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1 **Plant diversity in hedgerows and road verges across Europe**

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26 **Abstract**

- 27 1. Linear landscape elements such as hedgerows and road verges have the potential to mitigate the adverse effects
28 of habitat fragmentation and climate change on species, for instance, by serving as a refuge habitat or by
29 improving functional connectivity across the landscape. However, so far this hypothesis has not been evaluated
30 at large spatial scales, preventing us from making generalized conclusions about their efficacy and
31 implementation in conservation policies.
- 32 2. Here, we assessed plant diversity patterns in 336 vegetation plots distributed along hedgerows and road verges,
33 spanning a macro-environmental gradient across temperate Europe. We compared herb-layer species richness
34 and composition in these linear elements with the respective seed-source (core) habitats, i.e. semi-natural
35 forests and grasslands. Next, we assessed how these differences related to several environmental drivers acting
36 either locally, at the landscape level or along the studied macro-ecological gradient.
- 37 3. Across all regions, about 55 % of the plant species were shared between forests and hedgerows, and 52 %
38 between grasslands and road verges. Habitat-specialist richness was 11 % lower in the linear habitats than in
39 the core habitats, while generalist richness was 14 % higher. The difference in floristic composition between
40 both habitat types was mainly due to species turnover, and not nestedness. Most notably, forest-specialist
41 richness in hedgerows responded positively to tree cover, tree height and the proportion of forests in the
42 surrounding landscape, while generalist richness was negatively affected by tree height and buffering effect of
43 trees on sub-canopy temperatures. Grassland and road verge diversity was mainly influenced by soil properties,
44 with positive effects of basic cation levels on the number of specialists and of bio-available soil phosphorus
45 on generalist diversity.
- 46 4. *Synthesis and applications.* We demonstrate that linear landscape elements provide a potential habitat for plant
47 species across Europe, including slow-colonizing specialists. Additionally, our results stress the possibility for
48 land managers to modify local habitat features (e.g. canopy structure, sub-canopy microclimate, soil properties,
49 mowing regime) through management practices to enhance the colonization success of specialists in these
50 linear habitats. These findings underpin the management needed to better conserve biodiversity of agricultural
51 landscapes across broad geographical scales.

52 **Keywords:** hedgerows; landscape connectivity; linear landscape elements; macro-environmental gradient;
53 microclimate; multi-scale analysis; plant colonization dynamics; road verges.

54 1. Introduction

55 Land-use changes and agricultural intensification have converted complex natural ecosystems across the globe into
56 a patchwork of habitat fragments embedded in a matrix of production systems (T'scharntke *et al.* 2005). This
57 fragmentation of habitats may hamper species migrations (Guo, Lenoir & Bonebrake 2018), which could lead to a
58 dramatic increase in local extinction risk given that numerous species are currently changing their distribution range
59 towards higher latitudes or elevations in pursuit of the shifting climatic envelopes (Matlack 2005; Di Marco *et al.*
60 2019). Habitat specialist species are particularly sensitive to these global changes (Clavel, Julliard & Devictor 2011),
61 and safeguarding their persistence in a changing world constitutes a major challenge for nature conservationists in
62 the coming decades.

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

72 A variety of local-scale studies (e.g. Cousins 2006; Wehling & Diekmann 2009) have shown that hedgerows and
73 road verges are effective secondary habitats for species of conservation concern, and can even serve as dispersal
74 corridors between isolated habitat fragments. For instance, in north-western Germany, Wehling and Diekmann
75 (2009) showed that 77 % of all forest plant species occurring in forests were also found in adjacent hedgerows,
76 albeit with a higher representation of forest-dwelling generalists in the hedges. Likewise, Cousins (2006) reported
77 that small remnant habitats such as road verges may provide a refuge habitat for species restricted to semi-natural
78 grasslands in central Sweden, and thus contribute to the conservation of biodiversity in rural landscapes.

79 Yet, the utility of hedgerows and road verges as a conservation tool is still widely debated. While some studies
80 found no effect of these linear elements on the dispersal probabilities of certain species groups (e.g. butterflies;
81 Öckinger & Smith 2008), others even advocated that they may be detrimental to biodiversity (Davies & Pullin

82 2007), for instance, by acting as population sinks (Henein & Merriam 1990) or by spreading diseases and pathogens
83 (Hess 1994). Moreover, research has shown that the effectiveness of linear elements as habitat or migration
84 corridors for plant species varies depending on a wide range of environmental factors acting across different spatial
85 and temporal scales (Cousins 2006; Paal *et al.* 2017). For example, forest species richness in wooded corridors has
86 been linked to structural canopy characteristics (Wehling & Diekmann 2009), sub-canopy microclimate (Roy & de
87 Blois 2008), long-term connectivity to forest (Paal *et al.* 2017) and adjacent forest cover (Van Den Berge *et al.* 2018).
88 However, so far, studies investigating the drivers of plant distribution patterns in linear landscape elements are
89 almost exclusively restricted to local or regional studies (e.g. Corbit, Marks & Gardescu 1999; Cousins 2006; Liira
90 & Paal 2013; Litza & Diekmann 2019). At larger scales, it is still unclear which species will disperse, germinate,
91 establish their populations, and successively migrate through these linear structures, and how diversity patterns in
92 these habitats are shaped by multi-scale environmental factors. Consequently, an overall evaluation of linear
93 landscape elements in supporting and preserving diverse plant communities in agricultural regions is still lacking.

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

102 Specifically, we sought to test the following hypotheses:

103 (a) Herb-layer plant diversity and composition differs between the linear landscape elements (hedgerows and road
104 verges) and respective seed-source habitats (forests and semi-natural grasslands). In line with the preceding local-
105 scale studies, we expect a lower proportion of habitat specialists and higher proportion of generalists in the linear
106 elements.

