

1 **Contrasting vegetation change (1974-2015) in hedgerows and forests in**  
2 **an intensively used agricultural landscape**

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12 **Running head:** Opposite herbal changes in hedgerows and forests

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15 **ABSTRACT**

16 **Questions:** How did hedgerows and forests change in area between 1974 and 2015  
17 and did hedgerows still show the same vegetation composition in 2015? To what  
18 degree did the vegetation change in hedgerows and how do these changes compare  
19 to changes in forests? What is the nature of the species that changed and, from these,  
20 can we make general inferences about possible drivers of change?

21 **Location:** The countryside in the municipality of Turnhout, province of Antwerp,  
22 northern Belgium.

23 **Methods:** Through a resurvey of 54 and 20 quasi-permanent plots in hedgerows and  
24 forests, respectively, we investigated shifts in the herb layer over the period 1974-  
25 2015. The plot-level mean Ellenberg Indicator Values (EIVs) were calculated and soil  
26 samples were taken in 2015. We compared diversity statistics and used GLMM to  
27 detect trends in species richness (SR) and EIVs. Via a NMDS-ordination based on the  
28 Sørensen dissimilarity, we compared shifts at the community level.

29 **Results:** Our study shows severe, however opposite changes in SR in forests and  
30 hedgerows. In forests, SR declined and a homogenization occurred. The shifts in EIVs  
31 indicate that forest vegetation evolved to more shade tolerant and nutrient demanding  
32 species, likely due to eutrophication combined with natural forest succession. In  
33 hedgerows, SR significantly increased. The species pool became more diverse and  
34 more heterogeneous. Changes in EIVs suggest a change towards more light  
35 demanding species, possibly caused by fragmentation of the network, and towards  
36 species indicative for nutrient rich habitats, benefiting from eutrophication.

37 **Conclusions:** In general, SR in hedgerows is higher than in forests in our studied  
38 region, being a suitable habitat for a wide range of plant species in the countryside.

39 However, the loss of almost 30% of the hedgerow habitat in 41 years, confronts us  
40 with the challenge of protecting the hedgerow remnants, in the interest of the agro-  
41 biodiversity.

42 **KEYWORDS:** Hedgerows; small forests; resurvey; temporal vegetation shift; historical  
43 plot data; species richness; Ellenberg indicator values; eutrophication; acidification;  
44 semi-permanent plots

45 **NOMENCLATURE:** Lambinon et al. (2015) for plants; Runhaar et al. (2004) for plant  
46 communities

47 **ABBREVIATIONS:**

- 48 - Al: aluminum
- 49 - Ca: calcium
- 50 - C: carbon
- 51 - EIVs: Ellenberg indicator values
- 52 - K: potassium
- 53 - Mg: magnesium
- 54 - N: nitrogen
- 55 - P: phosphorus
- 56 - SR: species richness

57 **INTRODUCTION**

58 Improving the integration of biodiversity conservation into key policies for  
59 agriculture and forestry is one of the six targets of the EU 2020 Biodiversity Strategy.  
60 These two sectors combined are involved in the management of 72% of the land in  
61 the EU, therefore playing a major role in the status of Europe's biodiversity (EC 2015).  
62 Semi-natural habitats in agricultural landscapes (e.g. grass strips, single trees,

63 hedgerows and forest patches) support the vast majority of the species diversity in  
64 agro-ecosystems (Dover & Sparks 2000; Butet & Leroux 2001; Sullivan et al. 2012).  
65 However, agricultural landscapes have drastically changed in many countries as farms  
66 intensified their activities and became highly mechanized, at the expense of semi-  
67 natural habitats (Baudry et al. 2000). When situated on the field borders, semi-natural  
68 habitats may be removed to increase the field's cultivatable area or to allow for  
69 merging adjacent fields into larger parcels. This trend has led to a decrease in the  
70 diversity and abundance of fauna and flora in rural areas, sometimes even pushing  
71 species towards local extinction (Suding et al. 2005; Jennings & Pocock 2009).

72         Among the semi-natural habitats in agricultural areas, hedgerows and small  
73 forest patches provide relatively permanent habitats within a constantly disturbed  
74 environment, acting as suitable habitats for many plant and animal species (Roy & de  
75 Blois 2008; Decocq et al. 2016; Van Den Berge et al. 2018). They provide shelter,  
76 breeding sites, habitats and food resources for a range of invertebrates (Burel 1989;  
77 Duelli et al. 1990; Dover & Sparks 2000), birds (Dmowski & Koziakiewicz 1990;  
78 Clergeau & Burel 1997; Hinsley & Bellamy 2000), small mammals (Tattersall et al.  
79 2000; Butet & Leroux 2001; Gelling et al. 2007; Sullivan et al. 2012) and several  
80 carnivore species (Šálek et al. 2009; Cervinka et al. 2013; Dondina et al. 2016). Here  
81 we focus on the diversity and composition of the plant community, because of its  
82 importance for the functioning of these ecosystems, including their relationship with  
83 many trophic levels (Siemann et al. 1998; Steffan-Dewenter & Tschardtke 2001).

84         The largest contribution to plant diversity in both hedgerow (e.g. Deckers et al.  
85 2004) and forest ecosystems (e.g. Gilliam 2007) originates from the herb layer.  
86 Studies that aim at explaining what drives the spatial patterns of plant community  
87 diversity and composition are widely available for forests (e.g. Brunet et al. 2000; Kolb

88 & Diekmann 2004; Houle 2007; Gazol & Ibáñez 2010) and hedgerows (e.g. Le Coeur  
89 et al. 1997; de Blois et al. 2002; Deckers et al. 2004; Alignier & Baudry 2015; Van Den  
90 Berge et al. 2018). However, for decision-making in management and conservation  
91 strategies, we need to understand how these communities are changing over time as  
92 well. The drivers of spatial patterns may be used to infer how environmental change  
93 may cause the vegetation changes over time. Alternatively, resurveys of historical  
94 vegetation records provide direct data on decadal changes in vegetation, although the  
95 opportunities for such research are determined by the availability of high quality legacy  
96 data. Such resurveys have been widely used to study forest understory vegetation  
97 dynamics (e.g. Verheyen et al. 2017), but very few studies exist on temporal changes  
98 in vegetation in hedgerows (but see Huwer & Wittig 2012; Staley et al. 2013; Litza &  
99 Diekmann, 2017).

100         Syntheses across temperate forest vegetation resurvey studies have shown  
101 that several global and local environmental changes have a strong impact on forest  
102 plant diversity and composition. Changes include climate, altered forest management,  
103 nitrogen deposition, and herbivore mammal abundances (Verheyen et al. 2012; De  
104 Frenne et al. 2013; Bernhardt-Römermann et al. 2015; Perring et al. 2016). While it is  
105 tempting to assume vegetation in hedgerows in the same regions of these studied  
106 forests experiences similar changes, hedgerows actually form very distinct structures  
107 and are managed differently. Because of their linear structure, they are far more  
108 exposed to anthropogenic influences. Several studies (e.g. Schmucki et al. 2002;  
109 Deckers et al. 2004) show that important drivers for hedgerow vegetation are the  
110 adjacent land use and the agricultural practices in the neighboring fields; the use of  
111 pesticides, the ploughing of the land and the harvest of the crops influence hedgerow  
112 vegetation in a chemical or physical way. This clearly illustrates the potential value of

113 simultaneously focusing on temporal vegetation change in both hedgerows and forests  
114 in the same study area.

