

1 **Title:** Interactive effects of past land use and recent forest management on the understory community in
2 temperate oak forests in South Sweden

3 **Running title:** Effect of forest management on land-use legacies

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31 The Authors declare that there is no conflict of interest.

32

33 Abstract

34 **Questions:** Past agricultural land use and forest management have shaped and influenced the understorey
35 composition in European forests for centuries. We investigated whether understorey vegetation
36 assemblages are affected by (i) legacies from a historical infield/outland agricultural system (i.e. a system
37 with nutrient-enriched vs. nutrient-depleted areas), (ii) recent management intensity (i.e. thinning/felling
38 activities), and (iii) the interaction of recent management and potential legacies.

39 **Location:** Oak forests in Skåne, south Sweden.

40 **Methods:** We use three vegetation surveys (1983, 1993/94 and 2014) and notes on management and land-
41 use history, available for 62 permanent 500 m² plots. We conducted linear mixed effect modelling to detect
42 both main and interactive effects of past land use and recent management on understorey diversity
43 measures and vegetation indicator values for light and fertility. We combined nonmetric multidimensional
44 scaling (NMDS) with permutational multivariate analysis of variance (PERMANOVA) and indicator species
45 analysis to detect compositional differences caused by past land use and/or recent management.

46 **Results:** Understorey diversity was mainly affected by management activities, but the former
47 infield/outland agricultural system was an important determinant of understorey composition. Understorey
48 composition of former infields reflected higher nutrient availability and lower light availability compared to
49 former outland. Past land use and recent management had interactive effects on light-related understorey
50 variables: for the less intensively managed plots, the outland plots contained more light-demanding species
51 than the infield plots, while for the more intensively managed plots, the light-demanding signature of the
52 understorey was similar for infield and outland plots.

53 **Conclusions:** Different intensities of past land use as well as recent forest management influenced the
54 composition of the forest understorey, and interactions were present. Therefore, careful consideration of
55 both the long-term land-use history and the more recent disturbances due to forest management are
56 necessary when making future predictions of understorey composition and diversity.

57

58

59 Key words

60 past land use, land-use history, land-use legacies, forest management, understorey composition,
61 understorey diversity, forest herb layer

62

63 Introduction

64 Forests worldwide, as well as most other ecosystems, have been dominated, shaped and influenced by
65 human activities for centuries and more (Bürgi & Gimmi, 2007; Williams, 1993). Hence, the European
66 forests that we know today were created by a long history of human land-use changes, and only very few
67 forests exist free of legacies from former human influence (Bengtsson, Nilsson, Franc, & Menozzi, 2000;
68 Gossner et al., 2014). Human activities affecting forests are very diverse (Foster et al., 2003), comprising
69 episodes of deforestation and agricultural use (Foster, Motzkin, & Slater, 1998), wood harvesting with
70 different levels of intensity (Gossner et al., 2014), manipulation of animal populations (Foster et al., 2003),
71 litter collecting (Bürgi & Gimmi, 2007), and grazing by domestic animals (Bengtsson et al., 2000).

72 Understanding how both past and present anthropogenic disturbances influence biodiversity and species
73 assemblages is essential for conservation. Here, we focus on two aspects of anthropogenic disturbances
74 that are common in European forests, but which rarely have been studied in combination, namely different
75 intensities of both past agricultural land use and current forest management practices for wood harvesting.

76 We assess their effects on the forest understorey layer, which represents the majority of plant species
77 richness in temperate forests (Gilliam, 2007). This layer is most likely to reflect land-use legacies because it
78 exhibits slow dynamics and is less easily manipulated (by e.g. plantation) compared to the overstorey.

79 Most present-day European forests occur on lands that at some point in history were used for agriculture,
80 and many studies have demonstrated that these forests still bear imprints of their past land use, which we
81 call land-use legacies (Blondeel et al., 2019; Emanuelsson, 2009; Flinn & Marks, 2007; Hermy & Verheyen,
82 2007; Perring et al., 2016; Vellend, 2003). Land-use legacies are often found in forest understoreys, due to a
83 limited dispersal and recruitment capacity of typical forest species (De Frenne et al., 2011; Verheyen,
84 Honnay, Motzkin, Hermy, & Foster, 2003). As a result, forest understorey compositions may depend on
85 environmental conditions that no longer occur in a forest stand (Jonason et al., 2014). Land-use legacies
86 affect the understorey directly, by past elimination of plants and their diaspores, as well as indirectly, by
87 altering environmental conditions such as soil pH, soil nutrient concentrations, soil organic matter content
88 and light availability (Flinn & Marks, 2007; Hermy & Verheyen, 2007). Several studies found that forest soils

89 on former arable land are still richer in nutrients and hence more productive as a result of past fertilization
90 practices, compared to so-called ancient forests without a history of agricultural use (Falkengren-Grerup,
91 Ten Brink, & Brunet, 2006; Koerner, Dupouey, Dambrine, & Benoit, 1997; Naaf & Kolk, 2015; Verheyen,
92 Bossuyt, Hermy, & Tack, 1999). These higher nutrient contents in post-agricultural forests can influence the
93 composition of the established vegetation after abandonment of cultivation, due to a dominance of
94 competitive species which hamper the establishment of slow-colonizing herbs (Baeten, Hermy, &
95 Verheyen, 2009; Koerner et al., 1997).

96 In addition, most European temperate forests are or have been managed for timber production, with
97 varying levels of intensity (e.g. clear-cuts, shelterwood systems, coppicing, single tree selection) (Gossner et
98 al., 2014). Extracting timber changes the tree age structure, composition of tree species and vertical
99 stratification, causing changes in the soil, litter and microclimatic conditions. This results in the alteration or
100 disappearance of microhabitats (e.g. dead wood, cavities, root plates or mature trees) that host forest
101 biodiversity (Chaudhary, Burivalova, Koh, & Hellweg, 2016). According to a meta-analysis by Chaudhary et
102 al. (2016), forest management generally induces an overall decrease in forest biodiversity, but the effect of
103 forest management differs between taxonomic groups (such as vascular plants, birds, fungi, beetles), and
104 depends on the management type and intensity. For understorey vascular plants in particular, forest
105 management can affect their diversity and composition through altering the light regime by creating
106 canopy gaps at variable points in time, as well as the soil conditions, through compaction of the soil or
107 changing nutrient cycles (Brunet, Fritz, & Richnau, 2010; Godefroid & Koedam, 2004; Godefroid, Massant,
108 & Koedam, 2005; Vangansbeke et al., 2015; Wagner, Fischer, & Huth, 2011).

