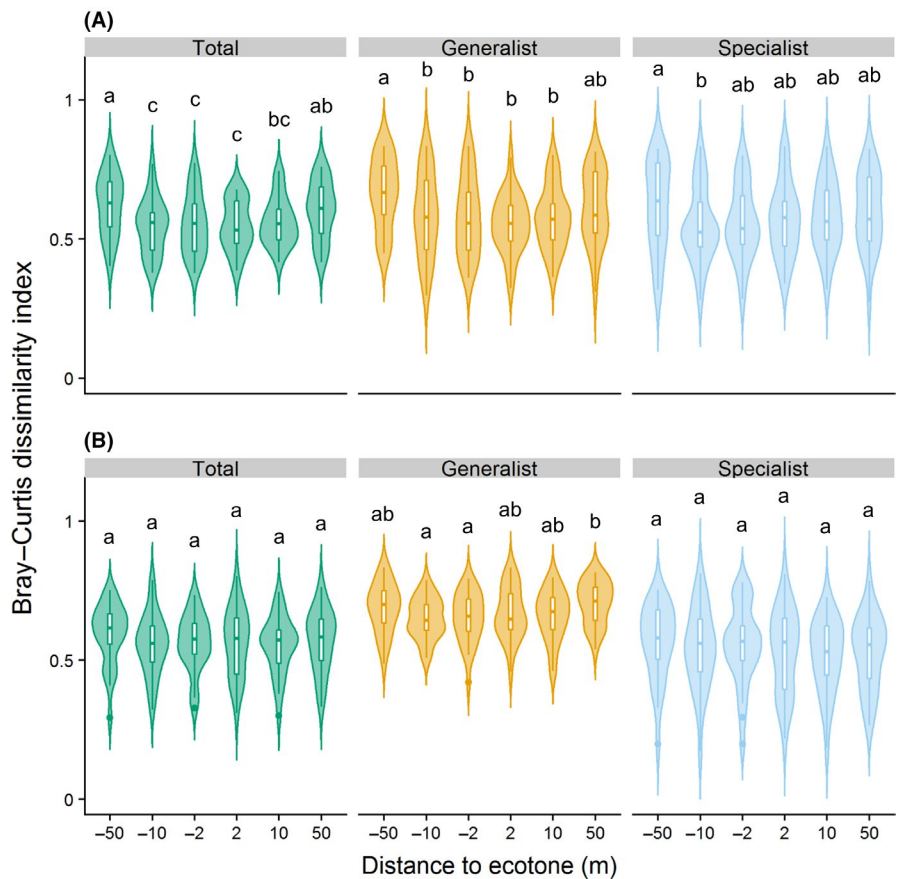


FIGURE 3 (A) Violin plots showing the plot-level Bray-Curtis dissimilarity index for all understorey plant species, generalists and specialists as a function of distance to the forest-hedgerow ecotone. (B) Violin plots showing the plot-level Bray-Curtis dissimilarity index for all plant species, generalists and specialists as a function to the grassland-road verge ecotone. Differences in Bray-Curtis dissimilarity among vegetation plots were tested with a generalized linear mixed-effect model with Poisson distribution (*Dissimilarity* ~ *Plot*), followed by a Tukey post hoc test for pairwise comparisons. Different letters denote significant differences

respectively. For generalists, the total β -diversity was 0.596 (± 0.087 SE), and the turnover and nestedness components of dissimilarity were 0.443 (± 0.134 SE) and 0.132 (± 0.092 SE) respectively. For specialists, the total β -diversity was 0.580 (± 0.186 SE), and the turnover and nestedness components of dissimilarity were 0.392 (± 0.138 SE) and 0.168 (± 0.085 SE) respectively. The plot-level compositional differentiation of generalists was highest in the forest interior, while the dissimilarity of specialists was lowest at 10 m in the forests (Figure 3).

In the grassland-road verge transects, the total β -diversity amounted to 0.568 (± 0.064 SE), whereas the turnover and nestedness components of dissimilarity were 0.529 (± 0.071 SE) and 0.039 (± 0.021 SE) respectively. For generalists, the total β -diversity was 0.671 (± 0.069 SE), and the turnover and nestedness components of dissimilarity were 0.580 (± 0.110 SE) and 0.085 (± 0.052 SE) respectively. For specialists, the total β -diversity was 0.544 (± 0.077 SE), and the turnover and nestedness components of dissimilarity were

0.444 (± 0.096 SE) and 0.096 (± 0.065 SE) respectively. The floristic dissimilarity of generalists was significantly higher in the outer plot of the road verges, while for specialists no differences in plot-level compositional differentiation were found (Figure 3).