115 Here we present the results of a vegetation resurvey study (1974 – 2015) in  
116 hedgerow and forest plots in an intensively used agricultural landscape in northern  
117 Belgium. The countryside in this region has a high degree of urbanization and  
118 agriculture has further intensified and increased in area between the surveys. We  
119 determined the shifts in plant community diversity and composition over the past four  
120 decades, including only understory plant species in our analysis, as woody species  
121 are often more driven by management choices than by natural processes (French &  
122 Cummins 2001). With these data we will answer the following research questions:

- 123 (1) How did the hedgerow and forest habitats change in area between 1974 and  
124 2015 and did hedgerows still show the same vegetation structure like 41 years  
125 ago?
- 126 (2) To what degree did the understory vegetation change over a period of 41 years  
127 in the hedgerows and how do these changes compare to changes in forest  
128 patches in the same region?
- 129 (3) What is the nature of the species that changed the most and, from these, can  
130 we make some general inferences about the possible drivers of change?

## 131 **METHODS**

### 132 **Study area and study systems**

133 The municipality of Turnhout (province of Antwerp, northern Belgium, Figure 1) has  
134 a total area of 56 km<sup>2</sup>, 16.42% of which are forests and 55.86% are agricultural  
135 landscapes (based on the CORINE methodology, European Environment Agency  
136 2013). Altitude varies between 18 and 35 m above sea level (Van der Veken et al.  
137 2004). The climate is temperate with a total annual rainfall of 755 mm and an average  
138 temperature of 10.1 °C. The region is dominated by Aeolian sandy soils, deposited  
139 during the last glacial period.

140 About three quarters (76%) of the studied hedgerows in the countryside (*anno*  
141 2015) are elevated (woody vegetation on artificial ground, so called 'wooded banks')  
142 and the remainder are at the same height as the surrounding land; however, all will be  
143 referred to as 'hedgerows'. The average width is  $3.1 \pm 1.7$  m and the average length  
144 is  $183.1 \pm 135.4$  m. *Quercus robur*, *Frangula alnus*, *Quercus rubra* and *Betula pendula*  
145 are the most frequent species in the tree and shrub layer (present in 94.4; 31.5; 24.9  
146 and 24.9% of the hedgerow plots, respectively). The studied forest patches have an  
147 average area of  $1.94 \pm 1.51$  ha; most common species in the tree layer are *Quercus*  
148 *robur* (in 55.5% of the plots) and *Betula pendula* (40.0%). *Sorbus aucuparia* (60.0%)  
149 and *Frangula alnus* (50.0%) are the most frequent species in the shrub layer.

### 150 **Vegetation (re)sampling**

151 During the summer of 1974 (July and August), a phytosociological vegetation  
152 study was carried out in Turnhout (Vanderschaeve 1975). The vegetation was  
153 recorded in a total of 81 plots in hedgerows and 26 plots in forests. Selection of  
154 hedgerows was done using this criterion: they showed a well-developed herb, shrub  
155 and tree layer to avoid already degraded hedgerows. The forest patches, on the other

156 hand, were randomly selected in the landscape. A representative part of the vegetation  
157 was recorded via plots varying between 25 - 150 m<sup>2</sup> and 60 – 150 m<sup>2</sup> for hedgerows  
158 and forests, respectively. The plot size was assigned to every single hedgerow and  
159 forest according to several a priori chosen sample sizes. Sizes were defined during an  
160 exploratory study (before the actual study took place) based on the “minimal area  
161 principle”: The minimal area of a community is the smallest area on which the  
162 community can develop its characteristic composition and structure (Cain & Oliveira-  
163 Castro 1959). Plots were chosen at a position in the middle of the hedgerow length  
164 and randomly in the forest patch. All species in the herb (< 0.5 m tall), shrub (< ca. 3  
165 m tall) and tree layer were identified and their percentage cover was estimated as a  
166 measure of their abundance (Barkman scale; Barkman et al. 1964). All plots were  
167 indicated on a topographical map and can be considered quasi-permanent (Kapfer et  
168 al. 2017).

169 During the summer of 2015 (July and August), the plots were revisited. We used  
170 the topographic map from the original study (scale 1/25000, marked with hand drawn  
171 plots) in combination with current aerial pictures with the digitized plots obtained via  
172 QGIS (QGIS Development Team 2016. Software version Desktop 2.18.18, QGIS  
173 Geographic Information System. Open Source Geospatial Foundation Project). In this  
174 way, we were able to relocate the sampled plots in a very accurate way.

175 In the field, each hedgerow was classified based on the general degradation  
176 status along its complete length (Appendix S1): ‘intact’ (hedgerow with well-developed  
177 herb, shrub and tree layer), ‘degraded’ (hedgerow with depleted or missing tree layer  
178 or shrub layer, mostly due to cutting) and ‘lost’ (hedgerow cleared). Also some  
179 additional attributes were recorded: whether or not the hedgerow was a wooded bank,  
180 presence of a ditch, and adjacent land use (arable land, forest, brushwood, grassland,



181 paved road, dirt road, garden, build-up area). We resurveyed 54 vegetation plots (3260  
182 m<sup>2</sup> in total) in the degraded and intact hedgerows analogous to the 1974 recordings  
183 (27 plots had disappeared). Likewise, 20 plots (1985 m<sup>2</sup> in total) in the forests were  
184 resurveyed (three plots had disappeared and three plots were no longer accessible).  
185 Some of the hedgerows became more narrow ( $n = 9$ ) or wider ( $n = 6$ ) and in both  
186 cases we respected the original plot size by adjusting the length of the plot. In the few  
187 occasions ( $n = 5$ ) that the original plot was no longer located within the hedgerow  
188 (hedgerow was shortened) we relocated it within the remnants, in the middle of the  
189 current length. Indeed, even though the exact location of the original sampling plot is  
190 not precise, still accurate vegetation changes can be determined (Kopecký & Macek  
191 2015). We estimated the abundance of all species in the herb, shrub and tree layer in  
192 percentage classes (Hennekens 2009). Since the original survey used the Barkman  
193 abundance scale, data were converted into percentage classes *sensu* Hennekens  
194 (2009) (Appendix S2).

### 195 **Environmental variables**

196 Because in the original study no soil samples were taken, we used Ellenberg  
197 indicator values (EIVs) to explore how environmental conditions have changed  
198 between the old and recent vegetation records. For each plot, we calculated  
199 unweighted mean EIVs for productivity (N), soil reaction (R), soil moisture (F) and light  
200 availability (L). We decided to use unweighted values to account for a possible  
201 consistent difference in abundance estimates between observers. Ellenberg values  
202 are known to be good proxies for these environmental conditions (Diekmann 2003).

203 Besides, we collected soil samples in a subset of the plots in both ecosystems  
204 during the summer of 2016 to allow for a better interpretation of patterns in EIVs in  
205 terms of the measured soil chemistry. A fraction of 40% of the plots was selected along

206 a gradient in mean Ellenberg R-values (weighted sample: hedgerows:  $n = 21$ , forests:  
207  $n = 9$ ). In each plot, we collected a mixed soil sample consisting of eight subsamples.  
208 All subsamples were taken with a gouge auger in the 0-10 cm mineral topsoil layer  
209 after removing the organic litter layer. Sample positions within the plot were randomly  
210 chosen over the entire plot area, but at least 1 m distance from trunks and edges to  
211 avoid edge and 'trunk' effects. In the laboratory, oven-dried (40 °C for a period of 48  
212 hours) and sieved soil was mixed in water in a 1/5 ratio, shaken for five minutes and  
213 left to stand for two hours. The pH-H<sub>2</sub>O-value was measured using a pH meter with  
214 Ross Sure-Flow combined electrode (Orion, USA). The carbon (C) and nitrogen (N)  
215 concentrations were determined with a vario MACRO cube (Elementar, Germany).  
216 The phosphorus (P) and base cation concentrations (potassium (K), calcium (Ca),  
217 magnesium (Mg), and aluminum (Al)) were measured after an ammonium lactate-  
218 EDTA extraction.

