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

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

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Abstract

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

Location: Oak forests in Skåne, south Sweden.

Methods: We use three vegetation surveys (1983, 1993/94 and 2014) and notes on management and land-use history, available for 62 permanent 500 m^2 plots. We conducted linear mixed effect modelling to detect both main and interactive effects of past land use and recent management on understorey diversity measures and vegetation indicator values for light and fertility. We combined nonmetric multidimensional scaling (NMDS) with permutational multivariate analysis of variance (PERMANOVA) and indicator species analysis to detect compositional differences caused by past land use and/or recent management.

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

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

Key words

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

Introduction

Forests worldwide, as well as most other ecosystems, have been dominated, shaped and influenced by human activities for centuries and more (Bürgi & Gimmi, 2007; Williams, 1993). Hence, the European forests that we know today were created by a long history of human land-use changes, and only very few forests exist free of legacies from former human influence (Bengtsson, Nilsson, Franc, & Menozzi, 2000; Gossner et al., 2014). Human activities affecting forests are very diverse (Foster et al., 2003), comprising episodes of deforestation and agricultural use (Foster, Motzkin, & Slater, 1998), wood harvesting with different levels of intensity (Gossner et al., 2014), manipulation of animal populations (Foster et al., 2003), litter collecting (Bürgi & Gimmi, 2007), and grazing by domestic animals (Bengtsson et al., 2000). Understanding how both past and present anthropogenic disturbances influence biodiversity and species assemblages is essential for conservation. Here, we focus on two aspects of anthropogenic disturbances that are common in European forests, but which rarely have been studied in combination, namely different intensities of both past agricultural land use and current forest management practices for wood harvesting. We assess their effects on the forest understorey layer, which represents the majority of plant species richness in temperate forests (Gilliam, 2007). This layer is most likely to reflect land-use legacies because it exhibits slow dynamics and is less easily manipulated (by e.g. plantation) compared to the overstorey.

Most present-day European forests occur on lands that at some point in history were used for agriculture, and many studies have demonstrated that these forests still bear imprints of their past land use, which we call land-use legacies (Blondeel et al., 2019; Emanuelsson, 2009; Flinn & Marks, 2007; Hermy & Verheyen, 2007; Perring et al., 2016; Vellend, 2003). Land-use legacies are often found in forest understoreys, due to a limited dispersal and recruitment capacity of typical forest species (De Frenne et al., 2011; Verheyen, Honnay, Motzkin, Hermy, & Foster, 2003). As a result, forest understorey compositions may depend on environmental conditions that no longer occur in a forest stand (Jonason et al., 2014). Land-use legacies affect the understorey directly, by past elimination of plants and their diaspores, as well as indirectly, by altering environmental conditions such as soil pH, soil nutrient concentrations, soil organic matter content and light availability (Flinn & Marks, 2007; Hermy & Verheyen, 2007). Several studies found that forest soils on former arable land are still richer in nutrients and hence more productive as a result of past fertilization practices, compared to so-called ancient forests without a history of agricultural use (Falkengren-Grerup, Ten Brink, & Brunet, 2006; Koerner, Dupouey, Dambrine, & Benoit, 1997; Naaf & Kolk, 2015; Verheyen, Bossuyt, Hermy, & Tack, 1999). These higher nutrient contents in post-agricultural forests can influence the composition of the established vegetation after abandonment of cultivation, due to a dominance of competitive species which hamper the establishment of slow-colonizing herbs (Baeten, Hermy, & Verheyen, 2009; Koerner et al., 1997).

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

Here, we are interested in how both recent forest management and past land-use intensity differences may have interactive effects on understorey assemblages and their trajectories over time. Reasons to believe such interactions are present arise from a study by Huston (2004), pointing out the importance of the disturbance-productivity interaction as a determinant of species richness. Within this framework, we consider the intensity of forest management as the disturbance factor, and different intensities of past agricultural land use as a proxy for the productivity factor. Several other studies argue that diversity may be a function of the interaction between disturbance and productivity, and therefore the productivity effects on diversity can only be assessed when they are stratified by disturbance regimes (e.g. Kondoh, 2001; Huston, 2014). For example, Proulx & Mazumder (1998) demonstrated that plant species richness increases with increasing disturbance (in this case grazing pressure) in a nutrient-rich environment, but decreases in a nutrient-poor environment. Furthermore, several studies highlight the occurrence of interactions between legacies of past land use with natural disturbance processes such as forest fires, hurricanes and droughts (Chazdon, 2003; Comita et al., 2010; Foster et al., 2003; Hogan, Zimmerman, Thompson, Nytch, & Uriarte, 2016). We believe that forest management actions can have similar effects on the forest vegetation as natural disturbances, and hence can interact with land-use legacies as well. Some recent studies indeed showed possible interactions between past land-use changes and alterations in present conditions through management practices on species richness and composition (Janssen et al., 2018; Kelemen, Kriván, & Standovár, 2014).