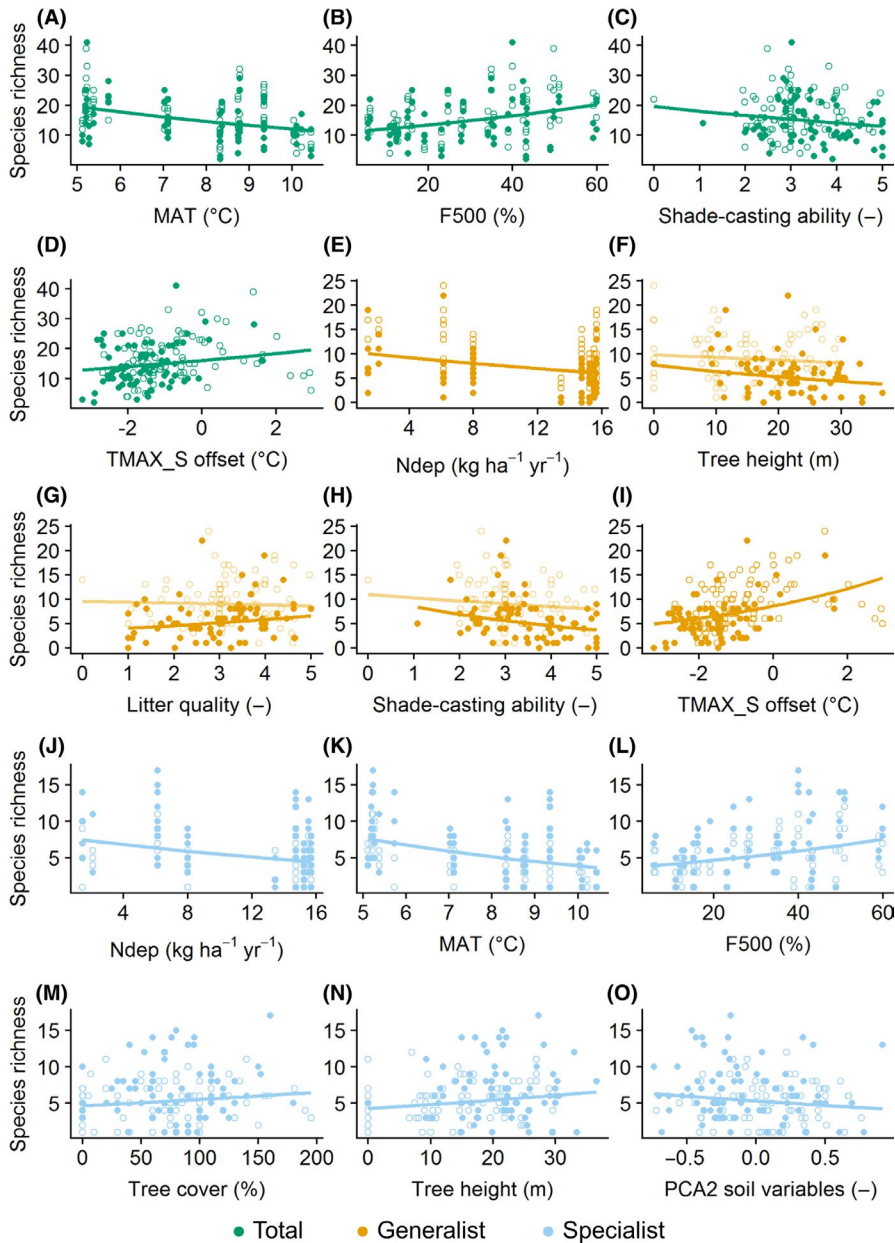
3.3 | Effect of environmental variables

In forests and hedgerows, N deposition and MAT tended to decrease the diversity of all species groups (albeit only marginally significant in some cases), but their effect did not interact with habitat type. The proportion of forest in a 500-m radius increased total and specialist plant diversity, while the effect on generalist richness interacted with habitat type. Regarding the canopy structure, three height was one of the most influential factors, with a strong negative effect on generalist richness and a highly positive effect on specialist richness. Furthermore, increasing

TABLE 1 Univariate statistical relationships between the total, generalist and specialist understorey plant species richness in forests and hedgerows, on the one hand, and the environmental variables, on the other hand. Values and symbols are chi-squared values and significances, respectively, from a likelihood ratio test of generalized linear mixed-effect models with Poisson distribution (*Species richness* ~ *Predictor* + *Habitat* + *Predictor* × *Habitat*). The direction of the effect is given as ‘↑’ for a positive effect of the predictor or a higher species richness in hedgerows than in forests, and ‘↓’ for a negative effect of the predictor or a lower species richness in hedgerows than in forests

	Total richness			Generalist richness			Specialist richness		
	Predictor	Habitat	Predictor × Habitat	Predictor	Habitat	Predictor × Habitat	Predictor	Habitat	Predictor × Habitat
Nitrogen deposition	↓3.1.	↑18.7***	n.s.	↓4.7*	↑72.7***	n.s.	↓4.1*	↓14.1***	n.s.
Mean annual temperature	↓6.0*	↑18.7***	n.s.	↓3.6.	↑72.7***	n.s.	↓10.0**	↓14.1***	n.s.
Mean annual precipitation	n.s.	↑18.7***	n.s.	n.s.	↑72.7***	n.s.	n.s.	↓14.1***	n.s.
Proportion of forest in 500-m radius	↑4.7*	↑18.7***	3.8.	↑2.8.	↑71.7***	4.7*	↑4.8*	↓14.1***	n.s.
Shrub cover	n.s.	↑18.7***	n.s.	↑3.2.	↑72.7***	n.s.	↓3.3.	↓14.1***	n.s.
Tree cover	n.s.	↑18.7***	n.s.	n.s.	↑72.7***	n.s.	↑4.0*	↓14.1***	n.s.
Shrub height	n.s.	↑18.7***	n.s.	n.s.	↑72.7***	n.s.	n.s.	↓14.1***	n.s.
Tree height	n.s.	↑12.0***	6.1*	↓7.2**	↑42.4***	5.3*	↑5.6*	↓14.1***	n.s.
Litter quality	n.s.	↑17.9***	6.4*	↑4.0*	↑67.9***	7.2**	n.s.	↓13.5***	n.s.
Shade-casting ability	↓6.4*	↑18.7***	n.s.	↓12.6***	↑61.5***	6.2*	n.s.	↓13.5***	n.s.
First PCA axis of soil variables	n.s.	↑18.7***	n.s.	n.s.	↑72.7***	↓3.8.	n.s.	↓14.1***	n.s.
Second PCA axis of soil variables	n.s.	↑18.7***	3.0.	n.s.	↑72.7***	n.s.	↓4.3*	↓14.1***	n.s.
Minimum summer temperature offset	n.s.	↑18.7***	n.s.	↓19.6***	↑72.7***	3.4.	↑3.0.	↓14.1***	n.s.
Maximum summer temperature offset	↑10.2**	↑18.7***	n.s.	↑36.2***	↑72.7***	3.7.	↓3.1.	↓14.1***	n.s.
Minimum winter temperature offset	n.s.	↑18.7***	n.s.	↓7.6**	↑72.7***	n.s.	n.s.	↓13.1***	3.9*
Maximum winter temperature offset	n.s.	↑18.7***	n.s.	↑7.3**	↑72.7***	n.s.	n.s.	↓14.1***	n.s.

Significances are indicated as ‘****’ for $p < 0.001$, ‘***’ for $p < 0.01$, ‘**’ for $p < 0.05$, ‘*’ for $p < 0.1$ and ‘n.s.’ for $p \geq 0.1$.



shade-casting ability negatively affected total and generalist plant diversity. Litter quality exhibited a positive relationship with the number of generalists, while a higher tree cover was positively related to the number of specialists. We also found a negative effect of the second PCA axis of soil variables on specialist diversity, which could be mainly related to the increasing levels of soil P and K along this axis. Finally, increasing maximum summer temperature offsets showed a positive relationship with total and generalist richness, while the effect on specialist richness was marginally negative. (Table 1; Figure 4).