## 219 **Data analysis**

### 220 Structural changes

221 Surface loss of forests and hedgerows over the 41-year period was calculated  
222 via QGIS. The association of the hedgerow status (lost, degraded, intact) with the  
223 features adjacent land use (converted to dummy variables), the presence of a ditch  
224 and whether or not the hedgerow was elevated was tested via a Chi<sup>2</sup>-test.

### 225 Vegetation changes and ecological characteristics of species

226 We looked into the ecology of the species by allocating every species to a  
227 particular species group *sensu* Runhaar et al. (2004) (pioneer species, grassland  
228 species, tall herb species and forest species) and looked up their EIVs *sensu*  
229 Ellenberg et al. (2001). For each species group, we counted the number of species  
230 (species richness = 'SR') and the mean abundance of these species in each plot. The  
231 plot-level mean EIVs were also calculated.

232 To illustrate the conservation status of the species in our inventories, we  
233 allocated a threat status to every species according to the red list for Belgium (Van  
234 Landuyt et al. 2006). Furthermore, we classified species according to their observed  
235 change in frequency over time: species that had disappeared by 2015 ('lost species'),  
236 species that appeared since 1974 ('new species'), and species that are common in  
237 both inventories. Among these common species, we classified 'losers' and 'winners'  
238 (present in 10% less and 10% more plots compared to 1974, respectively).

239 For both forest and hedgerow plots, we considered the size of the total species  
240 pool in each period ( $\gamma$  diversity), rarefied to the number of plots in 2015 (Chao et al.  
241 2014). So, by interpolation, the expected  $\gamma$  diversity could be correctly compared  
242 between the years (Colwell et al. 2004). Absolute numbers of species (in total and per  
243 species group) of the species pools in the two periods were compared via a Chi<sup>2</sup>-test.

244 Local plot-level taxonomic diversity (i.e.  $\alpha$  diversity) was estimated as a diversity  
245 of order zero (species richness;  ${}^0D$ ) and order one (exponential of Shannon;  ${}^1D$ ), the  
246 latter to take into account SR and abundance of each species within the plot. By taking  
247 the exponential of the Shannon index, the index is converted into an effective number  
248 of species, in this way two plots with equal diversity also acquire the same value. This  
249 facilitates the interpretation of the results (Jost 2006). Compositional differences  
250 between plots were assessed with pairwise dissimilarity metrics ( $\beta$  diversity). A  
251 Sørensen dissimilarity ( $\beta_{Sor}$ ) was used to quantify overall compositional differences  
252 and was further partitioned into its turnover ( $\beta_{Sim}$ ) and nestedness ( $\beta_{Nes}$ ) components  
253 to discriminate between species replacements across plots and richness differences  
254 leading to nestedness patterns across plots, respectively (Baselga 2010). The  
255 significance in differences for these diversity statistics between the two years was  
256 tested with a paired Wilcoxon signed-rank test (i.e. nonparametric test, when the data

257 were not normally distributed) or paired t-test (i.e. parametric test, when the data were  
258 normally distributed).

259 We used Generalized Linear Mixed-Effects Models (GLMMs) via the `glmer`  
260 function in the 'lme4' package (Bates et al. 2015) with Poisson distribution to detect  
261 significant trends in all these response variables (overall SR, SR of the four species  
262 groups, EIVs) over the two periods and between the two ecosystems (hedgerow and  
263 forest). Plot size was initially included in the models to check its influence on the  
264 response variables, but due to its small effect, we decided to leave it out in the final  
265 analyses. Plot identity was used as a random effect to account for the paired nature  
266 of the design (the same plot was recorded in two time points). To be able to plot the  
267 significance of the differences over time between the response variables within one  
268 ecosystem (i.e. forest or hedgerow), we used a paired t-test, as we could not use p-  
269 values from the models because of significant *year x ecosystem* interactions.

270 In order to compare the vegetation shifts at the community level, we performed  
271 a Non-metric multidimensional scaling ordination (NMDS) via the `metaMDS` function  
272 in the R package 'vegan' (Oksanen et al. 2015) with three a priori chosen dimensions  
273 for the hedgerows (stress was too high with two), two a priori chosen dimensions for  
274 the forests, and maximum 50 iterations. Our ordination was based on the Sørensen  
275 dissimilarity matrix of the full vegetation data sets (sets of 1974 containing only the  
276 plots that could be revisited). Significance of the effect of time on composition was  
277 tested with a permutational multivariate analysis of variance (PERMANOVA) on the  
278 same dissimilarity matrix (2000 permutations). An analysis of the multivariate  
279 dispersion (`betadisper` function in the `vegan` package) was performed to examine  
280 whether the multivariate spread was the same for the two periods or differed  
281 significantly. Correlations between the mean EIVs of the vegetation in the hedgerow

282 and forest plots and the two axes of the NMDS-analysis was assessed with the envfit  
283 function (also from the vegan package) and visualised by plotting the vectors onto the  
284 NMDS plots.

285 For the hedgerow plots, the influence of its status (intact vs degraded) on the  
286 average SR in the herb layer and on the species group-specific diversity, as well as  
287 on the average EIVs was tested with a t-test (when normally distributed) or Wilcoxon  
288 Signed-rank test (nonparametric statistics).

#### 289 Soil characteristics

290 The significance in differences for all measured soil characteristics between the  
291 two ecosystems was tested via a Wilcoxon signed-rank test, as these variables were  
292 not normally distributed. Spearman rank correlations were performed between the soil  
293 characteristics and mean EIVs of the plots for forests and hedgerows (only for the year  
294 2015).

295 All statistical tests were performed at the 5% level of significance, in R 3.2.3 (R  
296 Foundation for Statistical Computing, Vienna, AT).

## 297 RESULTS

### 298 Structural changes

299 The total surface of the studied forests decreased by ca 6.9%, from 45.88 ha in  
300 1974 to 42.71 ha in 2015. For the studied hedgerows, we found that the total length  
301 decreased by ca. 28.2%, from 20.93 km in 1974 to 15.02 km in 2015. Only 64.5% of  
302 the remaining network length was coded as 'intact' (9.69 km) and the remainder was  
303 'degraded' (Figure 1). Hedgerows without a ditch were more likely to become lost ( $p <$   
304  $0.05$ ). Of the remaining hedgerows, the wooded banks were more likely to remain  
305 intact ( $p < 0.001$ ). The status of the hedgerow (intact, degraded, lost) was not related  
306 to the current adjacent land use.

### 307 Vegetation changes in the hedgerow and forest plots

308 For hedgerows, the rarefied  $\gamma$  diversity significantly increased from 1974 to  
309 2015 ( $p < 0.001$ , Table 1). There were 53 species common to both surveys, among  
310 which nine winners and eight losers. 26 species were lost between the two surveys,  
311 and 67 species were new. In 1974, the species pool consisted for 93.6% of common  
312 species that are currently not threatened and 6.4% declining species: *Calluna vulgaris*,  
313 *Erica tetralix*, *Potentilla erecta*, *Salix repens*, *Solidago virgaurea* and *Melampyrum*  
314 *pratense*. In 2015, percentages in hedgerows shifted even more towards not  
315 threatened species (96.7% of the pool) and less declining species (2.5%: *P. erecta*,  
316 *C. vulgaris* and *M. pratense*) and one threatened species (*Juncus tenageia*). New  
317 species were mainly native except for *Conyza canadensis*, *Galinsoga quadriradiata*  
318 and *Impatiens parviflora* and scored generally high in EIVs (e.g. *Eupatorium*  
319 *cannabinum*, *Cirsium vulgare* and *Lamium album* with L-value = 7, 8, 7; N-value = 8,  
320 8, 9, respectively).