107 (b) Potential differences in species diversity and composition between both habitat types are driven by a range of
108 environmental factors, acting across multiple spatial scales. At the continental level, we expect that increased N
109 deposition and higher ambient temperatures negatively affect plant diversity in linear habitats, particularly by

110 inducing competitive exclusion of stress-tolerant habitat specialists by generalists. At the landscape level, we
111 hypothesize that a larger amount of surrounding seed-source habitats contributes to a higher overall species
112 richness (both specialists and generalists) in the linear structures. At the local scale, we expected to find a strong
113 relationship between habitat quality (related to edaphic properties, canopy structure and microclimatic buffering)
114 and species diversity of the linear elements, particularly the balance between specialists and generalists.

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

122 **2. Materials and methods**

123 **2.1 Study area and site selection**

124 This study was conducted in agricultural landscapes of nine different regions spanning a continental-scale
125 environmental gradient in climatic conditions (temperature and precipitation) as well as atmospheric N deposition
126 across the European temperate biome (Olson *et al.* 2001) (**Fig. 1a**). The mean annual temperature (MAT) between
127 1970-2000 ranged from 5.5 (Central Norway) to 10.3 °C (Belgium), mean annual precipitation (MAP) from 583
128 mm (Central Sweden) to 1057 mm (Central Norway) and N deposition in 2000 from 1.6 (Central Norway) to 23.8
129 kg N ha⁻¹ year⁻¹ (Belgium).

130 Within each region, four wooded habitat and or/four grassland sites were selected, according to a predefined set
131 of criteria (see **SI Materials and Methods; Table S1**). Each site was composed of a linear element (hedgerow or
132 graminoid-dominated road verge) and a corresponding core habitat (forest and semi-natural grassland,
133 respectively). Each selected hedgerow was connected to an ancient forest (i.e. always forest and no land-cover
134 change according to the oldest available sources), whereof the canopy was mainly composed of broadleaf species.
135 The selected road verges were connected to a species-rich, semi-natural grassland of the class *Molinio-Arrhenatheretea*
136 (Mucina *et al.* 2016).

137 2.2 Floristic surveys

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

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

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

159 2.3 Explanatory variables

160 2.3.1 Nitrogen deposition and climate data

161 Standardized N deposition data were obtained from the European Monitoring and Evaluation Program (EMEP)
162 (<http://www.emep.int>), while macroclimatic conditions were extracted from WorldClim 2.0
163 (<http://worldclim.org/version2>). We focused on MAT and MAP, which are generally considered as standard

164 variables for describing global patterns of species diversity (Fick & Hijmans 2017) (see **SI Materials and Methods**
165 for more details on the calculation of these variables; **Table S3–S4**).

166 *2.3.2 Habitat amount at landscape level*

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

172 *2.3.3 Canopy structure and composition*

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

178 *2.3.4 Soil properties*

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

187 *2.3.5 Microclimate*

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

191 (macroclimate) temperature data were obtained for each study site from nearby weather stations (using the sources
192 listed in **Table S6**). For each station, we extracted the daily mean, minimum and maximum statistics for the same
193 period as the in situ recordings. The magnitude of the temperature offset for daily mean, maximum and minimum
194 temperature values was then calculated as microclimate temperatures minus macroclimate temperatures. We mainly
195 focussed on the effect of minimum and maximum temperature offsets during summer (June, July and August) and
196 winter (December, January and February) (see **SI Materials and Methods; Table S3–S4**).

197 **2.4 Data analysis**

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

206 To quantify the dissimilarity in species composition (i.e. β diversity) within each site, we constructed distance
207 matrices using the abundance-based Bray-Curtis dissimilarity index (Bray & Curtis 1957). Next, we calculated the
208 compositional differentiation of each plot by averaging the pairwise dissimilarities against all other plots of that
209 particular site (i.e. plot-level dissimilarity; sensu Baeten *et al.* 2012). Differences in plot-level dissimilarity within
210 each site were then analysed with linear mixed-effect models (LMM) using the ‘lmer’ function. These models
211 contained ‘plot-level dissimilarity’ as response variable, ‘plot’ as fixed effect, and ‘region’ and ‘site’ (nested within
212 ‘region’) as random intercept terms. A Tukey’s post-hoc test was applied for pairwise comparisons using the ‘glht’
213 function of the ‘multcomp’ package (Hothorn, Bretz & Westfall 2008). The average site-level dissimilarity was
214 calculated as the mean of the six plot-level dissimilarities. Following Baselga (2013), we subsequently decomposed
215 the Bray-Curtis dissimilarity into its turnover (balanced variation in species abundances) and nestedness
216 (abundance gradient) components. All β diversity measures were computed using the ‘beta.pair.abund’ function of
217 the ‘betapart’ package (Baselga *et al.* 2018). In addition, nonmetric multidimensional scaling (NMDS) was adopted

218 to visualize differences in herb-layer species composition between core habitats and linear elements with the
219 ‘metaMDS’ function of the ‘vegan’ package (Oksanen *et al.* 2018) (**Fig. S4**).

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

226 **Results**

227 **3.1 Species richness**

228 In the understorey layer of the hedgerows, we recorded 224 vascular plant species across all surveyed sites with an
229 average of 16.6 (± 6.7 *SE*) species per plot, including 131 generalists and 61 forest specialists. In the forest
230 understorey, we found 195 species with an average of 14.0 (± 6.6 *SE*) species per plot, including 98 generalists and
231 72 forest specialists (**Table S8**). About 54.6 % of the total species pool occurring in forests was also found in
232 hedgerows, but the percentage of shared species among forest and hedgerow plots of the same site (i.e. paired
233 combinations of both habitat types) was, on average, only 4.8 % (**Table S9–S10**). Furthermore, we recorded a
234 significantly higher total number of species in the hedgerows than in the adjacent forests ($\chi^2 = 19.4$, $P < 0.001$).
235 The number of generalists was significantly higher in the hedgerow than in the forest ($\chi^2 = 64.1$, $P < 0.001$), while
236 the number of forest specialists was lower ($\chi^2 = 17.1$, $P < 0.001$) (**Fig. 2; Fig. S7**).