In grasslands and road verges, we found a negative effect of the proportion of grassland in a 500-m radius on the number of generalists. The first PCA axis of soil variables exhibited a negative effect on the total and specialist species richness. This effect was primarily driven by the decreasing basic cation contents along this axis. The second PCA axis of soil variables, on the other hand, showed

a positive effect on the generalist species richness. This effect was strongly defined by increasing levels of soil P along this axis. Finally, we also detected a negative relationship between maximum winter temperature offsets and generalist diversity (Table 2; Figure S9).

4 | DISCUSSION

Using an extensive dataset of 336 vegetation plots, we show that hedgerows and road verges serve as a habitat for plant species, including habitat specialists, and that plant diversity in these linear habitats responds to a variety of drivers acting across multiple geographical scales. Importantly, our results highlight the key role of local habitat features (e.g. soil properties, canopy structure and subcanopy microclimate) in shaping plant diversity patterns of linear landscape elements. Land managers can thus modify these

FIGURE 4 Relationship between the total understorey plant species richness in forests (*full circles*) and hedgerows (*open circles*), on the one hand, and mean annual temperature (MAT) (A), proportion of forest in 500-m radius (F500) (B), shade-casting ability (C) and maximum summer temperature (TMAX_S) offset (D), on the other hand. Relationship between generalist understorey plant species richness in forests (*full circles*) and hedgerows (*open circles*), on the one hand, and nitrogen deposition (Ndep) (E), tree height (F), litter quality (G), shade-casting ability (H) and maximum summer temperature (TMAX_S) offset (I), on the other hand. Relationship between specialist understorey species richness in forests (*full circles*) and hedgerows (*open circles*), on the one hand, and nitrogen deposition (Ndep) (J), mean annual temperature (MAT) (K), proportion of forest in 500-m radius (F500) (L), total tree cover (M), tree height (N) and second principal component axis (PCA2) of soil variables (O), on the other hand. Fitted regression lines are from generalized linear mixed-effect models with Poisson distribution ($Species\ richness \sim Predictor + Habitat + Predictor \times Habitat$). If the interaction term was significant in the models, two regression lines were plotted, that is one for forests (*dark-coloured regression line*) and one for hedgerows (*light-coloured regression line*)

TABLE 2 Univariate statistical relationships between the total, generalist and specialist plant species richness in grasslands and road verges, on the one hand, and the environmental variables, on the other hand. Values and symbols are chi-square values and significances, respectively, from a likelihood ratio test of generalized linear mixed-effect models with Poisson distribution (*Species richness* ~ *Predictor* + *Habitat* + *Predictor* × *Habitat*). The direction of the effect is given as ‘↑’ for a positive effect of the predictor or a higher species richness in road verges than in grasslands, and ‘↓’ for a negative effect of the predictor or a lower species richness in road verges than in grasslands

	Total richness			Generalist richness			Specialist richness		
	Predictor	Habitat	Predictor × Habitat	Predictor	Habitat	Predictor × Habitat	Predictor	Habitat	Predictor × Habitat
Nitrogen deposition	n.s.	↑3.6.	n.s.	↓3.0.	↑6.6*	n.s.	n.s.	n.s.	n.s.
Mean annual temperature	n.s.	↑3.6.	3.0.	↓3.4.	↑6.6*	n.s.	n.s.	n.s.	n.s.
Mean annual precipitation	n.s.	↑3.5.	9.3**	n.s.	↑6.4*	6.6*	n.s.	n.s.	3.2.
Proportion of grassland in 500-m radius	n.s.	↑3.6.	2.9.	↓4.3*	↑6.6*	3.3.	n.s.	n.s.	n.s.
First PCA axis of soil variables	↓4.9*	↑3.6.	n.s.	n.s.	↑6.6*	n.s.	↓4.3*	n.s.	n.s.
Second PCA axis of soil variables	n.s.	↑4.1*	5.0*	↑4.3*	↑7.5**	5.9*	n.s.	n.s.	n.s.
Minimum summer temperature offset	n.s.	↑3.6.	5.0*	n.s.	↑6.5*	4.3*	n.s.	n.s.	n.s.
Maximum summer temperature offset	n.s.	↑3.6.	n.s.	n.s.	↑6.6*	n.s.	↓3.5.	n.s.	n.s.
Minimum winter temperature offset	n.s.	↑3.6.	n.s.	n.s.	↑6.6*	3.0.	↑3.6.	n.s.	n.s.
Maximum winter temperature offset	n.s.	↑3.6.	4.1*	↓4.2*	↑6.4*	4.7*	n.s.	n.s.	n.s.

Significances are indicated as ‘****’ for $p < 0.001$, ‘***’ for $p < 0.01$, ‘**’ for $p < 0.05$, ‘.’ for $p < 0.1$ and ‘n.s.’ for $p \geq 0.1$.

local-scale features as a tool to improve the habitat quality and potential establishment success of plant species in linear habitats thereby contributing to the conservation of biodiversity of agroecosystems in a changing world.

4.1 | Linear landscape elements as habitat for plant species in agricultural landscapes across Europe