321 At the plot level, the mean  $\alpha$  diversity  ${}^0D$  and  ${}^1D$  significantly increased in  
322 hedgerows (Table 1). In terms of compositional variation, the mean Sørensen  
323 dissimilarity ( $\beta_{Sør}$ ) increased slightly between 1974 and 2015, though the individual  
324 turnover ( $\beta_{Sim}$ ) and nestedness ( $\beta_{Nes}$ ) components showed no significant change  
325 (Table 1).

326 In the intact hedgerows, the overall plot-level diversity ( ${}^0D$  and  ${}^1D$ ) and the  
327 species group-specific diversity (forest species; grassland species; tall herbs and  
328 pioneer species) were not significantly higher compared to the degraded hedgerows  
329 (*all comparisons*  $p > 0.05$ ). Diversity in both the intact and degraded hedgerows was  
330 significantly higher in 2015 compared to 1974 (both overall species richness and  
331 species group-specific diversity, *all comparisons*  $p < 0.001$ ). Mean EIVs in intact and  
332 degraded hedgerows did not differ significantly nor changed in a different way over  
333 time (*all comparisons*  $p < 0.001$ ).

334 In forests, the  $\gamma$  diversity decreased, however, not significantly ( $p > 0.05$ , Table  
335 1). There were 15 species common to both surveys (nine among which were losers),  
336 33 lost species and 9 new species. 91.7% of the species in forests in 1974 were not  
337 threatened and 8.3% were declining (*C. vulgaris* and *E. tetralix*). In 2015, only common  
338 species occurred in the forests. New species were native except for *I. parviflora* and  
339 scored generally low in L-values and high in N-values (e.g. *Geum urbanum* and *Ribes*  
340 *rubrum*). At the plot level, the mean  $\alpha$  diversity  ${}^0D$  and  ${}^1D$  decreased in forests. Also  
341 both  $\beta_{Sør}$  and  $\beta_{Sim}$  decreased significantly (Table 1).

342 The shift in EIVs at the community level is visualized in the NMDS analysis  
343 (*Stress* = 0.20): hedgerow surveys from 1974 and 2015 are clearly distinct on the first  
344 two axes (*PERMANOVA Pseudo-F* = 9.8,  $p < 0.001$ , Figure 2) and on the first vs. the

345 third axis (Appendix S3). The variance between the two years was almost the same  
346 (*ANOVA*,  $p > 0.05$ ). Correlations between the vectors of the EIVs and the (co)ordinates  
347 of site projections onto the first two axes are all significant ( $p < 0.001$ ). The first axis is  
348 strongly positively correlated with the N- and R-values ( $\rho = 0.96$  and  $\rho = 0.82$ ,  
349 respectively), to a lesser extent to the F value and negatively correlated with the L-  
350 value ( $\rho = 0.55$  and  $\rho = -0.50$ , respectively). The second axis is strongly positively  
351 correlated with the L-value ( $\rho = 0.82$ ); and to a lesser extent to the F-, R- and N-values  
352 ( $\rho = 0.77$ ,  $\rho = 0.56$ ,  $\rho = 0.26$ , respectively). Also forest surveys from 1974 and 2015  
353 were easily distinguished from each other in the NMDS-ordination (*Stress* = 0.16,  
354 *Pseudo-F* = 6.0,  $p < 0.001$ ). However, variation between the two years was not the  
355 same (*ANOVA*,  $p < 0.05$ ), possibly explaining a part of the difference between the two  
356 years. Correlations between the vectors of the EIVs and the two axes were all  
357 significant ( $p < 0.001$ ), except for the F-value ( $p > 0.05$ ). The first axis is strongly  
358 positively correlated with the F-, R and N-values ( $\rho = 0.99$ ,  $\rho = 0.96$  and  $\rho = 0.93$ ,  
359 respectively). The second axis is strongly positively correlated to the L-value ( $\rho = 0.99$ ,  
360 Figure 2).

### 361 **Ecological characteristics of the species**

362 In the species pool of hedgerow plots, representation of forest and pioneer  
363 species significantly increased ( $p < 0.05$ ); grassland species and tall herbs decreased.  
364 In the species pool found in the forests plots in 2015, pioneer species did not occur  
365 anymore and distribution had shifted towards more forest species and tall herbs and  
366 significantly less grassland species ( $p < 0.05$ ).

367 At the plot level, the mean number of forest species, grassland species, tall  
368 herbs and pioneer species consistently increased in the hedgerow plots and  
369 decreased in forest plots (Figure 3). Temporal patterns in the number of the species



370 groups were different between hedgerows and forests (*year x ecosystem interaction*  
371  $p < 0.01$ ). In both periods, hedgerow plots contained significantly more grassland  
372 species and tall herbs compared to forest plots and comparable amounts of forest  
373 species and pioneer species (Figure 3). Results for mean abundances of each species  
374 group were qualitatively similar, except for forest species and tall herbs in forests,  
375 which increased their abundance whereas their richness decreased (Appendix S4).

376 The mean EIVs changed consistently over time in hedgerow and forest plots:  
377 N-, R- and F-values increased whereas L-values decreased, although none of the  
378 shifts were significant (Figure 4). N-values and R-values were strongly correlated  
379 across plots in both ecosystems (*forests:  $\rho = 0.76, p < 0.05$ ; hedgerows:  $\rho = 0.71, p <$*   
380 *0.001*).

381 Soil characteristics in hedgerows and forests differed significantly (Appendix  
382 S5). Soil pH was significantly higher in hedgerow plots compared to forest plots ( $4.7 \pm$   
383  $0.6$  vs.  $4.1 \pm 0.3$ , respectively). In hedgerows, pH-values in almost all plots (76%)  
384 ranked above 4.2 and thus above the AI buffer range (Ulrich 1983). In forests, 78% of  
385 the plots showed pH-values below 4.2 units. In addition, ammonium lactate-P and  
386 base cation concentrations (K, Ca, and Mg) were significantly higher in hedgerow plots  
387 compared to forest plots. Only C, N and Al concentrations did not differ significantly  
388 across plots in both ecosystems (Appendix S5). Furthermore, N-values in both forest  
389 and hedgerow plots were positively correlated with the concentration of P in the soil  
390 (Appendix S5). In forest plots, R-values were also positively correlated with P  
391 concentrations and mean N-values were positively correlated with the concentration  
392 of K in the soil (Appendix S5). Mean R-values in hedgerow plots were negatively  
393 correlated with the concentration of Al. None of the EIVs were correlated with soil pH  
394 nor N, C, and Mg concentrations.

395 **DISCUSSION**

396 All over Europe, fragmentation of semi-natural habitats has continued to  
397 increase during the last 20 years (EEA 2011). Habitat patches are broken apart,  
398 reduced in size and become increasingly isolated. Consequently, the remaining  
399 ecological network provides less and less connectivity, negatively affecting ecological  
400 communities (EEA 2011). Also in our studied landscape, forest area has been lost and  
401 one third of the hedgerows was completely destructed over 41 years. However, in the  
402 remaining plots, (still) many plant species were found; hedgerow plots in particular  
403 hosted surprisingly many species (120 different species in total). In both ecosystems  
404 there were losses over the last four decades; the more threatened and rare species  
405 declined at the expense of generalists. Generally speaking, plant species richness in  
406 forests decreased clearly, whereas hedgerows strongly increased in plant diversity.