237 In the road verges, we found 152 species with an average of 11.8 (± 3.6 *SE*) species per plot, including 47 grassland
238 specialists and 104 generalists. In the semi-natural grasslands, 143 species were recorded, with an average of 10.9
239 (± 4.2 *SE*) species per plot, including 47 grassland specialists and 96 generalists (**Table S11**). About 51.5 % of all
240 species occurring in grasslands was also recorded in road verges, but the paired combinations of both habitat types
241 shared, on average, only 9.79 % of their species (**Table S12–S13**). Besides, we detected a marginally significant
242 difference in total species richness between the road verges and the grasslands ($\chi^2 = 2.79$, $P = 0.094$). The number
243 of generalists was higher in the road verges than in the grasslands ($\chi^2 = 13.3$, $P = 0.0003$), while the number of
244 specialists did not differ between both habitat types ($\chi^2 = 1.93$, $P = 0.165$) (**Fig. 2; Fig. S8**).

245 3.2 Community composition

246 Across all regions, the average site-level Bray-Curtis dissimilarity (total β diversity) along the forest-hedgerow
247 transects was 0.573 (± 0.071 SE), whereas the turnover and nestedness components of dissimilarity were 0.482
248 (± 0.096 SE) and 0.091 (± 0.054 SE), respectively. For generalists, the total β diversity was 0.596 (± 0.087 SE), and
249 the turnover and nestedness components of dissimilarity were 0.443 (± 0.134 SE) and 0.132 (± 0.092 SE),
250 respectively. For specialists, the total β diversity was 0.580 (± 0.186 SE), and the turnover and nestedness
251 components of dissimilarity were 0.392 (± 0.138 SE) and 0.168 (± 0.085 SE), respectively. The plot-level
252 compositional differentiation of generalists was highest in the forest interior, while the dissimilarity of specialists
253 was lowest at 10 m in the forests (**Fig. 3**).

254 In the grassland-road verge transects, the total β diversity amounted to 0.568 (± 0.064 SE), whereas the turnover
255 and nestedness components of dissimilarity were 0.529 (± 0.071 SE) and 0.039 (± 0.021 SE), respectively. For
256 generalists, the total β diversity was 0.671 (± 0.069 SE), and the turnover and nestedness components of
257 dissimilarity were 0.580 (± 0.110 SE) and 0.085 (± 0.052 SE), respectively. For specialists, the total β diversity was
258 0.544 (± 0.077 SE), and the turnover and nestedness components of dissimilarity were 0.444 (± 0.096 SE) and 0.096
259 (± 0.065 SE), respectively. The floristic dissimilarity of generalists was significantly higher in the outer plot of the
260 road verges, while for specialists no differences in plot-level compositional differentiation were found (**Fig. 3**).

261 3.3 Effect of environmental variables

262 In forests and hedgerows, N deposition and MAT tended to decrease the diversity of all species groups (albeit only
263 marginally significant in some cases), but their effect did not interact with habitat type. The proportion of forest
264 in a 500-m radius increased total and specialist plant diversity, while the effect on generalist richness interacted
265 with habitat type. Regarding the canopy structure, three height was one of the most influential factors, with a
266 strong negative effect on generalist richness and a highly positive effect on specialist richness. Furthermore,
267 increasing shade-casting ability negatively affected total and generalist plant diversity. Litter quality exhibited a
268 positive relationship with the number of generalists, while a higher tree cover was positively related to the number
269 of specialists. We also found a negative effect of the second PCA axis of soil variables on specialist diversity, which
270 could be mainly related to the increasing levels of soil P and K along this axis. Finally, increasing maximum summer
271 temperature offsets showed a positive relationship with total and generalist richness, while the effect on specialist
272 richness was marginally negative. (**Table 1; Fig. 4**).

273 In grasslands and road verges, we found a negative effect of the proportion of grassland in a 500-m radius on the
274 number of generalists. The first PCA axis of soil variables exhibited a negative effect on the total and specialist
275 species richness. This effect was primarily driven by the decreasing basic cation contents along this axis. The second
276 PCA axis of soil variables, on the other hand, showed a positive effect on the generalist species richness. This
277 effect was strongly defined by increasing levels of soil P along this axis. Finally, we also detected a negative
278 relationship between maximum winter temperature offsets and generalist diversity (**Table 2; Fig. S9**).

279 **Discussion**

280 Using an extensive dataset of 336 vegetation plots, we show that hedgerows and road verges serve as a habitat for
281 plant species, including habitat specialists, and that plant diversity in these linear habitats responds to a variety of
282 drivers acting across multiple geographical scales. Importantly, our results highlight the key role of local habitat
283 features (e.g. soil properties, canopy structure and sub-canopy microclimate) in shaping plant diversity patterns of
284 linear landscape elements. Land managers can thus modify these local-scale features as a tool to improve the habitat
285 quality and potential establishment success of plant species in linear habitats thereby contributing to the
286 conservation of biodiversity of agroecosystems in a changing world.

287 **4.1 Linear landscape elements as habitat for plant species in agricultural landscapes across** 288 **Europe**

289 The hedgerows harboured 55 % of all herbaceous species observed in adjacent forest patches. Moreover, 73 % of
290 the forest specialists was shared between both habitat types. This proportion is highly comparable to the findings
291 of Corbit, Marks and Gardescu (1999) from the USA as well as Wehling and Diekmann (2009) from north-western
292 Germany, where respectively 70 % and 77 % of the regional forest species pool was found in hedgerows. Given
293 the long-term connectivity between the surveyed hedgerows and forests, we expect that many of the forest
294 specialist species found in hedgerows likely colonized from source populations in the adjacent forests. This in turn
295 suggests that hedgerows may serve as potential movement conduits for typical forest herbs between isolated forest
296 fragments. Even so, we observed a consistently lower number of forest specialists in hedgerows than in adjacent
297 forests. This pattern is in accordance with our expectations and confirms a wide range of preceding studies
298 conducted in agricultural regions across Europe (e.g. Wehling & Diekmann 2009; Paal et al. 2017). Forest specialists
299 are typically characterized by a slow demography and short-range dispersal (De Frenne et al. 2011), limiting their
300 ability to readily colonize newly established forest-like habitats such as secondary woodlands (Brunet & Von