109 Here, we are interested in how both recent forest management and past land-use intensity differences may
110 have interactive effects on understorey assemblages and their trajectories over time. Reasons to believe
111 such interactions are present arise from a study by Huston (2004), pointing out the importance of the
112 disturbance-productivity interaction as a determinant of species richness. Within this framework, we
113 consider the intensity of forest management as the disturbance factor, and different intensities of past
114 agricultural land use as a proxy for the productivity factor. Several other studies argue that diversity may be
115 a function of the interaction between disturbance and productivity, and therefore the productivity effects

116 on diversity can only be assessed when they are stratified by disturbance regimes (e.g. Kondoh, 2001;
117 Huston, 2014). For example, Proulx & Mazumder (1998) demonstrated that plant species richness increases
118 with increasing disturbance (in this case grazing pressure) in a nutrient-rich environment, but decreases in a
119 nutrient-poor environment. Furthermore, several studies highlight the occurrence of interactions between
120 legacies of past land use with natural disturbance processes such as forest fires, hurricanes and droughts
121 (Chazdon, 2003; Comita et al., 2010; Foster et al., 2003; Hogan, Zimmerman, Thompson, Nytch, & Uriarte,
122 2016). We believe that forest management actions can have similar effects on the forest vegetation as
123 natural disturbances, and hence can interact with land-use legacies as well. Some recent studies indeed
124 showed possible interactions between past land-use changes and alterations in present conditions through
125 management practices on species richness and composition (Janssen et al., 2018; Kelemen, Kriván, &
126 Standovár, 2014).

127 In this study, we use a unique dataset containing three vegetation surveys (in 1983, 1993/94 and 2014),
128 extensive soil data (1983 and 2014) and notes on forest management and past land use for 62 permanent
129 plots in oak forest in Southern Sweden. Our aim is to assess the combined effects of both past land use and
130 recent disturbances due to management on understorey composition and diversity. In the early medieval
131 period, a so-called infield-outland agricultural system emerged in the region, resulting in a distinction
132 between plots on former outland, managed for grazing, and plots on former infields, intensively manured
133 for crop production and hay (Emanuelsson, 2009; Emanuelsson et al., 2002). In addition, plots across both
134 past land use types also differed in the level of management intensity they experienced since the first
135 survey in 1983. This crossing of past land use with a two-level management intensity factor allowed us to
136 investigate both their main and interactive effects on the composition and diversity of the forest
137 understorey community over a period of three decades. In contrast to previous studies on interactions
138 between past land use and recent management (e.g. Janssen et al., 2017; Kelemen et al., 2014; Kolb &
139 Diekmann, 2004), we are defining past land-use change as a distinction between former infields (nutrient-
140 enriched) and former outland (nutrient-depleted), rather than the classical ancient/recent forest
141 distinction. Furthermore, we have the opportunity to investigate trajectories of change in the understorey
142 communities, thanks to the availability of three vegetation surveys over a time span of three decades.

143 Specifically, we investigated the following research questions:

- 144 (i) Are legacies from the former infield/outland agricultural system reflected in the community
145 composition and diversity of the understorey? Have these land-used legacies changed over
146 time?
- 147 (ii) Does recent forest management intensity affect the community composition and diversity of
148 the understorey?
- 149 (iii) Have recent disturbances due to forest management interacted with land-use legacies, causing
150 changes in the dynamics of the understorey composition and diversity between 1983 and
151 2014?

152 Material and methods

153 Study area: past land use and recent management

154 The study area comprises the south Swedish province of Skåne, an area of ca 11 000 km² and ca 1.3 million
155 inhabitants. The border between the central-European sedimentary bedrock area (here mainly limestones
156 and clay shales) and the Fennoscandian shield of Precambrian crystalline rocks (granite and gneiss) crosses
157 the province from southeast to northwest, resulting in a gradient from the more densely populated
158 southwest with fertile agricultural soils to the northeastern part dominated by forests on less productive
159 soils (Figure 1, including forest distribution). Most soils have not developed directly upon bedrock but
160 originate from Quaternary deposits formed during and after the latest (Weichselian) glaciation which
161 completely covered Skåne with its icesheet.

162 We sampled 62 permanent forest plots, situated in forests dominated by oak (*Quercus robur* and in some
163 cases *Quercus petraea*) and hornbeam (*Carpinus betulus*) in the tree layer. Distances between study plots
164 varied strongly, ranging from 15 m to 111 km, with a median value of all distances between plots of 41 km.

165 To characterize the past land use of each plot, we distinguished between former infields and outland
166 (Emanuelsson, 2009). A permanent infield-outland system emerged in the early medieval period when
167 villages became sedentary. Infields were located close to settlements or farm-houses, and were intensively

168 manured. The infields were either used for crop production or managed as semi-open wooded meadows
169 which produced hay, small-dimension wood products from coppice, as well as some timber trees. The
170 outland was situated further from villages, and was managed jointly by the village for grazing, timber and
171 other wood-based products. The manure from grazers was then applied on the infield lands. The infield-
172 outland system was functional until ca. 1800-1850 (Emanuelsson et al., 2002). Outland area gradually
173 reduced in extent with the increasing demand for arable land due to continuous population increase since
174 the 1700s. Based on cadastral maps (mainly spanning the period 1730-1870) at the final phase of this land
175 use system, (<https://historiskakartor.lantmateriet.se/historiskakartor/search.html>), we classified 23 plots as
176 'Outland' (i.e. plots on former outland), and 39 plots as 'Infields' (i.e. plots on former infields) (Appendix
177 S3). According to the cadastral maps, none of the infield plots has been used as arable field since at least
178 ca. 1800. The majority of the stands are semi-natural, and developed from semi-open conditions to closed
179 stands when livestock grazing (outland) or wooded meadow/coppice management (infield) ceased. In some
180 sites (both infield and outland), oak was planted after felling of the previous stand. The evidence of
181 continuous presence of trees on the historical maps varies, but all plots have been wooded since at least
182 1900.

183 In the area, forests are or have been managed for timber production, comprising felling practices with
184 different levels of intensity. In this study, we made a rough distinction between 31 plots that were more
185 intensively managed over the period 1983-2014 (referred to as 'High' management), and 31 plots that were
186 less intensively managed (referred to as 'Low' management). We combined the different management
187 classification approaches applied during the three surveys to reach this final management category
188 (Appendix S2). We gave the most weight to the 1993 classification, because (i) it had a higher level of detail
189 as the surveyors were explicitly interested in vegetation responses to management, and (ii) management
190 intensity in the area was at its highest level around 1993, so differences between more and less intensively
191 managed plots should have been most clear during this survey. Counts of the number of stumps, available
192 in a subset of 35 plots in 2014, confirmed our management classification, as we found significantly
193 ($p=0.005$) more stumps in the more intensively managed plots (17.97 stumps on average), compared to the
194 less intensively managed plots (6.17 stumps on average) (see Appendix S2 and S3).