The hedgerows harboured 55% of all herbaceous species observed in adjacent forest patches. Moreover, 73% of the forest specialists was shared between both habitat types. This proportion is highly comparable to the findings of Corbit et al. (1999) from the United States as well as Wehling and Diekmann (2009) from north-western Germany, where 70% and 77%, respectively, of the regional forest species pool was found in hedgerows. Given the long-term connectivity between the surveyed hedgerows and forests, we expect that many of the forest-specialist species found in hedgerows likely colonized from source populations in the adjacent forests. This in turn suggests that hedgerows may serve as potential movement conduits for typical forest herbs between isolated forest fragments. However, we observed a consistently lower number of forest specialists in hedgerows than in adjacent forests. This pattern is in accordance with our expectations and confirms a wide

range of preceding studies conducted in agricultural regions across Europe (e.g. Paal et al., 2017; Wehling & Diekmann, 2009). Forest specialists are typically characterized by a slow demography and short-range dispersal (De Frenne et al., 2011), limiting their ability to readily colonize newly established forest-like habitats such as secondary woodlands (Brunet & Von Oheimb, 1998) and wooded corridors (Paal et al., 2017). Moreover, due to their recruitment limitation (Verheyen, Honnay, Motzkin, Hermy, & Foster, 2003), the establishment and survival of many shade-tolerant forest specialists may be inhibited in hedgerows owing to the poor habitat quality (e.g. more pronounced temperature extremes, stronger winds and increased inflow of agro-nutrients via drift from adjacent arable land; Aude et al., 2004). Likewise, our results indicated that the shift in floristic composition along the forest-hedgerow transects mainly resulted from a turnover of species, in particular from a higher abundance of specialists in the forest plots (average cover of 65.4% per plot) towards and increasing dominance of generalists in the hedgerow plots (average cover of 73.8%). This compositional difference between both habitat types confirms the observed patterns of α -diversity along our forest-hedgerow transects. Besides, the remarkably high species turnover and low nestedness could also result from the dispersal and/or recruitment limitation of forest herbs in wooded corridors (see Soininen, Heino, & Wang, 2017). Alternatively, the relatively small plot size could partly explain the

high turnover relative to nestedness in our study, because of missed species that were actually present just outside the plots.

Similar to hedgerows and forests, we found a consistently higher diversity of generalists in road verges compared to adjacent grasslands. Surprisingly, the number of grassland specialists did not significantly differ between both habitat types. These findings are corroborated by several observational studies (e.g. Cousins, 2006), indicating that linear grassland habitats such as road verges may harbour a considerable proportion of the grassland species pool. In particular, many grassland generalists are favoured by the edaphic conditions of road verges (e.g. drier soil conditions, increased soil nutrient availability and higher inflow of salts and pollutants; Cousins, 2006), and may benefit from the heterogeneity in management intensity and degree of disturbances (Jakobsson, Bernes, Bullock, Verheyen, & Lindborg, 2018). Semi-natural grasslands across the globe have suffered from the detrimental effects of habitat loss and degradation (Auffret, Kimberley, Plue, & Waldén, 2018), following the broad-scale abandonment or conversion of traditional, low-intensity management to specialized, intensive agriculture. In this respect, our findings highlight the key role of road verge networks in preserving and enhancing the diversity of typical semi-natural grassland species in otherwise degraded landscapes.

4.2 | Drivers of plant diversity in linear landscape elements across multiple spatial scales

To our knowledge, this is the first study to assess such a wide range of drivers of plant diversity in linear landscape elements (hedgerows and road verges) and their respective core habitats (forests and semi-natural grasslands) across multiple spatial scales. In line with our expectations, the number of generalists and specialists decreased with higher values of N deposition in our forest-hedgerow sites. N deposition has often been associated with a shift in understorey plant community composition and a decline in species diversity, largely through competitive exclusion as well as changes in soil properties (e.g. soil acidification; Dirnböck et al., 2014; but see Verheyen et al., 2012). In addition, we observed a decrease in species richness, particularly specialists, with rising ambient air temperatures. While macroclimate is widely considered as one of the main large-scale abiotic drivers of species diversity (McGill, 2010), other studies (Valdés et al., 2015) have highlighted that local habitat features may overrule the effect of macroclimate in explaining understorey plant diversity. Besides, macroclimatic changes across the temperate zone of Europe correlate strongly with N deposition. In this regard, a straightforward interpretation of the observed temperature effect remains difficult. Alternatively, echoing Wasof et al. (2013), we expect that climatic-niche divergence of many forest herbs is promoted in more extreme (e.g. colder) environments due to competitive release, which could in turn support species coexistence and, in the longer run, lead to a higher species richness. Even so, we found no differential effect of N deposition and macroclimate temperatures on plant diversity in our hedgerow versus forest sites. This

implies that hedgerow habitats in colder regions or areas with less atmospheric N inputs are not necessarily more similar to forests in terms of their species composition. In other words, the large-scale drivers investigated here appear to affect the regional herbaceous species pool, but will likely not influence the habitat quality and thus the colonization success of forest herb species in the linear features.

In addition to these large-scale drivers, the surrounding landscape (characterized by the proportion of forest around each site) strongly influenced the number of species, particularly specialists, in our forest-hedgerow systems. Indeed, a range of studies has acknowledged the presence of nearby forest habitats as a key driver of forest species richness in wooded corridors (Roy & de Blois, 2008; Van Den Berge et al., 2018). Nearby forests, in particular historically continuous forests, serve as a pool of dispersal propagules for wooded corridors, which could be all the more important for forest-specialist plants due to their limited colonization capacity and the absence of a persistent seed bank (De Frenne et al., 2011).

Finally, as anticipated, several local-scale habitat features exhibited a significant effect on species diversity patterns in hedgerows. For instance, our study revealed that the buffering effect of canopy cover on subcanopy temperatures negatively affected the diversity of generalists, whereas the effect on specialist richness was, albeit marginally significant, positive. This is one of our most striking results given that subcanopy temperature buffering as a driver of plant diversity in wooded corridors has not been tested so far. Overall, the magnitude of temperature buffering declined from the forest interior into the hedgerow along the sampled transects (Vanneste et al., 2020), causing plant communities to shift towards a higher abundance of light-demanding, warm-adapted species (conform the results of Bergès, Pellissier, Avon, Verheyen, & Dupouey, 2013).

Furthermore, we found a significant positive effect of total tree cover as well as marginally significant negative effect of shrub cover on forest-specialist diversity. These observations can be mainly attributed to the influence of light availability on the colonization dynamics of forest herbs (Paal et al., 2017; Wehling & Diekmann, 2009). Denser tree canopies diminish light penetration to the forest floor thereby creating a favourable environment for shade-tolerant forest specialists, whereas a denser shrub layer hampers the establishment of forest herbs through competition for light and rooting space. Interestingly, tree height had a contrasting effect on the diversity of forest specialists and generalists in our study sites. Tree height is a potential indicator for tree age (i.e. long-term continuity of shade) and structural maturation of the canopy, and will therefore also influence light transmittance to the understorey. In this regard, we expect that shade-tolerant specialists are favoured by the decreasing light availability under taller tree canopies, whereas the survival chances of light-demanding generalists are substantially reduced. The latter is also reflected by the respectively negative and positive effects of shade-casting ability and litter quality on generalist diversity. Germination and/or establishment of these light-demanding generalists is indeed hampered on sites where low-quality (and thus slow decomposing) litter has accumulated (Verheyen et al., 2012).