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

Specifically, we investigated the following research questions:

(i) Are legacies from the former infield/outland agricultural system reflected in the community composition and diversity of the understorey? Have these land-used legacies changed over time?

(ii) Does recent forest management intensity affect the community composition and diversity of the understorey?

(iii) Have recent disturbances due to forest management interacted with land-use legacies, causing changes in the dynamics of the understorey composition and diversity between 1983 and 2014?

Material and methods

Study area: past land use and recent management

The study area comprises the south Swedish province of Skåne, an area of ca 11 000 km^2 and ca 1.3 million inhabitants. The border between the central-European sedimentary bedrock area (here mainly limestones and clay shales) and the Fennoscandian shield of Precambrian crystalline rocks (granite and gneiss) crosses the province from southeast to northwest, resulting in a gradient from the more densely populated southwest with fertile agricultural soils to the northeastern part dominated by forests on less productive soils (Figure 1, including forest distribution). Most soils have not developed directly upon bedrock but originate from Quaternary deposits formed during and after the latest (Weichselian) glaciation which completely covered Skåne with its icesheet.

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

To characterize the past land use of each plot, we distinguished between former infields and outland (Emanuelsson, 2009). A permanent infield-outland system emerged in the early medieval period when villages became sedentary. Infields were located close to settlements or farm-houses, and were intensively manured. The infields were either used for crop production or managed as semi-open wooded meadows which produced hay, small-dimension wood products from coppice, as well as some timber trees. The outland was situated further from villages, and was managed jointly by the village for grazing, timber and other wood-based products. The manure from grazers was then applied on the infield lands. The infield-outland system was functional until ca. 1800-1850 (Emanuelsson et al., 2002). Outland area gradually reduced in extent with the increasing demand for arable land due to continuous population increase since the 1700s. Based on cadastral maps (mainly spanning the period 1730-1870) at the final phase of this land use system, (https://historiskakartor.lantmateriet.se/historiskakartor/search.html), we classified 23 plots as 'Outland' (i.e. plots on former outland), and 39 plots as 'Infields' (i.e. plots on former infields) (Appendix S3). According to the cadastral maps, none of the infield plots has been used as arable field since at least ca. 1800. The majority of the stands are semi-natural, and developed from semi-open conditions to closed stands when livestock grazing (outland) or wooded meadow/coppice management (infield) ceased. In some sites (both infield and outland), oak was planted after felling of the previous stand. The evidence of continuous presence of trees on the historical maps varies, but all plots have been wooded since at least 1900.

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

Soil and overstorey characterization

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

Regarding the overstorey characterization, plots with high and low intensity management had similar tree cover values in 1983 and 2014, while more intensively managed plots had a significantly lower tree cover during the intermediate survey in 1993, reflecting the peak in forest management activity in the region at the time of the intermediate survey. Dominant tree species were *Quercus robur* (or *Quercus petraea* in a few cases), *Carpinus betulus* and *Corylus avellana* (Figure 1b). At the time of the first survey (1983), both former infield plots and less intensively managed plots were characterized by more *Carpinus betulus* and *Corylus avellana* in the tree layer, and less *Quercus robur*/*petraea*, compared to former outland and more intensively managed plots respectively (Figure 1c/d). The shade-casting ability (SCA) of the tree layer (i.e. a cover weighted average of the SCA scores per species, listed in Appendix S6; see also Verheyen et al. (2012)) was similar between infield and outland plots within the more intensively managed plots, but clearly higher for infield than outland plots within the less intensively managed plots (see Appendix S7). We keep these soil and overstorey characteristics in mind when interpreting the results.

Vegetation surveys

In July-August 1983, 135 permanent plots were established by Professor em. Germund Tyler to study the relationships between soil, macrofungi and tree and herb layer species (e.g. Tyler, 1989). All these plots were resurveyed a first time in July-August 1993/1994 (further referred to as 1993) and a second time in August 2014, although only 62 of the plots were relocated at that time. All plots were 500 m² (20 m x 25 m). Criteria for the original plot selection in 1983 included no current livestock grazing and no thinning during approximately the five years prior to surveying (Brunet et al., 1996; Diekmann et al., 1999). Vegetation data were expressed as an estimated cover percentage for each individual species present. Two vegetation layers were distinguished: the *understorey* and the *tree layer*, respectively comprising all vascular plants below 5 m and above 5 m height (see Appendix S1 for details on the vegetation data).

Response variables

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

Statistical analyses

To test how contemporary management intensities interact with past land use to alter the plot characteristics over time, we conducted linear mixed effect modelling with four response variables related to the understorey (and described above): Shannon-Wiener index, Bray-Curtis dissimilarity, Ellenberg N, and L mean values. We confirmed that each response variable is normally distributed, using histograms.