195 Soil and overstorey characterization
196 During the 1983 and 2014 surveys, samples were taken from the upper 5 cm of the mineral soil (i.e. after
197 removal of the litter layer). For 1983, we have data on clay content and pH_{KCl} (see previous papers, such as
198 Brunet et al., 1996, Diekmann et al., 1999) for details on soil sampling and chemical analyses). For 2014, we
199 have data on soil total carbon (C), nitrogen (N) and phosphorus (P) (see Appendix S4 for details on soil
200 sampling and chemical analyses in 2014). Plots on former infields had a higher clay and total P content in
201 the soil, compared to former outland. Since texture is an intrinsic property of the soil, the differences in
202 clay content suggest that when the infield-outland agricultural system was established, richer and more
203 clayey soils were often chosen deliberately for infield use, given their potential for higher yields. The higher
204 total P concentrations in former infields are likely a result of their fertilization history, which can leave
205 imprints for at least a century after abandonment of agricultural use (Compton & Boone, 2000; Dupouey,
206 Dambrine, Laffite, & Moares, 2002; Fraterrigo, Turner, Pearson, & Dixon, 2005; Koerner et al., 1997).
207 Overall, the differences in soil chemistry between infield and outland plots are probably partly related to an
208 initial preference for richer clay soils for infield use (Flinn, Vellend, & Marks, 2005), after which the more
209 intensive land use on infields has probably reinforced the higher fertility and productivity that these soils
210 exhibit. Plots with a lower recent management intensity had significantly higher soil pH values and total P
211 content, likely caused by a higher degree of protection of richer oak forests, which are therefore less
212 intensively managed. There were no significant differences in total C and N content between either the
213 recent management or the past land-use categories (see Appendix 5 for soil data).

214 Regarding the overstorey characterization, plots with high and low intensity management had similar tree
215 cover values in 1983 and 2014, while more intensively managed plots had a significantly lower tree cover
216 during the intermediate survey in 1993, reflecting the peak in forest management activity in the region at
217 the time of the intermediate survey. Dominant tree species were *Quercus robur* (or *Quercus petraea* in a
218 few cases), *Carpinus betulus* and *Corylus avellana* (Figure 1b). At the time of the first survey (1983), both
219 former infield plots and less intensively managed plots were characterized by more *Carpinus betulus* and
220 *Corylus avellana* in the tree layer, and less *Quercus robur/petraea*, compared to former outland and more
221 intensively managed plots respectively (Figure 1c/d). The shade-casting ability (SCA) of the tree layer (i.e. a

222 cover weighted average of the SCA scores per species, listed in Appendix S6; see also Verheyen et al.
223 (2012)) was similar between infield and outland plots within the more intensively managed plots, but
224 clearly higher for infield than outland plots within the less intensively managed plots (see Appendix S7). We
225 keep these soil and overstorey characteristics in mind when interpreting the results.

226 Vegetation surveys

227 In July-August 1983, 135 permanent plots were established by Professor em. Germund Tyler to study the
228 relationships between soil, macrofungi and tree and herb layer species (e.g. Tyler, 1989). All these plots
229 were resurveyed a first time in July-August 1993/1994 (further referred to as 1993) and a second time in
230 August 2014, although only 62 of the plots were relocated at that time. All plots were 500 m² (20 m x 25
231 m). Criteria for the original plot selection in 1983 included no current livestock grazing and no thinning
232 during approximately the five years prior to surveying (Brunet et al., 1996; Diekmann et al., 1999).

233 Vegetation data were expressed as an estimated cover percentage for each individual species present. Two
234 vegetation layers were distinguished: the *understorey* and the *tree layer*, respectively comprising all
235 vascular plants below 5 m and above 5 m height (see Appendix S1 for details on the vegetation data).

236 Response variables

237 For each plot at each survey time, we characterized the understorey diversity by calculating the **Shannon-**
238 **Wiener index** (i.e. plot-level diversity), and the **Bray-Curtis dissimilarity** (Bray & Curtis, 1957) (i.e. diversity
239 among plots). We quantified the Bray-Curtis dissimilarity of each plot by creating a pairwise dissimilarity
240 matrix and calculating for each plot the mean of the dissimilarities to all other plots. To further enhance our
241 understanding of the processes and mechanisms behind possible changes in understorey composition and
242 diversity due to differences in past land use and recent management intensity levels, we investigated plot
243 characteristics related to the soil and light conditions. As a proxy of the prevailing plot-specific soil
244 properties and light conditions, we calculated **mean Ellenberg indicator values for soil fertility (N) and light**
245 **(L)**, based on presence/absence using the individual species' indicator values (Ellenberg & Leuschner, 2010).

246 Statistical analyses

247 To test how contemporary management intensities interact with past land use to alter the plot
248 characteristics over time, we conducted linear mixed effect modelling with four response variables related

249 to the understorey (and described above): Shannon-Wiener index, Bray-Curtis dissimilarity, Ellenberg N,
250 and L mean values. We confirmed that each response variable is normally distributed, using histograms.

251 We found the optimal model for each response variable according to the approach described by Zuur, Ieno,
252 Walker, Saveliev, & Smith (2009), starting from the *beyond optimal model* (Equation [1]).

253 Response variable \sim PastLandUse + Management + Year + PastLandUse:Management + PastLandUse:Year +
254 Management:Year + (1 | PLOT ID) Equation [1]

255 We added the variable *Year* to the model as a fixed effect, because we are interested in how each response
256 variable has changed over time. We modelled *Year* as a factor with three levels (i.e. 1983, 1993 and 2014),
257 rather than a continuous variable, to detect possible shifts in trends between the first period (1983-1993)
258 and the second period (1993-2014). *Management (High or Low)* and *Past Land Use (Infield or Outland)*
259 were both factors with two levels. To account for temporal pseudoreplication, given the fact that each plot
260 was surveyed three times, we added *PLOT ID* to the model as a random intercept. We added the
261 interaction between past land use and management to the model, to investigate whether the effect of
262 recent management practices on the response variables is dependent on the past land use category. For
263 both past land use and management, we also added the interaction with *Year* to the model; to study
264 whether the response variables exhibit different temporal trends for different past land use or recent
265 management categories. To detect possible multicollinearity among the explanatory variables, we
266 calculated variance inflation factors (VIF) according to Zuur et al. (2009). VIF values were very low (<1.1),
267 indicating low collinearity.