Forest-specialist richness was also favoured by a lower soil P availability in our study sites. At high soil P levels, these stress-tolerant specialists are more likely to be gradually outcompeted by fast-growing ruderal species (Litza & Diekmann, 2019). Hedgerow soils are often enriched in nutrients due to fertilizer misplacement or run off from adjacent fields. As a result, we expect that the habitat suitability and colonization success of forest specialists in hedgerows are improved when these corridors are bordered by less intensive land use (e.g. extensive grassland).

For the grasslands and road verges, the studied environmental variables showed only a limited number of significant effects on species diversity. We suspect that other factors, which are not accounted for in this study (e.g. differences in land-use history, management intensity or disturbance regimes, variable age of the road verges or differences in the applied sowing mixtures), play a more dominant role in structuring these grassland and roadside plant communities (Jakobsson et al., 2018). However, we observed a negative effect of the surrounding grassland cover on the number of generalists in our grassland-road verge sites, whereas the number of specialist was not affected. In other words, the relative contribution of generalists to the total species richness decreased in sites surrounded by a higher proportion of core habitat. This is somewhat unexpected given that generalist diversity usually increases with increasing source populations in the surrounding landscape matrix (Cousins, 2006).

Furthermore, we detected significant contributions of several soil properties to plant diversity in grasslands and road verges, with consistent positive effects of basic cation and extractable soil P levels on the specialists (as well as total) and generalist species richness respectively. The former is in agreement with Stevens, Thompson, Grime, Long, and Gowing (2010), indicating that higher levels of basic cations are associated with reduced soil acidification and therefore support higher species richness. The latter contradicts the overall assumption that soil P adversely affects plant diversity in grasslands (Ceulemans et al., 2014). Yet, our sampling was restricted to species-rich hay meadows, which are generally associated with low soil P availability (Gilbert, Gowing, & Wallace, 2009). Indeed, the median soil P content in our grasslands was only 20 mg P kg⁻¹ and 75% of all sampled patches showed a value below 50 mg P kg⁻¹. In these lower ranges of soil P, moderate increases in plant diversity with increasing soil P levels can still be expected. To illustrate, Janssens et al. (1998) reported that grassland diversity across Europe showed a humped-back curve with extractable soil P, and defined 50 mg P kg⁻¹ as a critical threshold for soil P above which the number of plant species, especially rare species, drastically decreased.

4.3 | Implications for management and biodiversity conservation

Our results underpin that linear landscape elements such as hedgerows and road verges may serve as a valuable secondary habitat or even a potential dispersal route for species associated with

semi-natural habitats, not only at regional scales but also at a continental extent. New policies aiming to preserve and (re-)establish these linear structures at larger scales are thus timely, given their potential to promote biodiversity in fragmented landscapes (Dainese et al., 2017) as well as to facilitate species migration under climate change (McGuire et al., 2016).

We show that the creation of new linear landscape elements should be prioritized in areas where historically continuous seed-source habitats such as ancient forests and species-rich semi-natural grasslands are already present (see also Cousins, 2006; Paal et al., 2017). Furthermore, the colonization success of specialist species along existing linear landscape elements can be enhanced through the modification of local habitat features. For instance, management practices that lead to a taller and denser overstorey tree layer in hedgerows could significantly improve the diversity of forest specialists. Potential strategies are to abate the frequency of pruning or coppicing and to preserve old and mature trees. Alternatively, the planting of sufficiently broad hedgerows should be considered, allowing that different rows of trees can be coppiced or pollarded per harvesting cycle, which in the longer term could support the maintenance of a denser tree layer. Such interventions also have a direct impact on the subcanopy microclimate of hedgerows, leading to more effective buffering of temperature extremes and hence promoting forest specialists over generalists. Likewise, with appropriate management, road verges may significantly contribute to the conservation of grassland plant diversity in landscapes with a historical decline of semi-natural grassland habitats. In practice, this could be achieved through suitable mowing regimes (preferably twice per year with the removal of hay after cutting); regular removal of shade-casting woody vegetation; diminishing the inflow of salts, pollutants and nutrients; and promoting the natural establishment of vegetation on road verges (as opposed to the traditionally applied sowing mixtures with highly competitive grass species; see also Jakobsson et al., 2018; Phillips, Gaston, Bullock, & Osborne, 2019). Meanwhile, while hedgerows or grass buffer strips are sometimes established in hilly landscapes to filter nutrients from surface runoff (Van Vooren et al., 2017), our results indicate that accumulation of soil P in hedgerows and road verges could be counteracted to improve the establishment success of specialist plant species. To illustrate, this could be achieved via optimized and potentially reduced application of P fertilizers or manures directly next to the linear structures. Following these guidelines, linear landscape elements could effectively extend 'core habitat conditions' into the agricultural landscape matrix, potentially alleviating the adverse impacts of habitat fragmentation and climate change on migrating plant species (Roy & de Blois, 2008).

It is also noteworthy that management strategies related to the maintenance and restoration of linear habitats in agricultural landscapes generally come at a relatively low cost (Dainese et al., 2017), but have a remarkable long-term benefit for biodiversity conservation especially in areas with relatively few non-crop habitats. Moreover, these actions require relatively little land from

crop production, have minimal (or sometimes even positive) effects on crop yield and do not involve changes in crop management (Garibaldi et al., 2014). Finally, we would like to point out that our results should be interpreted with care, given that we specifically focused on ancient linear elements with long-term connectivity to a seed-source habitat. These corridors already have a long history of stable habitat conditions, and have likely accumulated a higher number of slow-colonizing habitat specialists over time (Paal et al., 2017). Recent linear structures, on the other hand, typically lack these habitat specialists but given time and proper management they can develop into valuable habitats with diverse plant communities (Litza & Diekmann, 2019). From this perspective, we argue that land managers should promote the conservation of existing species-rich linear structures and remnant seed-source habitats. The emergence of new linear landscape elements should then be prioritized in the proximity of these ancient linear structures or historically continuous core habitats, serving as potential source populations (see Lenoir et al., 2019). Together this complex of linear structures and remnant habitat patches could form a functional network that facilitates the migration of species across degraded landscapes and contributes to the long-term conservation of otherwise isolated populations in the face of global environmental change.