301 Oheimb 1998) and wooded corridors (Paal et al. 2017). Moreover, due to their recruitment limitation (Verheyen
302 et al. 2003), the establishment and survival of many shade-tolerant forest specialists may be inhibited in hedgerows
303 owing to the poor habitat quality (e.g. more pronounced temperature extremes, stronger winds and increased
304 inflow of agro-nutrients via drift from adjacent arable land; Aude et al. 2004). Likewise, our results indicated that
305 the shift in floristic composition along the forest-hedgerow transects mainly resulted from a turnover of species,
306 in particular from a higher abundance of specialists in the forest plots (average cover of 65.4 % per plot) towards
307 and increasing dominance of generalists in the hedgerow plots (average cover of 73.8 %). This compositional
308 difference between both habitat types confirms the observed patterns of α diversity along our forest-hedgerow
309 transects. Besides, the remarkably high species turnover and low nestedness could also result from the dispersal
310 and/or recruitment limitation of forest herbs in wooded corridors (see Soininen, Heino & Wang 2017).
311 Alternatively, the relatively small plot size could partly explain the high turnover relative to nestedness in our study,
312 because of missed species that were actually present just outside the plots.

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

325 **4.2 Drivers of plant diversity in linear landscape elements across multiple spatial scales**

326 To our knowledge, this is the first study to assess such a wide range of drivers of plant diversity in linear landscape
327 elements (hedgerows and road verges) and their respective core habitats (forests and semi-natural grasslands)
328 across multiple spatial scales. In line with our expectations, the number of generalists and specialists decreased

329 with higher values of N deposition in our forest-hedgerow sites. N deposition has often been associated with a
330 shift in understorey plant community composition and a decline in species diversity, largely through competitive
331 exclusion as well as changes in soil properties (e.g. soil acidification) (Dirnböck *et al.* 2014; but see Verheyen *et al.*
332 2012). In addition, we observed a decrease in species richness, particularly specialists, with rising ambient air
333 temperatures. While macroclimate is widely considered as one of the main large-scale abiotic drivers of species
334 diversity (McGill 2010), other studies (Valdés *et al.* 2015) have highlighted that local habitat features may overrule
335 the effect of macroclimate in explaining understorey plant diversity. Besides, macroclimatic changes across the
336 temperate zone of Europe correlate strongly to N deposition. In this regard, a straightforward interpretation of
337 the observed temperature effect remains difficult. Alternatively, echoing Wasof *et al.* (2013), we expect that
338 climatic-niche divergence of many forest herbs is promoted in more extreme (e.g. colder) environments due to
339 competitive release, which could in turn support species coexistence and, in the longer run, lead to a higher species
340 richness. Even so, we found no differential effect of N deposition and macroclimate temperatures on plant
341 diversity in our hedgerow vs. forest sites. This implies that hedgerow habitats in colder regions or areas with less
342 atmospheric N inputs are not necessarily more similar to forests in terms of their species composition. In other
343 words, the large-scale drivers investigated here appear to affect the regional herbaceous species pool, but will likely
344 not influence the habitat quality and thus the colonization success of forest herb species in the linear features.

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

352 Finally, as anticipated, several local-scale habitat features exhibited a significant effect on species diversity patterns
353 in hedgerows. For instance, our study revealed that the buffering effect of canopy cover on sub-canopy
354 temperatures negatively affected the diversity of generalists, whereas the effect on specialist richness was, albeit
355 marginally significant, positive. This is one of our most striking results given that sub-canopy temperature buffering
356 as a driver of plant diversity in wooded corridors has not been tested so far. Overall, the magnitude of temperature
357 buffering declined from the forest interior into the hedgerow along the sampled transects (Vanneste *et al.* 2020),

358 causing plant communities to shift towards a higher abundance of light-demanding, warm-adapted species
359 (conform the results of Bergès *et al.* 2013).

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

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

378 For the grasslands and road verges, the studied environmental variables showed only a limited number of
379 significant effects on species diversity. We suspect that other factors, which are not accounted for in this study
380 (e.g. differences in land-use history, management intensity or disturbance regimes, variable age of the road verges
381 or differences in the applied sowing mixtures), play a more dominant role in structuring these grassland and
382 roadside plant communities (Jakobsson *et al.* 2018). Even so, we observed a negative effect of the surrounding
383 grassland cover on the number of generalists in our grassland-road verge sites, whereas the number of specialist
384 was not affected. In other words, the relative contribution of generalists to the total species richness decreased in

385 sites surrounded by a higher proportion of core habitat. This is somewhat unexpected given that generalist diversity
386 usually increases with increasing source populations in the surrounding landscape matrix (Cousins 2006).

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

399 **4.3 Implications for management and biodiversity conservation**

400 Our results underpin that linear landscape elements such as hedgerows and road verges may serve as a valuable
401 secondary habitat or even a potential dispersal route for species associated with semi-natural habitats, not only at
402 regional scales but also at a continental extent. New policies aiming to preserve and (re-)establish these linear
403 structures at larger scales are thus timely, given their potential to promote biodiversity in fragmented landscapes
404 (Dainese *et al.* 2017) as well as to facilitate species migration under climate change (McGuire *et al.* 2016).