268 Next, we performed backwards elimination of the explanatory variables using maximum likelihood-fitted
269 models at a 5% level of significance (Zuur et al., 2009), leading to the optimal model. For each response
270 variable, we refitted the optimal model with restricted maximum likelihood (REML). For the final (optimal)
271 model of each response variable, we inspected model diagnostic plots to check validity; all were
272 satisfactory. For each model, we calculated the marginal and conditional R^2 , representing the variance
273 explained by fixed factors and the variance explained by both fixed and random factors, respectively
274 (*MuMIn* package; (Nakagawa & Schielzeth, 2013)). Given the high number of parameters in the *beyond*

275 *optimal model*, compared to a sample size of 62 plots, there is a possibility of overfitting. Therefore, we also
276 performed a model comparison based on information criteria (AIC), which resulted in the same final
277 (optimal) model for each response variable (Appendix S8). Additionally, we repeated the backwards
278 elimination procedure for separate models for each year, which reduces the number of explanatory
279 variables and thus the risk of overfitting. This additional analysis led to identical qualitative findings for all
280 response variables except Ellenberg N, where an effect of recent management was identified in 2014 that
281 was absent in other analysis approaches (Appendix S9).

282 To evaluate differences in understorey community composition in each survey year, between former infield
283 plots and former outland plots, and between plots with high and low levels of management intensity, we
284 conducted a permutational multivariate analysis of variance (PERMANOVA; *vegan* package; Anderson,
285 2001) using Bray-Curtis dissimilarities with 999 permutations (based on abundance data; Bray & Curtis,
286 1957). A significant PERMANOVA can result from differences among groups in their mean (centroid) values
287 or the dispersion (i.e. spread) of values around the centroid of each group (Anderson, Ellingsen, & McArdle,
288 2006; Brudvig, Grman, Habeck, Orrock, & Ledvina, 2013). The Bray-Curtis dissimilarity as described above
289 (and used in the linear mixed effect modelling) on the other hand, only contains information on the
290 dispersion. Hence, a PERMANOVA analysis can reveal compositional differences among groups resulting
291 from differences in their mean (centroid) values, which would be overlooked when only focussing on the
292 Bray-Curtis dissimilarity. We followed the PERMANOVA with a test for homogeneity of multivariate
293 dispersion (PERMDISP), which evaluates the mean distance of each plot to the group centroid (Brudvig et
294 al., 2013). We used nonmetric multidimensional scaling (NMDS) to visualize the compositional differences
295 in the understorey vegetation. To identify species that typified the different plot groups (i.e. former infields
296 vs. outland, and high vs. low intensity management), we also conducted an indicator species analysis
297 (Dufrêne & Legendre, 1997) for the understorey data in each survey year, with the infield/outland and the
298 high/low management distinction as classification variables (function *multipatt*; *indicspecies* package;
299 Ampoorter et al., 2015; De Cáceres & Legendre, 2009). We performed t-tests to compare the mean
300 Ellenberg N and L values of the indicator species.

301 To visualize changes in the understorey composition over time, for the different land-use and management
302 categories, we made a NMDS plot showing the mean and standard error of the NMDS coordinates of the
303 plots for each of the 12 plot groups, i.e. all possible combinations of survey year, past land use and recent
304 management. To facilitate interpretation, we added the following variables to the NMDS-plot: Ellenberg N
305 and L, tree cover, shade-casting ability, soil total P and clay content, and soil pH. All data analyses were
306 performed in R version 3.4.3 (R Core Team, 2017).

307 Results

308 For all four models, marginal R^2 (R^2_m) was quite low (between 0.06 and 0.17) (Figure 2; Appendix S10),
309 suggesting that the fixed effects *Year*, *Past Land Use* and *Disturbance* only explained a small part of the
310 variance. Values for conditional R^2 (R^2_c) were higher (between 0.48 and 0.86), indicating that a high
311 proportion of the variance can be explained by the random effect *PLOT ID*. This suggests that other
312 (unmeasured or unmodelled) variables could be important. We did not investigate such variables as the
313 focus of our study was to detect main and interactive effects of past land use intensity and recent
314 management.

315 For both the Bray-Curtis dissimilarity (beta diversity) and the Shannon-Wiener index (alpha diversity), the
316 only significant predictor that was retained after model selection was the factor *Year* (Figure 2; Appendix
317 S10). Hence, these diversity measures changed significantly over time, but the changes were not related to
318 either the past land use or recent management category. The Shannon-Wiener biodiversity index increased
319 significantly between 1983 and 1993 (+0.27 on average), but then decreased again to a level not
320 significantly different from the original 1983 level. Bray-Curtis dissimilarity only started to increase
321 significantly after the second survey, but the increases were minor (+0.042 on average between 1993 and
322 2014).

323 Ellenberg N values were significantly affected by past land use, with values being 0.46 units higher in
324 former infield plots compared to former outland plots. In addition, during 1983-2014, we observed a small
325 (+0.16) but significant increase in Ellenberg N values (Figure 2; Appendix S10); there was no evidence for
326 interactions.

327 We observed a small but significant increase in Ellenberg L values (+0.14) between 1983 and 1993. After
328 1993, Ellenberg L values decreased again to a level not significantly different from the original 1983 level.
329 Over the entire period, we found a significant interactive effect between past land use and recent
330 management disturbances on Ellenberg L values. For the plots with low recent management, Ellenberg L
331 values were on average 0.48 units higher in outland compared to infields. For the plots with more intensive
332 recent management, Ellenberg L values of infield and outland plots were closer to each other (Figure 2;
333 Appendix S10).

334 With PERMANOVA, we found a significant difference in the understorey composition between infield and
335 outland plots in each survey year (Figure 3). The permutational test for homogeneity of multivariate
336 dispersion (PERMDISP) indicated that this difference was driven by different mean multivariate
337 composition between infield and outland plots, and not the degree of multivariate dispersion (Figure 3).
338 This explains why no significant effects of past land use on the Bray-Curtis dissimilarity were found with the
339 linear mixed effect modelling approach. Differences in the understorey composition between plots with
340 high and low levels of management intensity were also significant in each survey year, although significance
341 was often marginal and R^2 values were lower compared to the infield/outland PERMANOVA tests (Figure 3).
342 Differences in community composition between infield and outland plots can be related to the richer clay
343 soils and the higher tree cover and SCA found in infield plots, compared to the outland plots (Figure 3).
344 Compositional differences between less and more intensively managed plots can also be related to the
345 richer clay soils and the higher tree cover and SCA, which occur in the plots with lower management
346 intensity.