ACKNOWLEDGEMENTS

We are grateful to the Research Foundation—Flanders (FWO) for funding the scientific research network FLEUR. T.V. was funded by the Special Research Fund (BOF) from Ghent University (01N02817), S.G. by the FWO (G0H1517N), P.D.F., P.V.G. and C.M. by the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (ERC Starting Grant FORMICA 757833) and K.V. through ERC Consolidator Grant (PASTFORWARD 614839). We also thank Domien Vanneste, Robbe De Beelde, Kris Ceunen and Fabien Spicher for their assistance during the fieldwork, Emiel De Lombaerde for his help with the statistical analysis, and Luc Willems and Greet De Bruyn for performing the chemical analysis.

AUTHORS' CONTRIBUTIONS

T.V., P.D.F. and K.V. conceived and designed the study; T.V. and P.D.F. conducted the statistical analyses and wrote the first draft of the paper. All the authors were involved in the site selection and data collection, contributed to revisions and gave approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the figshare <https://doi.org/10.6084/m9.figshare.8104499> (Vanneste et al., 2019).

ORCID

Thomas Vanneste  <https://orcid.org/0000-0001-5296-917X>

Sanne Govaert  <https://orcid.org/0000-0002-8939-1305>

Sanne Van Den Berge  <https://orcid.org/0000-0001-6155-7097>

Pieter Vangansbeke  <https://orcid.org/0000-0002-6356-2858>

Camille Meeussen  <https://orcid.org/0000-0002-5869-4936>

Jörg Brunet  <https://orcid.org/0000-0003-2667-4575>

Guillaume Decocq  <https://orcid.org/0000-0001-9262-5873>

Per-Ola Hedwall  <https://orcid.org/0000-0002-0120-7420>

Kenny Helsen  <https://orcid.org/0000-0001-6856-7095>

Jonathan Lenoir  <https://orcid.org/0000-0003-0638-9582>

Jaan Liira  <https://orcid.org/0000-0001-8863-0098>

Kathrin Litza  <https://orcid.org/0000-0003-3568-2825>

Jan Plue  <https://orcid.org/0000-0002-6999-669X>

Kris Verheyen  <https://orcid.org/0000-0002-2067-9108>

Pieter De Frenne  <https://orcid.org/0000-0002-8613-0943>

REFERENCES

- Aude, E., Tybirk, K., Michelsen, A., Ejrnæs, R., Hald, A. B., & Mark, S. (2004). Conservation value of the herbaceous vegetation in hedgerows – Does organic farming make a difference? *Biological Conservation*, 118, 467–478. <https://doi.org/10.1016/j.biocon.2003.09.022>
- Auffret, A. G., Kimberley, A., Plue, J., & Waldén, E. (2018). Super-regional land-use change and effects on the grassland specialist flora. *Nature Communications*, 9, 3464. <https://doi.org/10.1038/s41467-018-05991-y>
- Baeten, L., Vangansbeke, P., Hermy, M., Peterken, G., Vanhuysse, K., & Verheyen, K. (2012). Distinguishing between turnover and nestedness in the quantification of biotic homogenization. *Biodiversity and Conservation*, 21, 1399–1409. <https://doi.org/10.1007/s10531-012-0251-0>
- Baselga, A. (2013). Separating the two components of abundance-based dissimilarity: Balanced changes in abundance vs. abundance gradients. *Methods in Ecology and Evolution*, 4, 552–557. <https://doi.org/10.1111/2041-210X.12029>
- Baselga, A., Orme, D., Villeger, S., De Bortoli, J., & Leprieux, F. (2018). betapart: Partitioning beta diversity into turnover and nestedness components. R package version 1.5.0. Retrieved from <https://CRAN.R-project.org/package=betapart>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.
- Baudry, J., Bunce, R. G. H., & Burel, F. (2000). Hedgerows: An international perspective on their origin, function and management. *Journal of Environmental Management*, 60, 7–22. <https://doi.org/10.1006/jema.2000.0358>
- Bergès, L., Pellissier, V., Avon, C., Verheyen, K., & Dupouey, J.-L. (2013). Unexpected long-range edge-to-forest interior environmental gradients. *Landscape Ecology*, 28, 439–453. <https://doi.org/10.1007/s10980-012-9841-1>
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution*, 24, 127–135. <https://doi.org/10.1016/j.tree.2008.10.008>
- Bonebrake, T. C., Brown, C. J., Bell, J. D., Blanchard, J. L., Chauvenet, A., Champion, C., ... Pecl, G. T. (2018). Managing consequences of climate-driven species redistribution requires integration of ecology, conservation and social science. *Biological Reviews*, 93, 284–305. <https://doi.org/10.1111/brv.12344>
- Bray, J. R., & Curtis, J. T. (1957). An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*, 27, 325–349. <https://doi.org/10.2307/1942268>
- Brunet, J., & Von Oheimb, G. (1998). 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>