407 **Hedgerows vs. forest patches in the agricultural landscape**

408 Comparing both habitat types, we found clearly higher diversity in plants in  
409 hedgerows compared with forests. The species pool in hedgerows was much larger  
410 and the distribution among species groups more balanced. Even though the sampled  
411 area in hedgerows and forests was not the same (bigger sampled area in hedgerows)  
412 so the comparison is not completely fair, it is clear that hedgerows offer suitable  
413 habitats to more different plant species than do forests in our studied region.  
414 Hedgerows are typical edge habitats. They are structurally more heterogeneous than  
415 core habitats, including shaded parts as well as forest edge conditions. There is also  
416 variation in exposure to solar radiation and wind, creating even more niches (Critchley  
417 et al. 2013; French and Cummins 2001). In addition, hedgerow soils seem to have  
418 more suitable soil properties for plant growth compared to forest soils in our studied  
419 region, as we found higher pH and higher availability of P and basic cations. The soil

420 characteristics in our studied forests demand a more customized life strategy of the  
421 vegetation resulting in a smaller species pool.

#### 422 **Biodiversity decrease in forests**

423         The plant biodiversity in the forest fragments in this agricultural landscape  
424 decreased over the past four decades, in terms of local diversity within forests as well  
425 as compositional variation between forests. Similar patterns have been shown in  
426 several other forest resurvey studies (e.g. Keith et al. 2009, but not in others e.g.  
427 Verheyen et al. 2012). In our study, forest communities clearly shifted towards more  
428 shade tolerant species (lower L-value), at the expense of the more light demanding  
429 grassland species and pioneers – the latter totally gone in 2015. This indicates that  
430 forest succession might be ongoing. Most of the forests in the Campine region were  
431 planted during the 19<sup>th</sup> or 20<sup>th</sup> century, when afforestation of former heathland took  
432 place (Kint et al. 2010). Young forests growing older entails the establishment of more  
433 shading trees and shrubs, being a possible driver of plant biodiversity loss, as only  
434 well-adapted species can survive beneath a densely closed forest cover (Baeten et al.  
435 2009).

436         In addition, the subtle community shift towards more nutrient demanding  
437 species (higher N-value), indirectly indicates an increase in the availability of nutrients.  
438 Natural forest succession might also be a possible explanation here, as in general,  
439 this leads to eutrophication of the soil via the building up of organic matter (Hédli et al.  
440 2010). The correlation of the N-values of the vegetation with the amount of P and K in  
441 the soil – these two elements being main elements of fertilizers – also indicates  
442 eutrophication is ongoing. Fertilization of adjacent fields, combined with atmospheric  
443 deposition of reactive nitrogen from agriculture, traffic and industry (Bobbink et al.  
444 2010) is probably contributing to the eutrophication of the forests. Although

445 atmospheric deposition has declined in recent decades, the long-term accumulation  
446 has caused nitrogen-saturated ecosystems (De Schrijver et al. 2007). This  
447 eutrophication is mirrored as a decline in forest vegetation richness, at the expense of  
448 more specialized forest species, such as *Teucrium scorodonia* and *Vaccinium*  
449 *myrtillus*.

450         Deposition of atmospheric nitrogen and other acidifying pollutants, can also  
451 lead to forest soil acidification (Heisner et al. 2003; Van Calster et al. 2007; Baeten et  
452 al. 2009). Indeed, acidification is a widespread pattern in agro-ecosystems, mainly  
453 caused by the input of organic fertilizers that contain ammonium, which is oxidized to  
454 nitrate by which protons are released (Barak et al. 1997). Surprisingly, we found higher  
455 R-values for the forest community in 2015, whereas an acidification signal would be  
456 indicated by a decrease in R. However, there is no evidence for an ongoing  
457 deacidification nor acidification, as mean R-values were actually not correlated to the  
458 measured pH-values. R-values were, just like N-values, correlated with the amount of  
459 P in the soil, and both R- and N-values showed positive covariation. Such correlations  
460 between indicator values can create problems in the interpretation of ecological  
461 resurvey studies (Diekmann 2003; Naaf and Kolk 2015; Litza and Diekmann 2017).  
462 The pH-values in our resurvey were all situated in the Al buffer range (buffering stage  
463 “Al hydroxides”: pH 4.2-2.8), which is characterized by a high bioavailability of Al  
464 (Ulrich 1983; Appendix S5). Inhibition of root growth and function is the primary effect  
465 of Al on plants. Owing to Al inhibition of primary and lateral root growth, the growth of  
466 root systems is strongly reduced, negatively affecting the survival chances of a species  
467 (Lukac & Godbold 2011). Even though we cannot compare pH-values over time, it is  
468 plausible that Al toxicity might have become a factor decreasing species diversity in  
469 the forests.

470 **Biodiversity increase in hedgerows**

471 Hedgerows became more diverse (both in overall plant diversity and in diversity  
472 of the forest species, grassland species, tall herbs and pioneers) and taxonomically  
473 more heterogeneous over time. This is quite a different result compared to the findings  
474 of previous hedgerow resurvey studies, which have consistently reported a decline in  
475 overall diversity (Huyer and Wittig 2012; Staley et al. 2013; Litza and Diekmann 2017)  
476 and most also reported an increasing homogenization of the vegetation (e.g. Staley et  
477 al. 2013). However, in our study, a transition phase might be ongoing where original  
478 vegetation is still present and newly established vegetation increases the number of  
479 species, but reorganization may follow.

480 Fragmentation might be one of the underlying factors in our study of maintaining  
481 and increasing beta diversity. Due to fragmentation, the edge-to-core ratio of the  
482 hedgerows increases even more – being already quite high, as they are typical edge  
483 habitats – when they are shortened or when gaps appear. Edge habitat is influenced  
484 more profoundly by the surroundings, supporting the establishment of disturbed  
485 vegetation such as pioneers (Runhaar et al. 2004). This might also explain the shift in  
486 the species pool towards a composition of more light demanding species (higher L-  
487 value).

488 Over time, also more species indicative for nutrient rich soils found their way to  
489 the hedgerow habitats, resulting in higher diversity. Again, eutrophication seems to be  
490 the logical explanation for this shift (cf. also the findings of Staley et al. 2013; Litza and  
491 Diekmann 2017). Hedgerows – especially those located in agricultural fields – are  
492 exposed to high inputs of fertilizers. Moreover, crop plants in bordering agricultural  
493 fields tend to grow less strong because the shading of the hedgerow, using less of the  
494 applied fertilizers, possibly causing accumulation of fertilizers in the soil over time

495 (Mette 1994). Additionally, just like forests, hedgerows are exposed to atmospheric  
496 depositions causing further eutrophication and acidification of the ecosystem. The  
497 edge character of the hedgerows causes locally an increased wind turbulence, which  
498 allows an even higher nitrogen deposition and deposition of other acidifying pollutants  
499 compared to the deposition inside forest patches. The observed shift of hedgerow  
500 vegetation towards species with higher R-values would indicate a deacidification is  
501 ongoing, even though they were not correlated to the measured soil pH. Also Litza  
502 and Diekmann (2017) stated that in their studied hedgerows, the increasing nutrient  
503 availability (reflected in increasing mean N) overruled the responses of species to pH,  
504 as they found proof that soil pH decreased over 50 years while the mean R-values  
505 increased. The pH-values in our resurvey were almost all above the AI buffer range.  
506 However, the proportion of acid-tolerant species was strongly determined by AI  
507 concentrations in the soil (strong negative correlation between R-value of the  
508 vegetation and AI concentration in the soil). If soil acidification continues, AI-toxicity  
509 might become a problem for plant species diversity in the hedgerows.