347 Typical species on former infields were *Convallaria majalis* and *Poa nemoralis*, while typical former outland
348 species included *Dryopteris carthusiana*, *Juncus effusus* and *Carex pilulifera* (but these species were not
349 indicators in 2014). *Mercurialis perennis*, *Melica nutans* and *Hepatica nobilis* (not in 2014) were indicative
350 of a less intensive management, while *Betula pubescens/pendula* was indicative of a higher management
351 intensity (Figure 3, Appendix S11). The following commonly prevailing herbaceous species seemed
352 indifferent for both past land use and recent management intensities, and were found in all plot groups:
353 *Oxalis acetosella*, *Maianthemum bifolium*, *Viola spp.*, *Rubus idaeus*, and *Galeopsis spp.*. Comparison of

354 mean Ellenberg N and L values between indicator species groups only revealed significant differences in
355 Ellenberg N values in 1983 (infield indicators: 6.14; outland indicators: 3.71; $t_{9,98} = 2.69$; $p = 0.023$).

356 For all outland plots, and for the infield plots with high management intensity, the direction of
357 compositional change indicated by the mean NMDS (Figure 4) showed similar patterns, first going down
358 along the second axis, and then going up along the same axis. For the infield plots with low management
359 intensity, we observed an initial small upwards shift along the second axis between 1983 and 1993,
360 followed by a bigger shift in the same direction between 1993 and 2014. The understorey compositions of
361 more intensively managed infield and outland plots are converging over time, compared to the less
362 intensively managed plots. As Ellenberg L values are negatively related to the second axis of variation, it
363 seems that the compositional shift over time is partly related to an initial increase in light-demanding
364 species between 1983 and 1993, followed by a decrease in these species after 1993. All former outland
365 plots had negative means along the first axis of variation, while means for former infields were centred
366 around zero or had positive values. This shows that compositional differences between former infields and
367 outland can mainly be seen along the first axis. Also, the first axis of variation was strongly correlated with
368 Ellenberg N and to a lesser extent shade-casting ability and tree cover, which indicates that more nutrient-
369 demanding understorey species and more shade casting overstorey species have a higher affinity for
370 infields compared to outland.

371 Discussion

372 This is the first study, to our knowledge, investigating both the main and interactive effects from legacies of
373 a historical infield/outland system and recent management intensity levels on contemporary understorey
374 compositions and their trajectories over time. We found that plot-level understorey diversity (i.e. alpha
375 diversity) depended mainly on recent management intensities, and not on past land use. Higher levels of
376 disturbance due to management positively affected alpha diversity. We found dissimilarities in species
377 composition (i.e. beta diversity) among plots with different past land uses, and (to a lesser extent) different
378 recent management intensities. Legacies from the former infield/outland agricultural system clearly
379 persisted in the nutrient-demanding signature of the understorey. Interestingly, we also found an indirect

380 effect of past land use on the light levels at the forest floor, through its effect on the soil nutrient
381 availability. The more nutrient-rich soils of former infields seemed to result in forest canopies casting a
382 deeper shade. However, recent management activities overruled this effect of past land use on the light-
383 demanding signature of the understorey, resulting in similar indicator values for light regardless of past
384 land use when plots were intensively managed.

385 Research question 1: Land-use legacies in the understorey

386 We found clear compositional differences in the understorey between former infields and former outland
387 (Figure 3). Compositional differences in the forest understorey due to past land use have been consistently
388 reported in the literature (e.g. Brudvig et al., 2013; Hermy & Verheyen, 2007), and can be related to
389 fragmentation, dispersal limitations, and recruitment limitations due to differences in soil properties
390 (Baeten et al., 2009). While fragmentation and dispersal limitations are outside the scope of this study, we
391 present evidence that at least part of the compositional differences in our study plots are related to the
392 higher soil nutrient contents in the infield plots. Both the direction of the environmental variables on the
393 NMDS-plots (Figure 3) and the significantly higher amount of nutrient-demanding species in the
394 understorey of former infields suggest that nutrient availability drives compositional differences between
395 infield and outland plots. Similar findings have been noted where more extreme land use comparisons (i.e.
396 ancient vs. recent forest) have been made (e.g. Dupouey et al., 2002; Koerner et al., 1997).

397 Research question 2: impact of recent management on the understorey

398 We found that different levels of recent management intensity affected the community composition of our
399 study plots, in terms of their mean position in the ordination figures. We also observed an increase in plot-
400 level diversity between 1983 and 1993, followed by an overall decrease between 1993 and 2014 across all
401 past land use/management combinations. These changes are probably related to the overall management
402 intensity trajectory for the entire region. Overall management intensity in the region increased after the
403 ratification of the *Swedish Broadleaves Act* in 1984, which prescribed that oak/hornbeam stands larger than
404 0.5 ha must not be converted to coniferous plantations, but regenerated with oak or other temperate
405 hardwoods, and which stimulated interest in active management of hardwood forests. After 1993,
406 management intensity decreased again due to changes in the Swedish forest policy that now gave more

407 importance to the environmental goal of forests whereby biodiversity was to be secured and ecosystems
408 conserved (Simonsson, Gustafsson, & Östlund, 2015). This suggests that management intensity and alpha
409 diversity are positively correlated. Several other studies reported similar findings, where forest
410 management has a positive effect on species richness of the understorey vegetation (e.g. Brunet,
411 Falkengren-Grerup, & Tyler, 1997). The dissimilarity in species composition among plots increased slightly
412 between 1993 and 2014, and displayed the opposite trend to alpha diversity. This result can be explained
413 by the dependence of the Bray-Curtis index on alpha diversity, where both measures are inversely
414 correlated due to the multiplicative definition ($\alpha \times \beta = \gamma$) (Jost, 2007). Hence, a decrease in
415 alpha diversity due to the disappearance of some species can result in plots becoming more dissimilar and
416 thus an increase in beta diversity.

417 The level of recent management intensity, according to our classification, did not affect the nutrient-
418 demanding signature of the understorey. However, we observed an overall eutrophication signal over time
419 since 1983 over all plot groups. This can be attributed to the closing of the canopy related to an overall
420 decrease in management activities after 1993 as well as (but probably to a lesser extent) increased
421 atmospheric N depositions (Verheyen et al., 2012).

422 The light-demanding signature of the understorey was affected by both the overall change in management
423 intensity over time due to the Swedish forest policy and the more subtle management differences between
424 plots. The overall increase in light-demanding species during 1983-1993 is likely the result of the increased
425 management activity, creating more canopy openings (see Figure 1b), followed by an overall decrease in
426 light-demanding species once management activity started decreasing again. Additionally, the significant
427 main positive effect of management intensity on the light requirement of the understorey reflects our
428 distinction between plots with high and low management intensity. This effect can be related to the higher
429 share of *Carpinus betulus* and *Corylus avellana* in the less intensively managed plots, which cause higher
430 shade levels at the forest floor (see 'Soil and overstorey characterization').