- Ceulemans, T., Stevens, C. J., Duchateau, L., Jacquemyn, H., Gowing, D. J. G., Merckx, R., ... Honnay, O. (2014). Soil phosphorus constrains biodiversity across European grasslands. *Global Change Biology*, 20, 3814–3822. <https://doi.org/10.1111/gcb.12650>
- Clavel, J., Julliard, R., & Devictor, V. (2011). Worldwide decline of specialist species: Toward a global functional homogenization? *Frontiers in Ecology and the Environment*, 9, 222–228. <https://doi.org/10.1890/080216>
- Corbit, M., Marks, P., & Gardescu, S. (1999). Hedgerows as habitat corridors for forest herbs in central New York, USA. *Journal of Ecology*, 76, 119–121.
- Cousins, S. A. O. (2006). Plant species richness in midfield islets and road verges – The effect of landscape fragmentation. *Biological Conservation*, 127, 500–509. <https://doi.org/10.1016/j.biocon.2005.09.009>
- Dainese, M., Montecchiari, S., Sitzia, T., Sigura, M., Marini, L., & Kleijn, D. (2017). High cover of hedgerows in the landscape supports multiple ecosystem services in Mediterranean cereal fields. *Journal of Applied Ecology*, 54, 380–388. <https://doi.org/10.1111/1365-2664.12747>
- Davies, Z. G., & Pullin, A. S. (2007). Are hedgerows effective corridors between fragments of woodland habitat? An evidence-based approach. *Landscape Ecology*, 22, 333–351. <https://doi.org/10.1007/s10980-006-9064-4>
- De Frenne, P., Baeten, L., Graae, B. J., Brunet, J., Wulf, M., Orczewska, A., ... Verheyen, K. (2011). Interregional variation in the floristic recovery of post-agricultural forests. *Journal of Ecology*, 99, 600–609. <https://doi.org/10.1111/j.1365-2745.2010.01768.x>
- Di Marco, M., Ferrier, S., Harwood, T. D., Hoskins, A. J., & Watson, J. E. M. (2019). Wilderness areas halve the extinction risk of terrestrial biodiversity. *Nature*, 573, 582–585. <https://doi.org/10.1038/s41586-019-1567-7>
- Dirnböck, T., Grandin, U., Bernhardt-Römermann, M., Beudert, B., Canullo, R., Forsius, M., ... Uziębło, A. K. (2014). Forest floor vegetation response to nitrogen deposition in Europe. *Global Change Biology*, 20, 429–440. <https://doi.org/10.1111/gcb.12440>
- Ellenberg, H., Weber, H. E., Düll, R., Wirth, V., Werner, W., & Paulissen, D. (1991). *Zeigerwerte von Pflanzen in Mitteleuropa*. Goltze, Göttingen: Scripta Geobotanica.
- Fick, S. E., & Hijmans, R. J. (2017). Worldclim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37(12), 4302–4315. <https://doi.org/10.1002/joc.5086>
- Garibaldi, L. A., Carvalheiro, L. G., Leonhardt, S. D., Aizen, M. A., Blaauw, B. R., Isaacs, R., ... Winfree, R. (2014). From research to action: Enhancing crop yield through wild pollinators. *Frontiers in Ecology and the Environment*, 12, 439–447. <https://doi.org/10.1890/130330>
- Gilbert, J., Gowing, D., & Wallace, H. (2009). Available soil phosphorus in semi-natural grasslands: Assessment methods and community tolerances. *Biological Conservation*, 142, 1074–1083. <https://doi.org/10.1016/j.biocon.2009.01.018>
- Guo, F., Lenoir, J., & Bonebrake, T. C. (2018). Land-use change interacts with climate to determine elevational species redistribution. *Nature Communications*, 9, 1315. <https://doi.org/10.1038/s41467-018-03786-9>
- Heinken, T. (2019). European forest vascular plant species list. *figshare*. <https://doi.org/10.6084/m9.figshare.8095217.v1>
- Henein, K., & Merriam, G. (1990). The elements of connectivity where corridor quality is variable. *Landscape Ecology*, 4, 157–170. <https://doi.org/10.1007/BF00132858>
- Hess, G. R. (1994). Conservation corridors and contagious disease: A cautionary note. *Conservation Biology*, 8, 256–262. <https://doi.org/10.1046/j.1523-1739.1994.08010256.x>
- Hodgson, J. A., Moilanen, A., Wintle, B. A., & Thomas, C. D. (2011). Habitat area, quality and connectivity: Striking the balance for efficient conservation. *Journal of Applied Ecology*, 48, 148–152. <https://doi.org/10.1111/j.1365-2664.2010.01919.x>
- Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, 50, 346–363. <https://doi.org/10.1002/bimj.200810425>
- Jakobsson, S., Bernes, C., Bullock, J. M., Verheyen, K., & Lindborg, R. (2018). How does roadside vegetation management affect the diversity of vascular plants and invertebrates? A systematic review. *Environmental Evidence*, 7, 17. <https://doi.org/10.1186/s13750-018-0129-z>
- Janssens, F., Peeters, A., Tallowin, J. R. B., Bakker, J. P., Bekker, R. M., Fillat, F., & Oomes, M. J. M. (1998). Relationship between soil chemical factors and grassland diversity. *Plant and Soil*, 202, 69–78.
- Lenoir, J., Decocq, G., Spicher, F., Gallet-Moron, E., Buridant, J., & Closset-Kopp, D. (2019). Historical continuity and spatial connectivity ensure hedgerows are effective corridors for forest plants: Evidence from the species-time-area relationship. *Journal of Vegetation Science*, 1–14. <https://doi.org/10.1111/jvs.12845>
- Leuschner, C., & Ellenberg, H. (2017). *Ecology of Central European non-forest vegetation: Coastal to alpine, natural to man-made habitats: Vegetation ecology of Central Europe (Vol. II)*. Cham, Switzerland: Springer International Publishing AG.
- Liira, J., & Paal, T. (2013). Do forest-dwelling plant species disperse along landscape corridors? *Plant Ecology*, 214, 455–470. <https://doi.org/10.1007/s11258-013-0182-1>
- Litza, K., & Diekmann, M. (2019). Hedgerow age affects the species richness of herbaceous forest plants. *Journal of Vegetation Science*, 30(3), 553–563. <https://doi.org/10.1111/jvs.12744>
- Matlack, G. R. (2005). Slow plants in a fast forest: Local dispersal as a predictor of species frequencies in a dynamic landscape. *Journal of Ecology*, 93, 50–59. <https://doi.org/10.1111/j.1365-2745.2004.00947.x>
- McGill, B. J. (2010). Matters of scale. *Science*, 328, 575. <https://doi.org/10.1126/science.1188528>
- McGuire, J. L., Lawler, J. J., McRae, B. H., Nuñez, T. A., & Theobald, D. M. (2016). Achieving climate connectivity in a fragmented landscape. *Proceedings of the National Academy of Sciences*, 113(26), 7195–7200. <https://doi.org/10.1073/pnas.1602817113>
- Mucina, L., Bültmann, H., Dierßen, K., Theurillat, J.-P., Raus, T., Čarni, A., ... Tichý, L. (2016). Vegetation of Europe: Hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. *Applied Vegetation Science*, 19, 3–264. <https://doi.org/10.1111/avsc.12257>
- Öckinger, E., & Smith, H. G. (2008). Do corridors promote dispersal in grassland butterflies and other insects? *Landscape Ecology*, 23, 27–40. <https://doi.org/10.1007/s10980-007-9167-6>
- Oksanen, J., Blanchet, G. F., Friendly, M., Kindt, R., Legendre, P., McGinn, D. J., ... Wagner, H. H. (2018). *vegan: Community ecology package*. R package version 2.4-6. Retrieved from <https://CRAN.R-project.org/package=vegan>
- Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., ... Kassem, K. R. (2001). Terrestrial ecoregions of the world: A new map of life on earth. *BioScience*, 51, 933–938. [https://doi.org/10.1641/0006-3568\(2001\)051\[0933:TEOTWA\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2)
- Paal, T., Kütt, L., Löhmus, K., & Liira, J. (2017). Both spatiotemporal connectivity and habitat quality limit the immigration of forest plants into wooded corridors. *Plant Ecology*, 218, 417–431. <https://doi.org/10.1007/s11258-017-0700-7>
- Phillips, B. B., Gaston, K. J., Bullock, J. M., & Osborne, J. L. (2019). Road verges support pollinators in agricultural landscapes, but are diminished by heavy traffic and summer cutting. *Journal of Applied Ecology*, 56, 2316–2327. <https://doi.org/10.1111/1365-2664.13470>
- QGIS Development Team. (2018). QGIS geographic information system. Open Source Geospatial Foundation Project. Retrieved from <http://qgis.osgeo.org>
- R Core Team. (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