510 In our studied hedgerows, a shift of typical vegetation well suited within the  
511 syntaxa one had in mind for the original thesis, to a kind of frame communities with  
512 the presence of non-typical species (e.g. more grassland species and pioneers), may  
513 have occurred. This shift may have resulted in a biodiversity increase for now.  
514 However, challenges such as climate change, further fragmentation and immigration  
515 of new plant species can enhance reorganization and dominance of single species in  
516 the future (Smith et al. 2009). Follow-up research remains needed to study the  
517 temporal vegetation changes in hedgerows and forests in intensively used agricultural  
518 lands.

519 **CONCLUSION**

520 In a period of four decades, major changes in both the structure and species  
521 composition of our semi-natural habitats in the countryside occurred. Over time,  
522 several threatened species were lost in both ecosystems, as eutrophication may have  
523 led to a shift towards more competitive species typical for nutrient rich habitats.  
524 Additionally, forest succession led to a strong light-determined diversity decline,  
525 whereas hedgerows hosted significantly more species in 2015. These different  
526 temporal vegetation shifts demonstrate the importance of considering diversity  
527 patterns in more than one ecosystem at once at a landscape scale, to get a broader  
528 idea about vegetation changes at this scale.

529 Irrespective of the fact that species richness in hedgerow networks is not  
530 declining and the existing species pool is relatively species rich, it is striking that in a  
531 period of 41 years, almost one third of the studied length of the network was cleared.  
532 In 100 years from now, hedgerows may be gone if this 'business as usual' continues  
533 (i.e. when considering a constant loss of 150 m/year). Even though it is more likely  
534 that only a specific proportion and not all of the hedgerows will be lost in our studied  
535 agro-ecosystem, it is clear that we are losing significant amounts of hedgerows. They  
536 are clearly suitable habitats to many different plant species, hosting a bigger variety of  
537 functional plant species groups and more threatened species than forests in our  
538 studied region. Proportionally much more hedgerow habitat than forest habitat  
539 disappeared during our studied period. The extent to which we will do efforts to ensure  
540 conservation of these hedgerows, will definitely determine the future biological content  
541 of the landscape.

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### 783 **SUPPORTING INFORMATION**

784 Additional supporting information may be found online in the Supporting Information  
785 section at the end of the article.

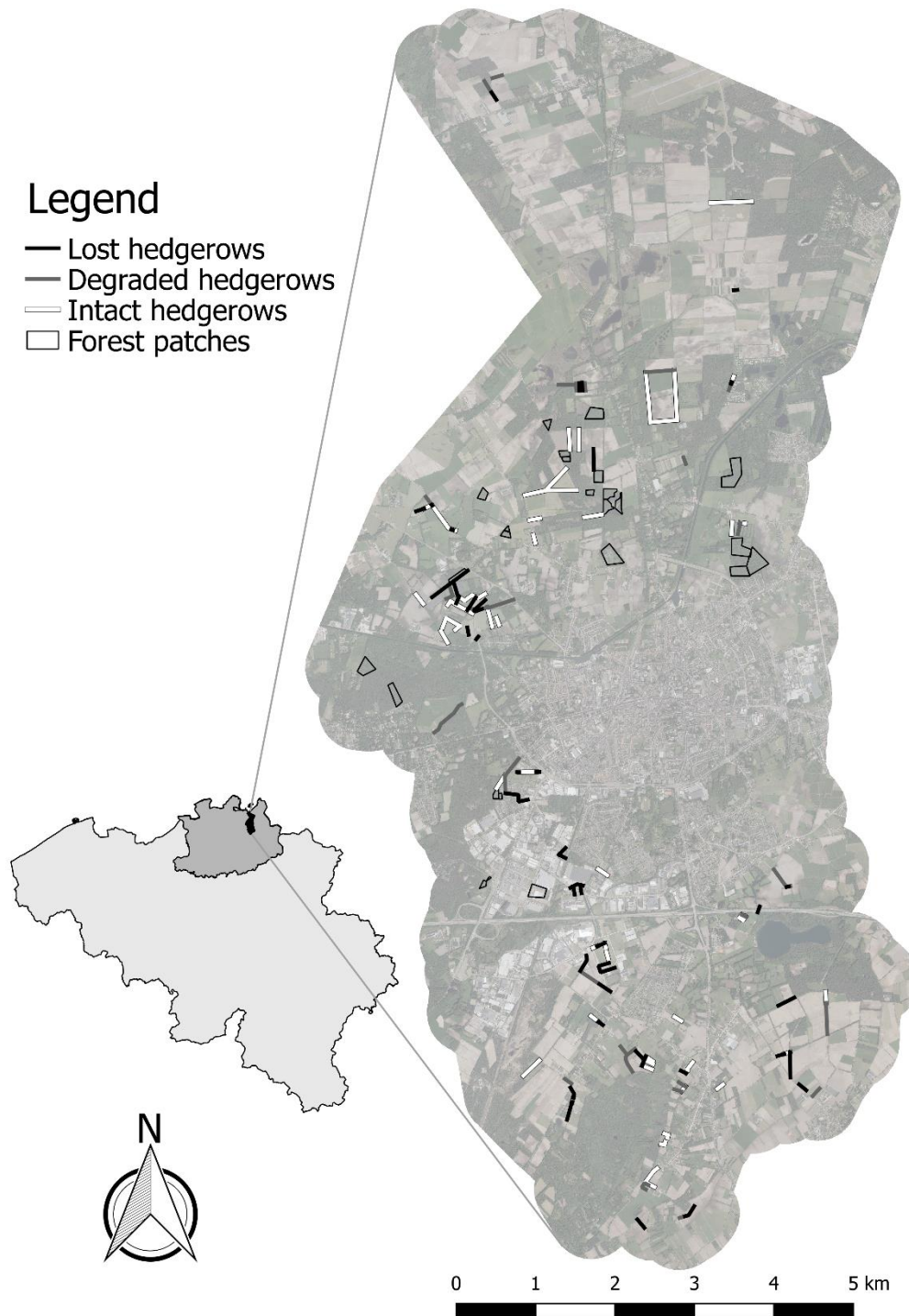
786 APPENDIX S1. Intact, degraded and lost hedgerows.