431 Research question 3: interactive effects of past land use and recent management on the
432 understorey
433 We found a clear interactive effect between past land use and recent management levels on the light
434 requirement of the understorey. Within the less intensively managed plots, infield plots had fewer light-
435 demanding species than outland plots. This decline is likely associated with the higher soil nutrient content
436 in infield plots, resulting in a denser (sub)canopy and lower light availability at the forest floor compared to
437 the less nutrient-rich outland plots. Indeed, when characterizing the overstorey of the study plots (see '*Soil*
438 *and overstorey characterization*') we found that former infield plots had a higher share of *Corylus avellana*
439 and *Carpinus betulus* in their (sub)canopy, which can cause high shade levels. Similar examples of lower
440 light transmission on richer soils, potentially due to a denser layer of subcanopy trees, have been reported
441 in other parts of the world (e.g. Coomes & Grubb, 1996; Coomes et al., 2009; Tilman, 1988). Within the
442 more intensively managed plots however, the understorey light requirements of infield and outland plots
443 were similar, indicating that recent disturbances in the tree and shrub layer due to management practices
444 have caused similar light levels at the forest floor, regardless of soil fertility, and thus regardless of the past
445 land use. In other words: recent management disturbances might have 'overruled' differences in light
446 availability due to past land use. We also observed an overruling effect of recent management disturbances
447 for compositional differences among plot groups. Across both land-use intensities, the intensively managed
448 plots have become more similar over time, while this was not the case for the group of less intensively
449 managed plots, where communities on former infield and outland are still very distinct from each other in
450 2014. These findings contrast with Jonason et al. (2016), who observed that clear-cutting sustained legacies
451 from former use as meadowland. However, they observed only small differences in soil nutrients between
452 land-use types (i.e. forest history vs. meadow history), while soil nutrient content was an important driver
453 behind land-use legacies (resulting from infield vs. outland use) in our study.

454 Conclusion

455 Recent forest management intensity had a positive effect on plot-level diversity. The former infield/outland
456 agricultural system was an important determinant of both the nutrient- and light-demanding signature of
457 the understorey composition. The level of disturbance intensity due to recent management practices
458 interacted with this past land-use effect, but only on the light-demanding signature of the understorey,

459 where differences resulting from past land use had disappeared in the more intensively managed plots. Our
460 results differ from previous studies, where disturbances were found to preserve legacies from past land use
461 (e.g. Hogan et al., 2016; Jonason et al., 2016).

462 Our findings suggest that while increasing the management intensity could increase plot-level diversity, it
463 might reduce diversity in community composition. Especially with regard to light-demanding species,
464 understoreys in infield and outland plots will become more similar when management intensity increases.

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472 Data availability statement

473 We intend to archive all data used in this paper on our public website: www.pastforward.ugent.be.

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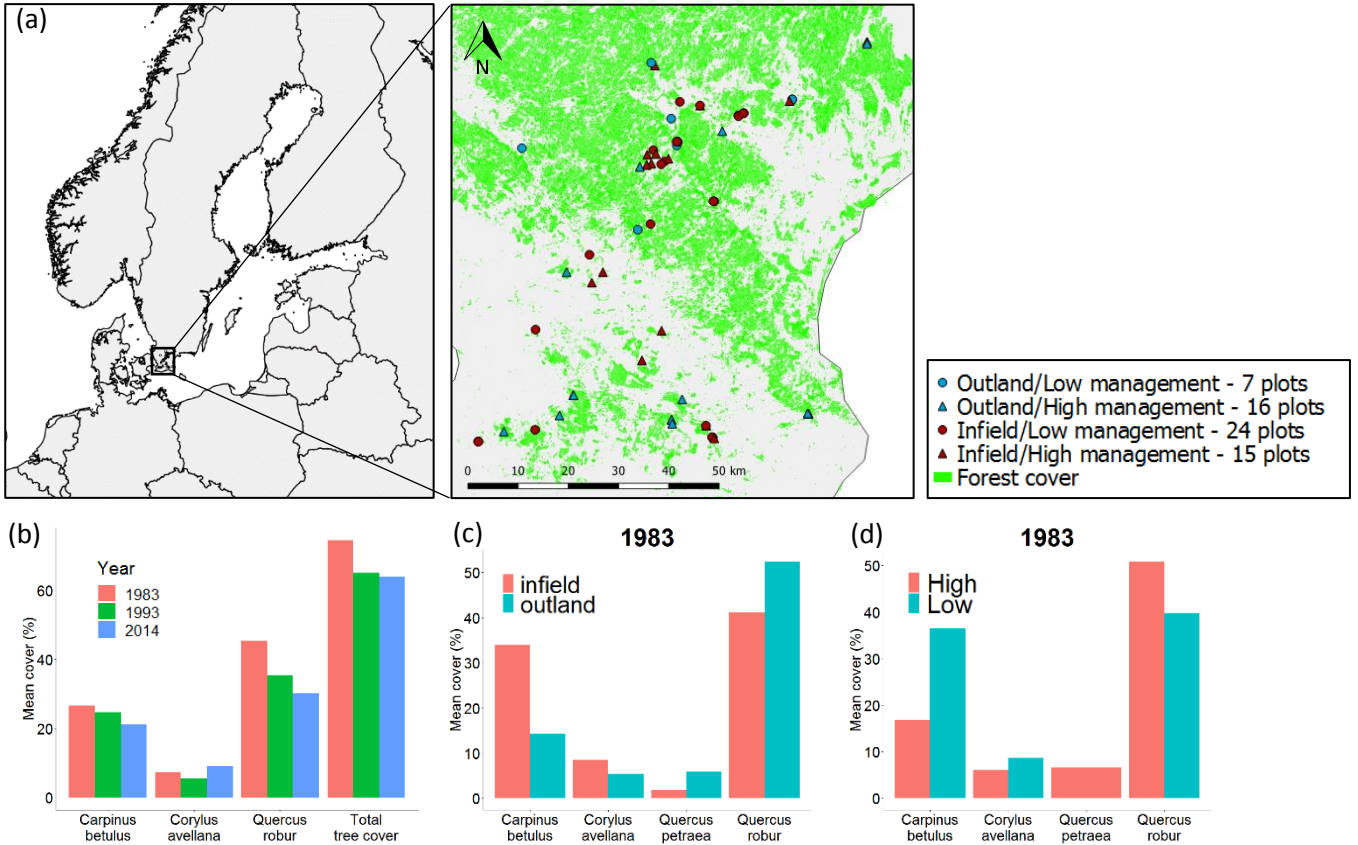
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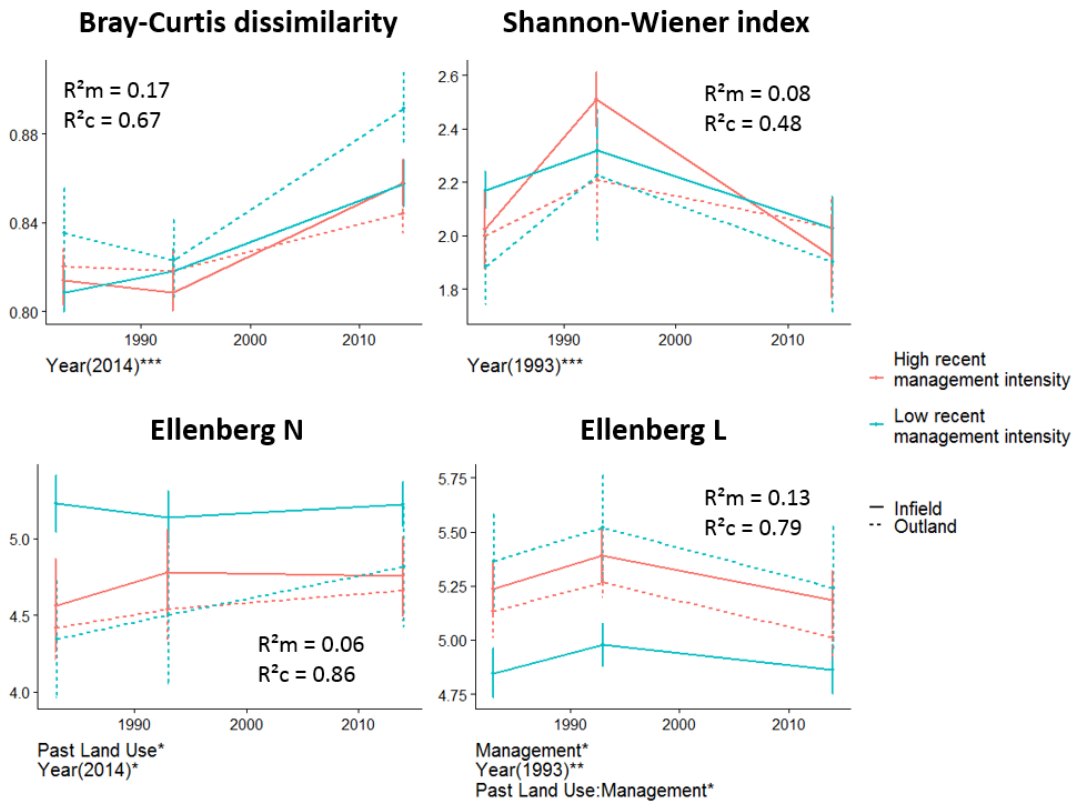
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650 Figures