405 We show that the creation of new linear landscape elements should be prioritized in areas where historically
406 continuous seed-source habitats such as ancient forests and species-rich semi-natural grasslands are already present
407 (see also Cousins 2006; Paal *et al.* 2017). Furthermore, the colonization success of specialist species along existing
408 linear landscape elements can be enhanced through the modification of local habitat features. For instance,
409 management practices that lead to a taller and denser overstorey tree layer in hedgerows could significantly improve
410 the diversity of forest specialists. Potential strategies are to abate the frequency of pruning or coppicing and to
411 preserve old and mature trees. Alternatively, the planting of sufficiently broad hedgerows should be considered,
412 allowing that different rows of trees can be coppiced or pollarded per harvesting cycle, which in the longer term

413 could support the maintenance of a denser tree layer. Such interventions also have a direct impact on the sub-
414 canopy microclimate of hedgerows, leading to more effective buffering of temperature extremes and hence
415 promoting forest specialists over generalists. Likewise, with appropriate management, road verges may significantly
416 contribute to the conservation of grassland plant diversity in landscapes with a historical decline of semi-natural
417 grassland habitats. In practice, this could be achieved through suitable mowing regimes (preferably twice per year
418 with the removal of hay after cutting), regular removal of shade-casting woody vegetation, diminishing the inflow
419 of salts, pollutants and nutrients, and promoting the natural establishment of vegetation on road verges (as opposed
420 to the traditionally applied sowing mixtures with highly competitive grass species) (see also Jakobsson *et al.* 2018;
421 Phillips *et al.* 2019). Meanwhile, while hedgerows or grass buffer strips are sometimes established in hilly landscapes
422 to filter nutrients from surface runoff (Van Vooren *et al.* 2017), our results indicate that accumulation of soil P in
423 hedgerows and road verges could be counteracted to improve the establishment success of specialist plant species.
424 To illustrate, this could be achieved via optimized and potentially reduced application of P fertilizers or manures
425 directly next to the linear structures. Following these guidelines, linear landscape elements could effectively extent
426 ‘core habitat conditions’ into the agricultural landscape matrix, potentially alleviating the adverse impacts of habitat
427 fragmentation and climate change on migrating plant species (Roy & de Blois 2008).

428 It is also noteworthy that management strategies related to the maintenance and restoration of linear habitats in
429 agricultural landscapes generally come at a relatively low cost (Dainese *et al.* 2017), but have a remarkable long-
430 term benefit for biodiversity conservation especially in areas with relatively few non-crop habitats. Moreover, these
431 actions require relatively little land from crop production, have minimal (or sometimes even positive) effects on
432 crop yield and do not involve changes in crop management (Garibaldi *et al.* 2014). Finally, we would like to point
433 out that our results should be interpreted with care, given that we specifically focused on ancient linear elements
434 with long-term connectivity to a seed-source habitat. These corridors already have a long history of stable habitat
435 conditions, and have likely accumulated a higher number of slow-colonizing habitat specialists over time (Paal *et*
436 *al.* 2017). Recent linear structures, on the other hand, typically lack these habitat specialists but given time and
437 proper management they can develop into valuable habitats with diverse plant communities (Litza & Diekmann
438 2019). From this perspective, we argue that land managers should promote the conservation of existing species-
439 rich linear structures and remnant seed-source habitats. The emergence of new linear landscape elements should
440 then be prioritized in the proximity of these ancient linear structures or historically continuous core habitats,
441 serving as potential source populations (see Lenoir *et al.* 2019). Together this complex of linear structures and

442 remnant habitat patches could form a functional network that facilitates the migration of species across degraded
443 landscapes and contributes to the long-term conservation of otherwise isolated populations in the face of global
444 environmental change.

445 **Authors' contributions**

446 TV, PDF and KV conceived and designed the study. All authors were involved in the site selection and data
447 collection. TV and PDF conducted the statistical analyses. TV and PDF wrote the first draft of the paper, while
448 all authors contributed to revisions. All authors gave approval for publication.