787 Appendix S2. Abundance scale *sensu* Barkman and *sensu* Hennekens.

788 Appendix S3. NMDS-ordination diagrams of hedgerow plots (Axis 1 vs Axis 3; Axis 2  
789 vs Axis 3).

790 Appendix S4. Shift in abundance of considered species groups.

791 Appendix S5. Results of soil analyses (2015).

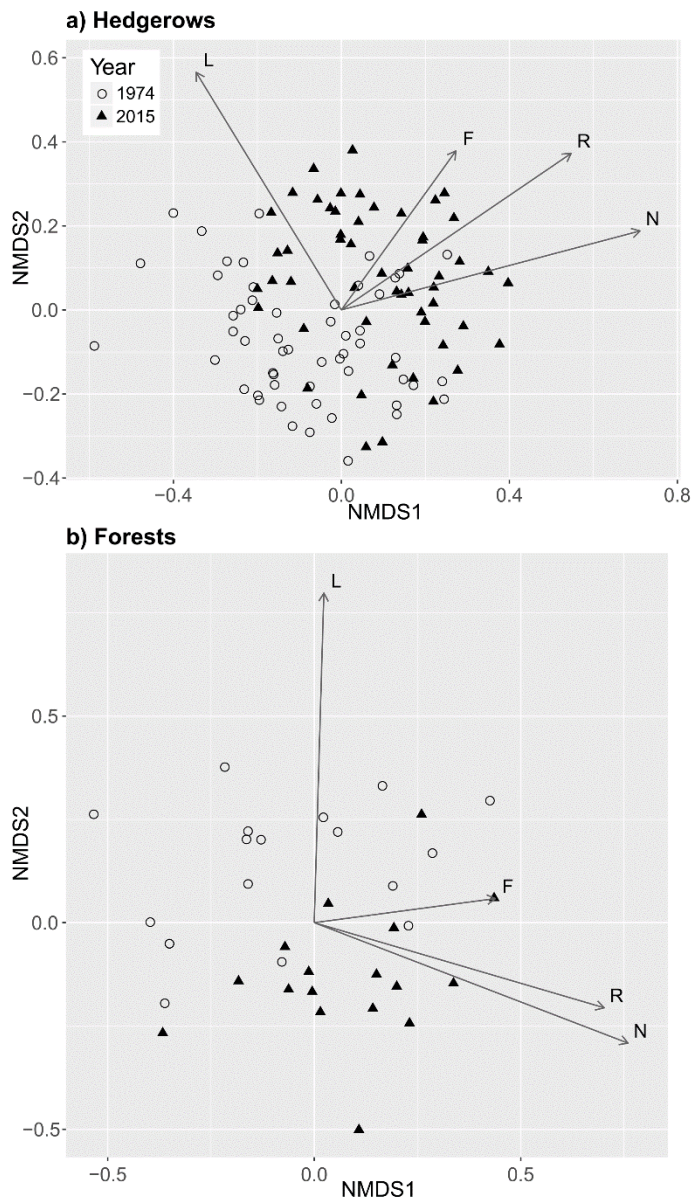


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795 **Figure 1. Study area.** Map showing the location of the study area in the province of Antwerp  
796 in the north of Belgium. The municipality of Turnhout is presented in detail with indication of  
797 studied hedgerows and forests. Source aerial picture: Geopunt Vlaanderen.

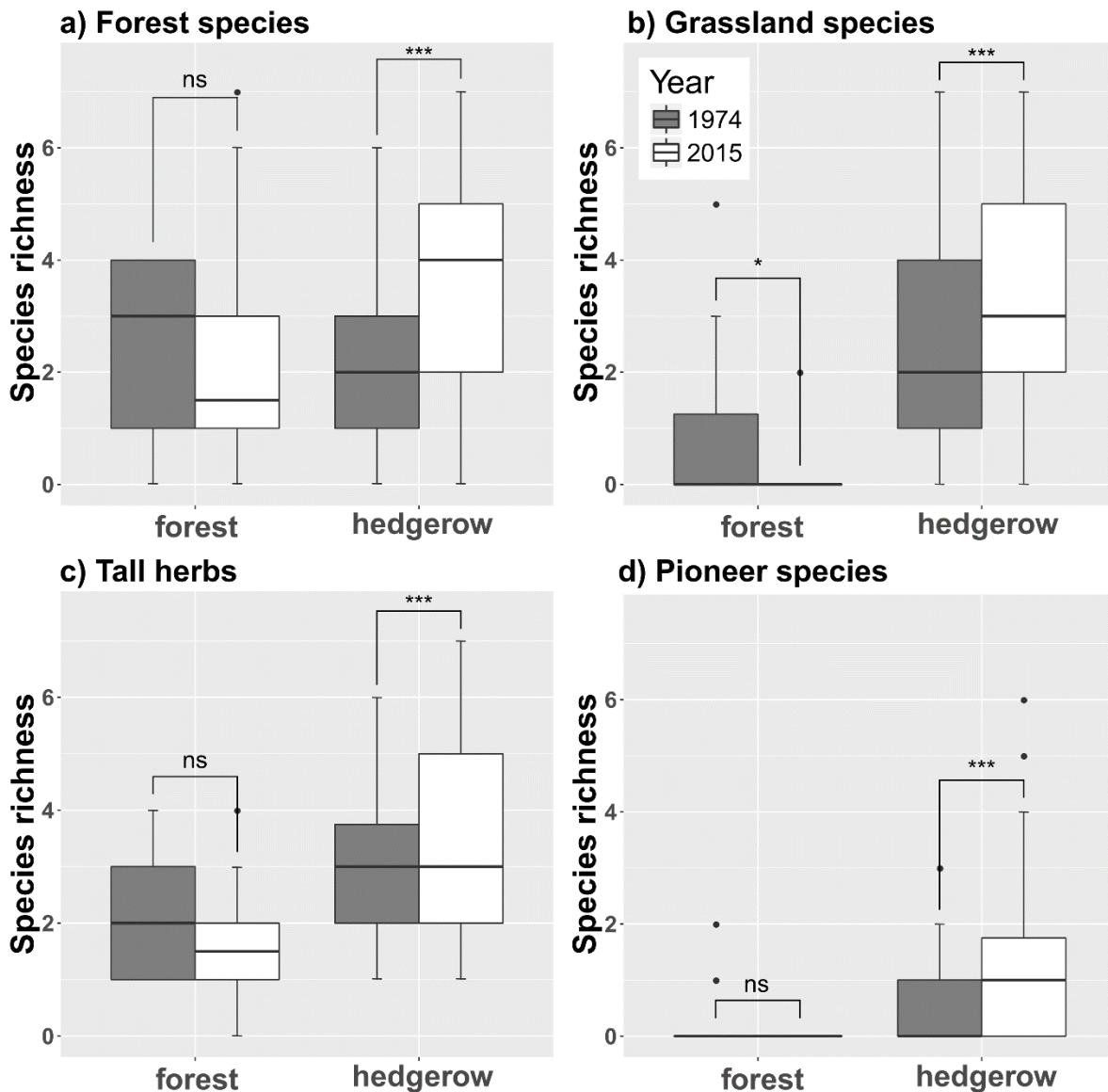
798

799 **Figure 2**



814

815 **Figure 2. NMDS analysis showing temporal vegetation shift.** NMDS-ordination diagrams  
816 (ordination based on Sørensen dissimilarity) for hedgerow plots (a) and forest plots (b) are  
817 shown. The diagrams include the original plots ( $n = 54$  for hedgerows and  $n = 20$  for forests)  
818 and the resurveyed plots ( $n = 54$  for hedgerows and  $n = 20$  for forests). The vectors generated  
819 via the 'envfit' analysis (function in the R package vegan) indicate the correlation of the axes  
820 with the Ellenberg indicator values.