658 *Figure 1 (a) Geographical location and distribution of the 62 study plots. The number of plots in each land use category, which is the*
 659 *combination of past land use and recent management intensity, is shown in the legend. (b) Mean cover (%) of the three most*
 660 *dominant tree species, as well as the total tree layer in each survey year. (c) Mean cover of the dominant tree species in 1983 for*
 661 *infield and outland plots. (d) Mean cover of the dominant tree species in 1983 for plots with high and low recent*
 662 *management intensity.*

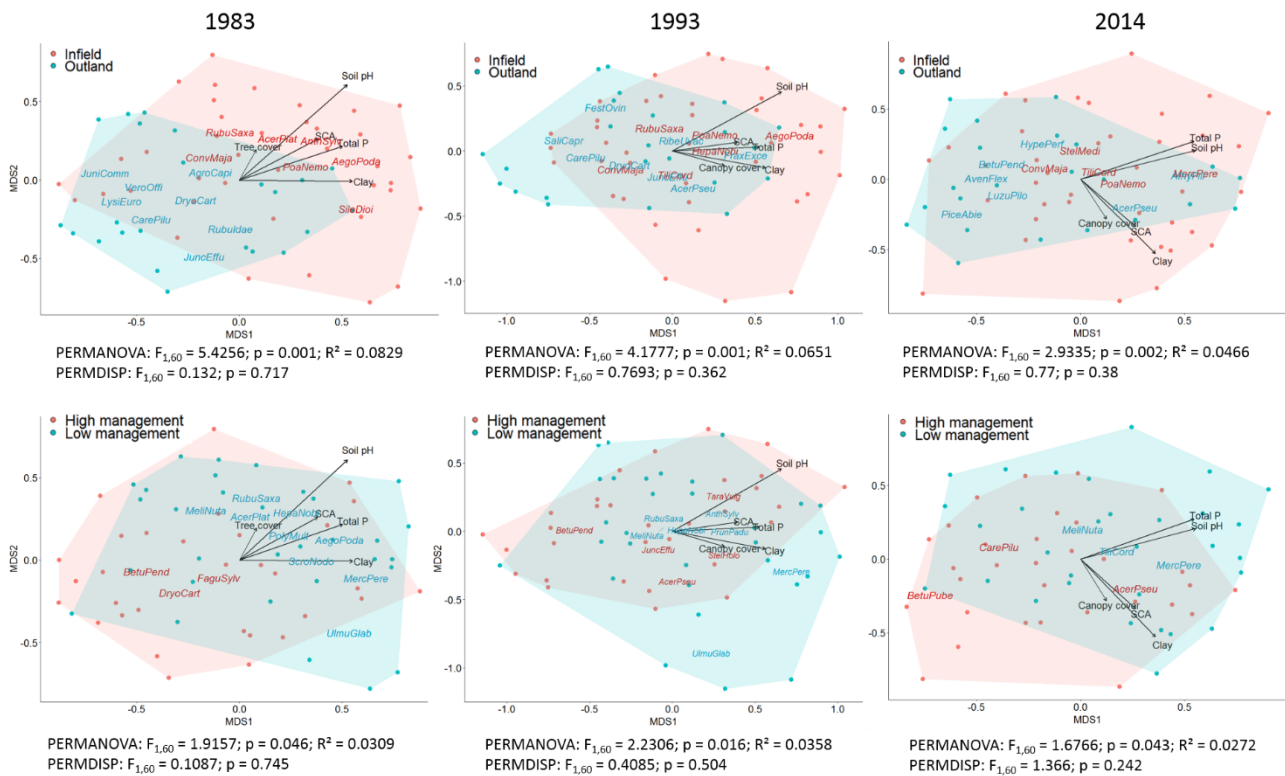
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665