449 **Data availability statement**

450 Data available from the Figshare repository DOI: 10.6084/m9.figshare.8104499 (Vanneste *et al.* 2019).

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617

618 **Tables**

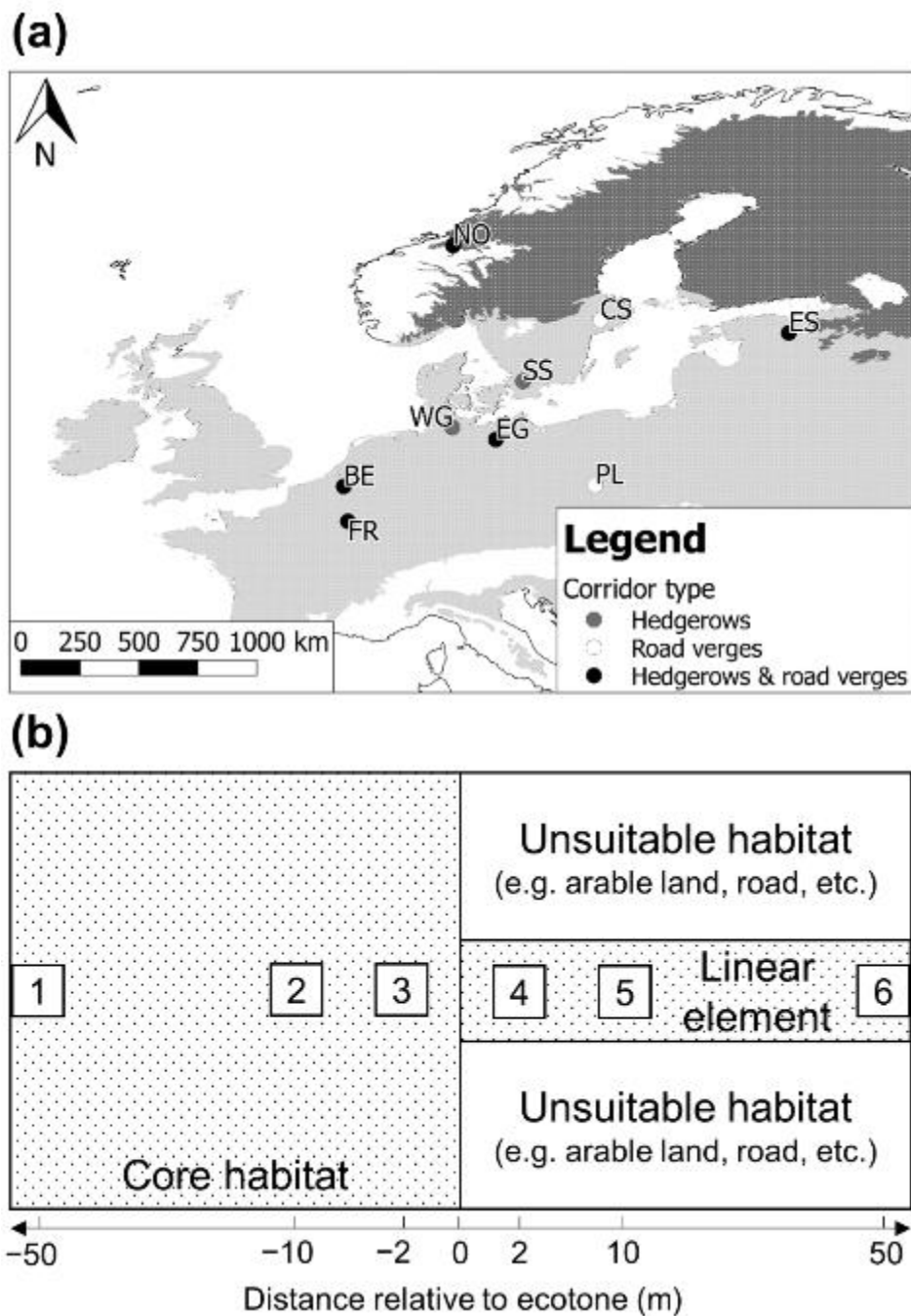
619 **Table 1.** Univariate statistical relationships between the total, generalist and specialist understorey plant species richness in forests and hedgerows, on the one hand, and the
620 environmental variables, on the other hand. Values and symbols are χ^2 -values and significances, respectively, from a likelihood ratio test of generalized linear mixed-effect
621 models with Poisson distribution ($Species\ richness \sim Predictor + Habitat + Predictor \times Habitat$). The direction of the effect is given as “ \uparrow ” for a positive effect of the predictor or
622 a higher species richness in hedgerows than in forests, and “ \downarrow ” for a negative effect of the predictor or a lower species richness in hedgerows than in forests. Significances
623 are indicated as “***” for $P < 0.001$, “**” for $P < 0.01$, “*” for $P < 0.05$ “.” for $P < 0.1$ and “n.s.” for $P \geq 0.1$.

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

624 **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
625 environmental variables, on the other hand. Values and symbols are χ^2 -values and significances, respectively, from a likelihood ratio test of generalized linear mixed-effect
626 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
627 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.
628 Significances are indicated as “***” for $P < 0.001$, “**” for $P < 0.01$, “*” for $P < 0.05$ “.” for $P < 0.1$ and “n.s.” for $P \geq 0.1$.

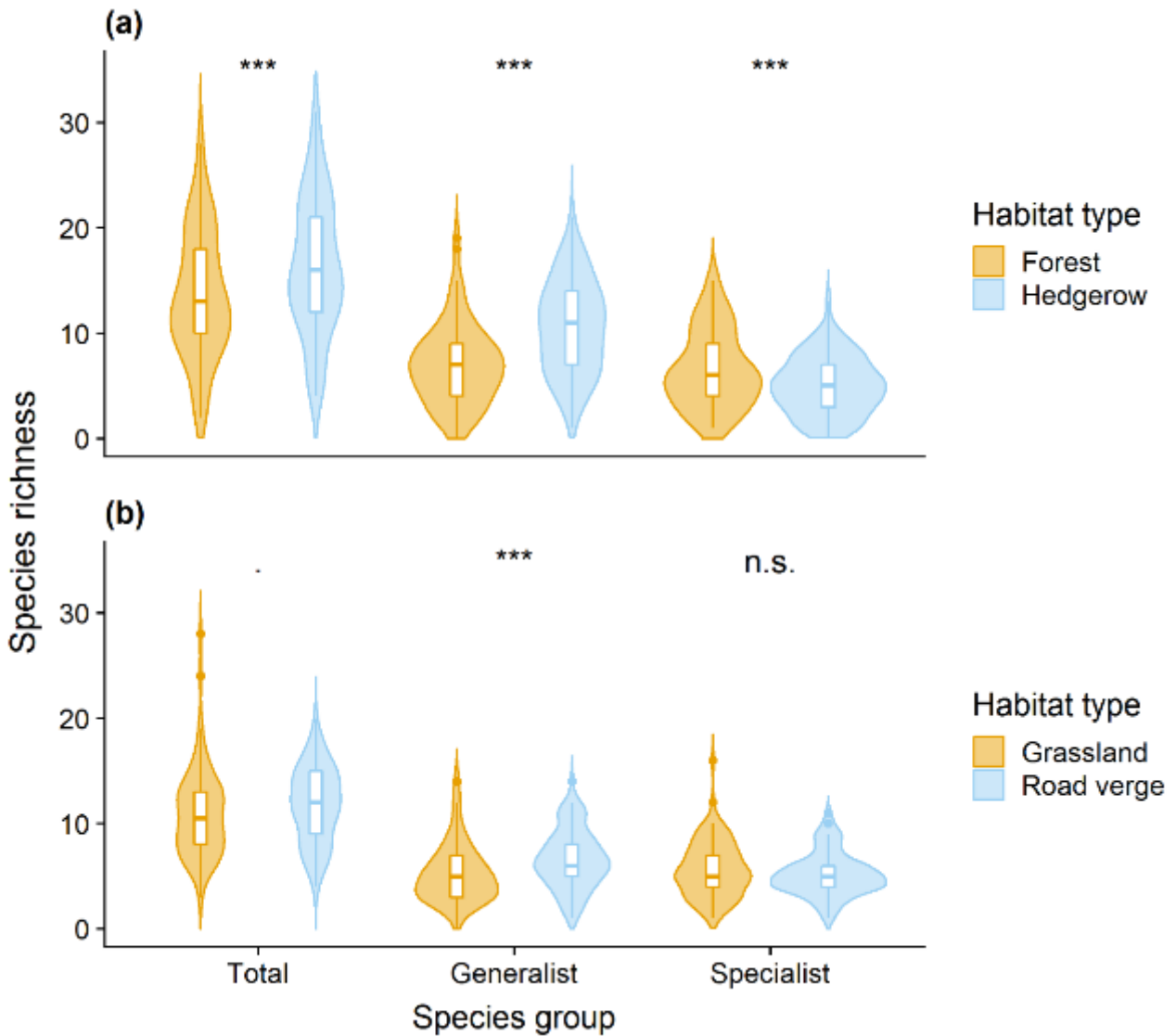
	Total richness			Generalist richness			Specialist richness		
	Predictor	Habitat	Predictor × Habitat	Predictor	Habitat	Predictor × Habitat	Predictor	Habitat	Predictor × Habitat
Nitrogen deposition	n.s.	↑3.6.	n.s.	↓3.0.	↑6.6*	n.s.	n.s.	n.s.	n.s.
Mean annual temperature	n.s.	↑3.6.	3.0.	↓3.4.	↑6.6*	n.s.	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.