- Roy, V., & de Blois, S. (2008). Evaluating hedgerow corridors for the conservation of native forest herb diversity. *Biological Conservation*, 141, 298–307. <https://doi.org/10.1016/j.biocon.2007.10.003>
- Soininen, J., Heino, J., & Wang, J. (2017). A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. *Global Ecology and Biogeography*, 27, 96–109. <https://doi.org/10.1111/geb.12660>
- Stevens, C. J., Thompson, K., Grime, J. P., Long, C. J., & Gowing, D. J. G. (2010). Contribution of acidification and eutrophication to declines in species richness of calcifuge grasslands along a gradient of atmospheric nitrogen deposition. *Functional Ecology*, 24, 478–484. <https://doi.org/10.1111/j.1365-2435.2009.01663.x>
- Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity – Ecosystem service management. *Ecology Letters*, 8, 857–874. <https://doi.org/10.1111/j.1461-0248.2005.00782.x>
- Valdés, A., Lenoir, J., Gallet-Moron, E., Andrieu, E., Brunet, J., Chabrierie, O., ... Decocq, G. (2015). The contribution of patch-scale conditions is greater than that of macroclimate in explaining local plant diversity in fragmented forests across Europe. *Global Ecology and Biogeography*, 24, 1094–1105. <https://doi.org/10.1111/geb.12345>
- Van Den Berge, S., Baeten, L., Vanhellemont, M., Ampoorter, E., Proesmans, W., Eeraerts, M., ... Verheyen, K. (2018). Species diversity, pollinator resource value and edibility potential of woody networks in the countryside in northern Belgium. *Agriculture, Ecosystems & Environment*, 259, 119–126. <https://doi.org/10.1016/j.agee.2018.03.008>
- Van Vooren, L., Reubens, B., Broekx, S., De Frenne, P., Nelissen, V., Pardon, P., & Verheyen, K. (2017). Ecosystem service delivery of agri-environment measures: A synthesis for hedgerows and grass strips on arable land. *Agriculture, Ecosystems & Environment*, 244, 32–51. <https://doi.org/10.1016/j.agee.2017.04.015>
- Vanneste, T., Govaert, S., De Kesel, W., Van Den Berge, S., Vangansbeke, P., Meeussen, C., ... De Frenne, P. (2019). Data for 'Multi-scale drivers of plant diversity in linear landscape elements across Europe – Implications for management'. *figshare*. <https://doi.org/10.6084/m9.figshare.8104499.v1>
- Vanneste, T., Govaert, S., Spicher, F., Brunet, J., Cousins, S. A. O., Decocq, G., ... De Frenne, P. (2020). Contrasting microclimates among hedgerows and woodlands across temperate Europe. *Agricultural and Forest Meteorology*, 281, 107818. <https://doi.org/10.1016/j.agrfor.2019.107818>
- Vanneste, T., Valdés, A., Verheyen, K., Perring, M. P., Bernhardt-Römermann, M., Andrieu, E., ... De Frenne, P. (2018). Functional trait variation of forest understorey plant communities across Europe. *Basic and Applied Ecology*, 34, 1–14. <https://doi.org/10.1016/j.baae.2018.09.004>
- Verheyen, K., Baeten, L., De Frenne, P., Bernhardt-Römermann, M., Brunet, J., Cornelis, J., ... Verstraeten, G. (2012). Driving factors behind the eutrophication signal in understorey plant communities of deciduous temperate forests. *Journal of Ecology*, 100, 352–365. <https://doi.org/10.1111/j.1365-2745.2011.01928.x>
- Verheyen, K., Honnay, O., Motzkin, G., Hermy, M., & Foster, D. R. (2003). Response of forest plant species to land-use change: A life-history trait-based approach. *Journal of Ecology*, 91, 563–577. <https://doi.org/10.1046/j.1365-2745.2003.00789.x>
- Wasof, S., Lenoir, J., Gallet-Moron, E., Jamoneau, A., Brunet, J., Cousins, S. A. O., ... Decocq, G. (2013). Ecological niche shifts of understorey plants along a latitudinal gradient of temperate forests in north-western Europe. *Global Ecology and Biogeography*, 22, 1130–1140. <https://doi.org/10.1111/geb.12073>
- Wehling, S., & 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>

SUPPORTING INFORMATION

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

How to cite this article: Vanneste T, Govaert S, De Kesel W, et al. Plant diversity in hedgerows and road verges across Europe. *J Appl Ecol*. 2020;00:1–14. <https://doi.org/10.1111/1365-2664.13620>