666 *Figure 2 Temporal changes in mean values (and standard errors) of the four response variables representing understorey diversity*
 667 *and composition. The level of recent disturbance by forest management is indicated by the line color (red = high; blue = low), while*
 668 *the past land use category is indicated by the line type (continuous = infield; dotted = outland). Below each graph, the significant*
 669 *predictors that were retained in the final model of the response variable are shown, with their level of significance ('***' for*
 670 *p<0.001; '**' for p<0.01; '*' for p<0.05). Interactions between predictors are indicated with ':'. The marginal and conditional R²*
 671 *(R²m and R²c respectively) for the final model of each response variable are also given. See Appendix S10 for the full model results.*

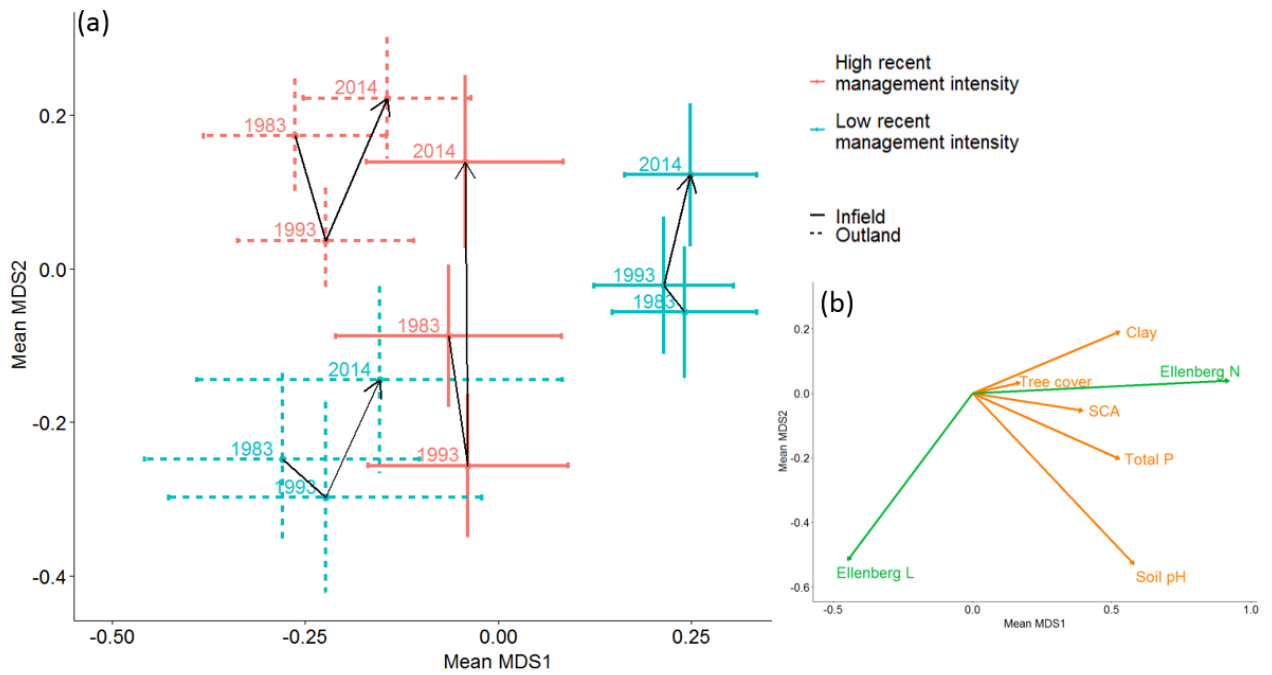
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673

674 Figure 3 NMDS of understory composition for each survey year. In the upper row, red dots represent former infield plots and the
 675 species in red are the indicator species of infield plots; blue dots represent former outland plots and the
 676 species in blue are the indicator species of outland plots. In the lower row, red dots represent plots with high levels of management intensity and their
 677 respective indicator species are shown in red; blue dots represent plots with low levels of management intensity and their respective
 678 indicator species are shown in blue. The arrows indicate the variables characterizing the soil and overstorey of the plots, i.e. soil pH,
 679 soil clay and total P content, tree cover, and shade-casting ability. Species are abbreviated with the first four characters of the genus
 680 and species name. The following species occur on the figure: *Acer platanoides*, *Acer pseudoplatanus*, *Aegopodium podagraria*,
 681 *Agrostis capillaris*, *Anthriscus sylvestris*, *Athyrium filix-femina*, *Avenella flexuosa*, *Betula pendula*, *Betula pubescens*, *Carex pilulifera*,
 682 *Convallaria majalis*, *Dryopteris carthusiana*, *Fagus sylvatica*, *Festuca ovina*, *Fraxinus excelsior*, *Hepatica nobilis*, *Hypericum*
 683 *perforatum*, *Juncus effusus*, *Juniperus communis*, *Luzula pilosa*, *Lysimachia europaea*, *Melica nutans*, *Mercurialis perennis*, *Picea*
 684 *abies*, *Poa nemoralis*, *Polygonatum multiflorum*, *Ribes uva-crispa*, *Prunus padus*, *Rubus idaeus*, *Rubus saxatilis*, *Salix caprea*,
 685 *Scrophularia nodosa*, *Silene dioica*, *Stellaria holostea*, *Stellaria media*, *Taraxacum vulgare*, *Tilia cordata*, *Ulmus glabra*, *Veronica*
 686 *officinalis* (see Appendix S11).

687



688

689 *Figure 4 (a) Mean and standard error of the NMDS-coordinates for each survey year and for each plot category (resulting in 12*
 690 *possible combinations of year, past land use and recent management level). The level of recent disturbance by forest management*
 691 *is indicated by the line colour (red = high; blue = low), while the past land use category is indicated by the line type (continuous =*
 692 *infield; dotted = outland). The black arrows visualize the trajectories of the understory compositions over time. (b) Correlation of*
 693 *relevant plot characteristics (orange arrows: soil clay and total P content, soil pH, cover and shade-casting ability (SCA) of the tree*
 694 *layer) and community descriptors (green arrows: mean Ellenberg N and L values) with the plot positions on the NMDS ordination*
 695 *figure. The length of the arrows indicates the degree of correlation.*

696	Supporting information
697	Appendix S1. Vegetation data manipulation
698	Appendix S2. Determining the level of recent management intensity for each plot
699	Appendix S3. Land-use and management classification for all 62 plots
700	Appendix S4. Details on soil sampling and analyses during our own sampling campaign in 2014
701	Appendix S5. Soil data for 1983 and 2014
702	Appendix S6. Shade-casting ability scores
703	Appendix S7. Shade-casting ability of the tree layer
704	Appendix S8. AIC model comparison results
705	Appendix S9. Backwards model selection for each year separately
706	Appendix S10. Details of linear mixed effect modelling results for the four response variables
707	Appendix S11. Indicator species analysis
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