629



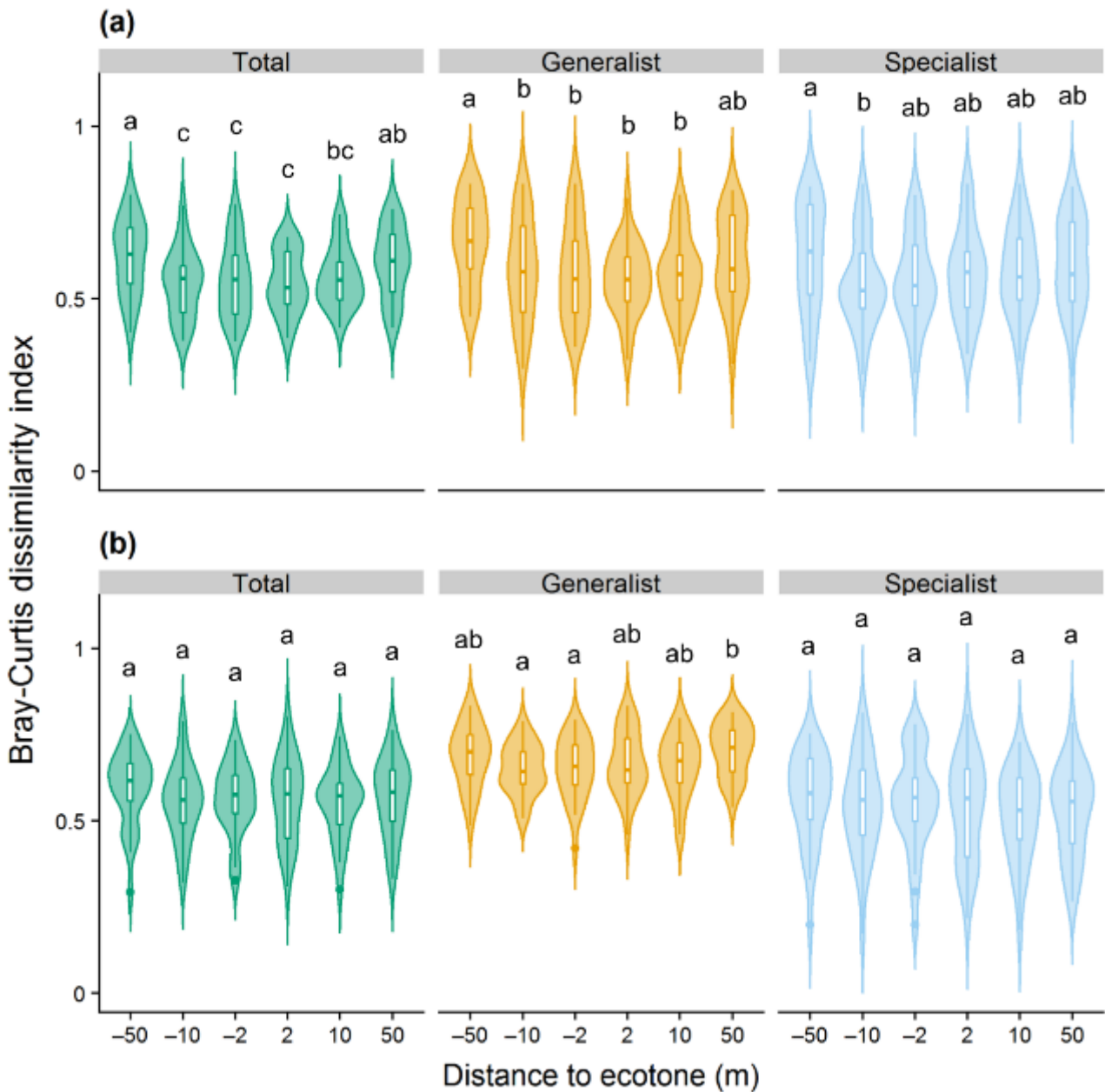
631

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



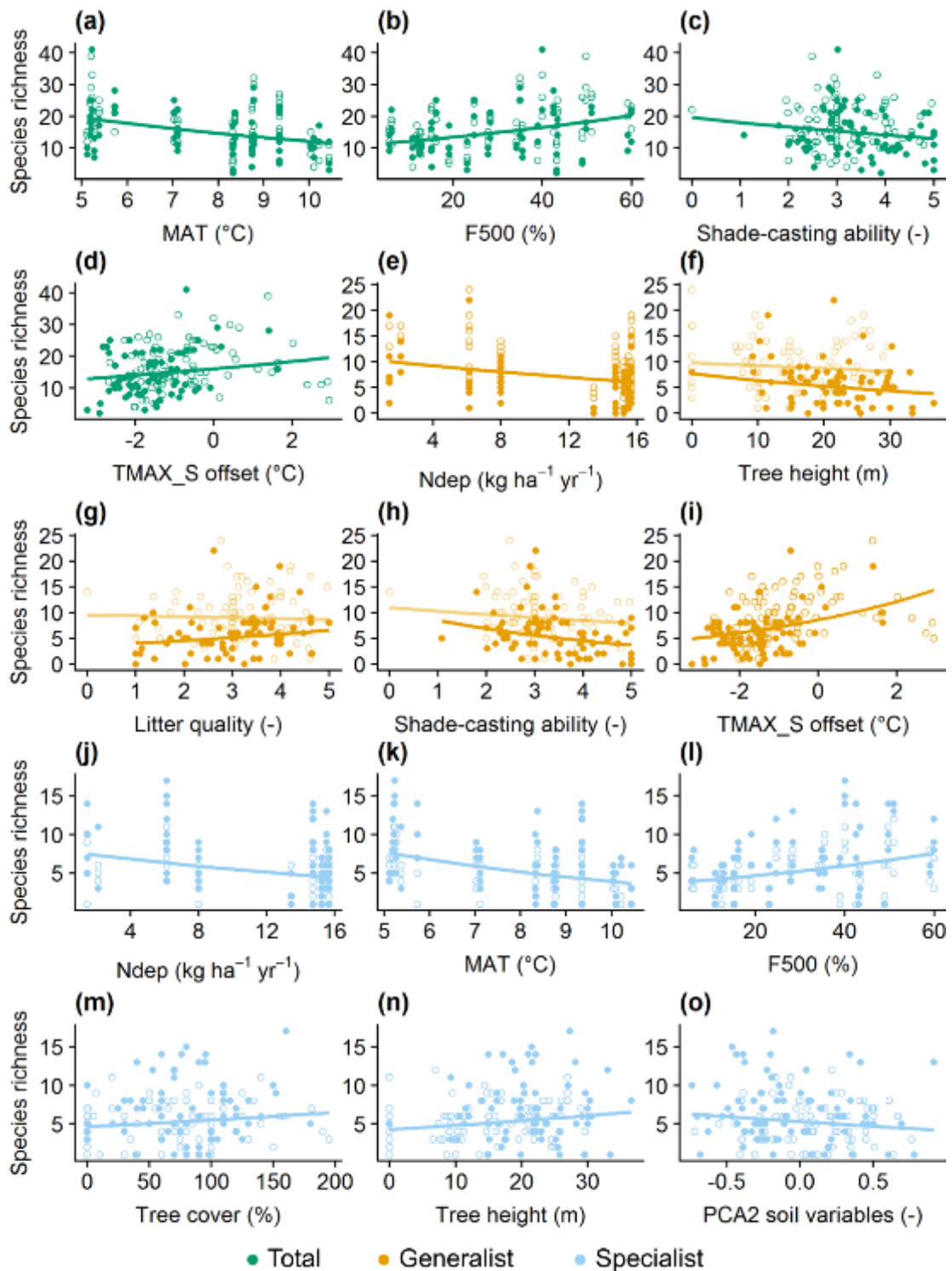
638

639 **Fig. 2. (a)** Violin plots showing the total, generalist and specialist understorey plant species richness in forests and
 640 hedgerows. **(b)** Violin plots showing the total, generalist and specialist plant species richness in grasslands and road
 641 verges. The difference in species richness between both habitat types (core habitat vs. linear habitat) was tested
 642 with a generalized linear mixed-effect model with Poisson distribution ($Species\ richness \sim Habitat$). Significant
 643 differences are indicated as: “****” for $P < 0.001$, “***” for $P < 0.01$, “**” for $P < 0.05$, “*” for $P < 0.1$ and “n.s.”
 644 for $P > 0.1$.



645

646 **Fig. 3. (a)** Violin plots showing the plot-level Bray-Curtis dissimilarity index for all understorey plant species,
 647 generalists and specialists as a function of distance to the forest-hedgerow ecotone. **(b)** Violin plots showing the
 648 plot-level Bray-Curtis dissimilarity index for all plant species, generalists and specialists as a function to the
 649 grassland-road verge ecotone. Differences in Bray-Curtis dissimilarity among vegetation plots were tested with a
 650 generalized linear mixed-effect model with Poisson distribution ($Disimilarity \sim Plot$), followed by a Tukey post hoc
 651 test for pairwise comparisons. Different letters denote significant differences.



652