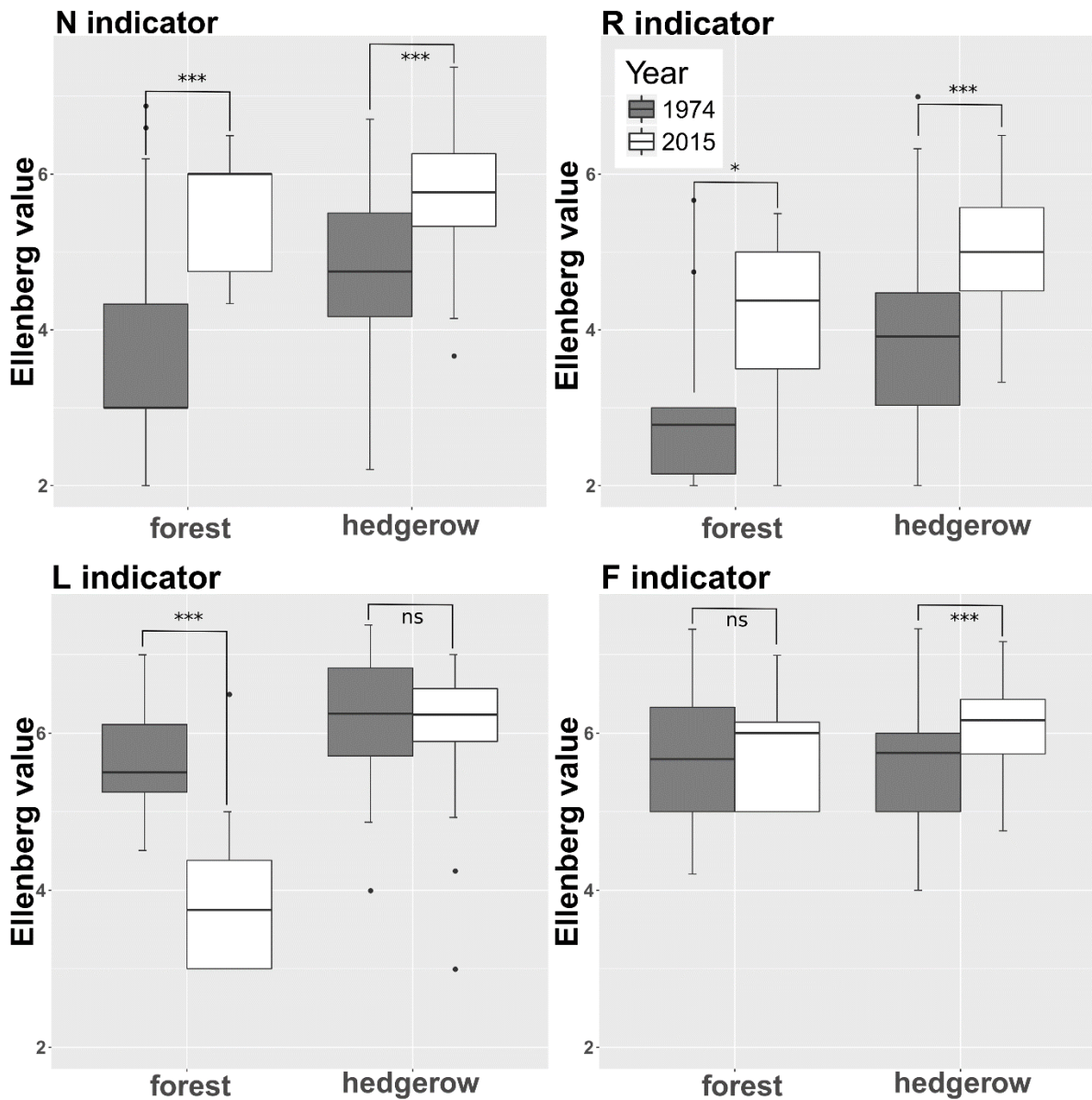


822

823 **Figure 3. Temporal vegetation change.** Changes in mean species richness in hedgerows  
 824 and forests between 1974 and 2015 for forest species (a), grassland species (b), tall herbs (c)  
 825 and pioneer species (d) (*sensu* Runhaar et al. 2004). The boxes indicate the 25% and 75%  
 826 quartile, with a median line and 2 whiskers showing the 10% and 90% quantiles. Significant  
 827 differences in species richness as derived from paired t-tests are indicated with asterisks (*p*-  
 828 value levels ns: not significant; \*\*\*:  $p \leq 0.001$ ).



829 **Figure 4**



830

831 **Figure 4. Shifts in Ellenberg indicator values.** Changes in mean Ellenberg values for soil  
832 fertility N (a), soil reaction R (b), light L (c), and soil moisture F (d) (*sensu* Ellenberg et al.  
833 2001) in hedgerows and forests between 1974 and 2015. The boxes indicate the 25% and  
834 75% quartile, with a median line and 2 whiskers showing the 10% and 90% quantiles.  
835 Significant differences in mean Ellenberg values as derived from paired t-tests are indicated  
836 with asterisks (*p*-value levels ns: not significant; \*:  $p \leq 0.05$ ; p\*\*\*:  $p \leq 0.001$ ).

837 **Table 1**838 **Table 1. Diversity statistics for 1974 & 2015.**

839 Diversity statistics for the vegetation in hedgerow plots and forest plots in 1974 and 2015:  
 840 species pool ( $\gamma$  diversity), average species richness ( $\alpha$  diversity  $^0D$ ), exponential of Shannon  
 841 ( $\alpha$  diversity  $^1D$ ) and beta diversity in terms of Sørensen dissimilarity ( $\beta_{Sor}$ ), turnover ( $\beta_{Sim}$ ) and  
 842 nestedness ( $\beta_{Nes}$ ) are shown. For the year 1974,  $\gamma$  diversity is presented in absolute number  
 843 of species (*cf.* original number of sampled plots *anno* 1974: hedgerows = 81; forests = 26) and  
 844 in rarefied number of species (*cf.* rarefied number of sampled plots *anno* 1974: hedgerows =  
 845 54; forests = 20). The significance in differences for these statistics between the two years is  
 846 indicated for the Chi squared test ( $Chi^2$ ), paired Wilcoxon signed-rank test ( $W$ ) or paired t-test  
 847 ( $T$ ), where the superscripts display the p-value levels (*ns*: not significant; \*:  $p \leq 0.05$ ; \*\*\*:  $p \leq$   
 848  $0.001$ ).

849

	1974	2015	Statistical test
<b>Hedgerows</b>			
Species pool ( $\gamma$ diversity)	79 ( $n = 81$ ); 70 ( $n = 54$ )	120 ( $n = 54$ )	$Chi^{2***}$ ( $n = 54$ )
Species richness ( $\alpha$ diversity $^0D$ )	mean = $8.69 \pm 2.93$ SD	mean = $13.20 \pm 6.13$ SD	$T^{***}$
Exponential of Shannon ( $\alpha$ diversity $^1D$ )	mean = $4.14 \pm 1.54$ SD	mean = $6.14 \pm 3.65$ SD	$W^{***}$
$\beta_{Sor}$	mean = $0.72 \pm 0.05$ SD	mean = $0.74 \pm 0.04$ SD	$W^*$
$\beta_{Sim}$	mean = $0.55 \pm 0.08$ SD	mean = $0.56 \pm 0.07$ SD	$T^{ns}$
$\beta_{Nes}$	mean = $0.10 \pm 0.05$ SD	mean = $0.12 \pm 0.06$ SD	$W^{ns}$
<b>Forests</b>			
Species pool ( $\gamma$ diversity)	33 ( $n = 26$ ); 30 ( $n = 20$ )	24 ( $n = 20$ )	$Chi^{2ns}$ ( $n = 20$ )
Species richness ( $\alpha$ diversity $^0D$ )	mean $5.60 \pm 3.47$ SD	mean $3.65 \pm 2.85$ SD	$T^{ns}$
Exponential of Shannon ( $\alpha$ diversity $^1D$ )	mean $2.92 \pm 1.97$ SD	mean $2.1 \pm 1.75$ SD	$W^{ns}$
$\beta_{Sor}$	mean $0.73 \pm 0.06$ SD	mean $0.67 \pm 0.09$ SD	$T^*$
$\beta_{Sim}$	mean $0.59 \pm 0.12$ SD	mean $0.52 \pm 0.09$ SD	$T^*$
$\beta_{Nes}$	mean $0.14 \pm 0.07$ SD	mean $0.153 \pm 0.04$ SD	$W^{ns}$

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