653 **Fig. 4.** Relationship between the total understorey plant species richness in forests (*full circles*) and hedgerows (*open*
654 *circles*), on the one hand, and mean annual temperature (MAT) **(a)**, proportion of forest in 500-m radius (F500)
655 **(b)**, shade-casting ability **(c)** and maximum summer temperature (TMAX_S) offset **(d)**, on the other hand.
656 Relationship between generalist understorey plant species richness in forests (*full circles*) and hedgerows (*open circles*),
657 on the one hand, and nitrogen deposition (Ndep) **(e)**, tree height **(f)**, litter quality **(g)**, shade-casting ability **(h)** and
658 maximum summer temperature (TMAX_S) offset **(i)**, on the other hand. Relationship between specialist

659 understory species richness in forests (*full circles*) and hedgerows (*open circles*), on the one hand, and nitrogen
660 deposition (Ndep) (**j**), mean annual temperature (MAT) (**k**), proportion of forest in 500-m radius (F500) (**l**), total
661 tree cover (**m**), tree height (**n**) and second principal component axis (PCA2) of soil variables (**o**), on the other
662 hand. Fitted regression lines are from generalized linear mixed-effect models with Poisson distribution (*Species*
663 *richness* ~ *Predictor* + *Habitat* + *Predictor* × *Habitat*). If the interaction term was significant in the models, two
664 regression lines were plotted, i.e. one for forests (*dark coloured regression line*) and one for hedgerows (*light coloured*
665 *regression line*).