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

Response variable ~ PastLandUse + Management + Year + PastLandUse:Management + PastLandUse:Year + Management:Year + (1|PLOT ID) Equation [1]

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

Next, we performed backwards elimination of the explanatory variables using maximum likelihood-fitted models at a 5% level of significance (Zuur et al., 2009), leading to the optimal model. For each response variable, we refitted the optimal model with restricted maximum likelihood (REML). For the final (optimal) model of each response variable, we inspected model diagnostic plots to check validity; all were satisfactory. For each model, we calculated the marginal and conditional R^2, representing the variance explained by fixed factors and the variance explained by both fixed and random factors, respectively (*MuMIn* package; (Nakagawa & Schielzeth, 2013)). Given the high number of parameters in the *beyond* *optimal model*, compared to a sample size of 62 plots, there is a possibility of overfitting. Therefore, we also performed a model comparison based on information criteria (AIC), which resulted in the same final (optimal) model for each response variable (Appendix S8). Additionally, we repeated the backwards elimination procedure for separate models for each year, which reduces the number of explanatory variables and thus the risk of overfitting. This additional analysis led to identical qualitative findings for all response variables except Ellenberg N, where an effect of recent management was identified in 2014 that was absent in other analysis approaches (Appendix S9).

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

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

Results

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

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

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

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

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

Typical species on former infields were *Convallaria majalis* and *Poa nemoralis*, while typical former outland species included *Dryopteris carthusiana, Juncus effusus* and *Carex pilulifera* (but these species were not indicators in 2014). *Mercurialis perennis, Melica nutans* and *Hepatica nobilis* (not in 2014) were indicative of a less intensive management, while *Betula pubescens/pendula* was indicative of a higher management intensity (Figure 3, Appendix S11). The following commonly prevailing herbaceous species seemed indifferent for both past land use and recent management intensities, and were found in all plot groups: *Oxalis acetosella*, *Maianthemum bifolium, Viola spp., Rubus idaeus,* and *Galeopsis spp.*. Comparison of mean Ellenberg N and L values between indicator species groups only revealed significant differences in Ellenberg N values in 1983 (infield indicators: 6.14; outland indicators: 3.71; $t_{9.98}$ = 2.69; p = 0.023).

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

Discussion

This is the first study, to our knowledge, investigating both the main and interactive effects from legacies of a historical infield/outland system and recent management intensity levels on contemporary understorey compositions and their trajectories over time. We found that plot-level understorey diversity (i.e. alpha diversity) depended mainly on recent management intensities, and not on past land use. Higher levels of disturbance due to management positively affected alpha diversity. We found dissimilarities in species composition (i.e. beta diversity) among plots with different past land uses, and (to a lesser extent) different recent management intensities. Legacies from the former infield/outland agricultural system clearly persisted in the nutrient-demanding signature of the understorey. Interestingly, we also found an indirect effect of past land use on the light levels at the forest floor, through its effect on the soil nutrient availability. The more nutrient-rich soils of former infields seemed to result in forest canopies casting a deeper shade. However, recent management activities overruled this effect of past land use on the light-demanding signature of the understorey, resulting in similar indicator values for light regardless of past land use when plots were intensively managed.

Research question 1: Land-use legacies in the understorey

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

Research question 2: impact of recent management on the understorey

We found that different levels of recent management intensity affected the community composition of our study plots, in terms of their mean position in the ordination figures. We also observed an increase in plot-level diversity between 1983 and 1993, followed by an overall decrease between 1993 and 2014 across all past land use/management combinations. These changes are probably related to the overall management intensity trajectory for the entire region. Overall management intensity in the region increased after the ratification of the *Swedish Broadleaves Act* in 1984, which prescribed that oak/hornbeam stands larger than 0.5 ha must not be converted to coniferous plantations, but regenerated with oak or other temperate hardwoods, and which stimulated interest in active management of hardwood forests. After 1993, management intensity decreased again due to changes in the Swedish forest policy that now gave more importance to the environmental goal of forests whereby biodiversity was to be secured and ecosystems conserved (Simonsson, Gustafsson, & Östlund, 2015). This suggests that management intensity and alpha diversity are positively correlated. Several other studies reported similar findings, where forest management has a positive effect on species richness of the understorey vegetation (e.g. Brunet, Falkengren-Grerup, & Tyler, 1997). The dissimilarity in species composition among plots increased slightly between 1993 and 2014, and displayed the opposite trend to alpha diversity. This result can be explained by the dependence of the Bray-Curtis index on alpha diversity, where both measures are inversely correlated due to the multiplicative definition (alpha x beta = gamma) (Jost, 2007). Hence, a decrease in alpha diversity due to the disappearance of some species can result in plots becoming more dissimilar and thus an increase in beta diversity.

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

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

Research question 3: interactive effects of past land use and recent management on the understorey

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

Conclusion

Recent forest management intensity had a positive effect on plot-level diversity. The former infield/outland agricultural system was an important determinant of both the nutrient- and light-demanding signature of the understorey composition. The level of disturbance intensity due to recent management practices interacted with this past land-use effect, but only on the light-demanding signature of the understorey, where differences resulting from past land use had disappeared in the more intensively managed plots. Our results differ from previous studies, where disturbances were found to preserve legacies from past land use (e.g. Hogan et al., 2016; Jonason et al., 2016).

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

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Data availability statement

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

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Figures

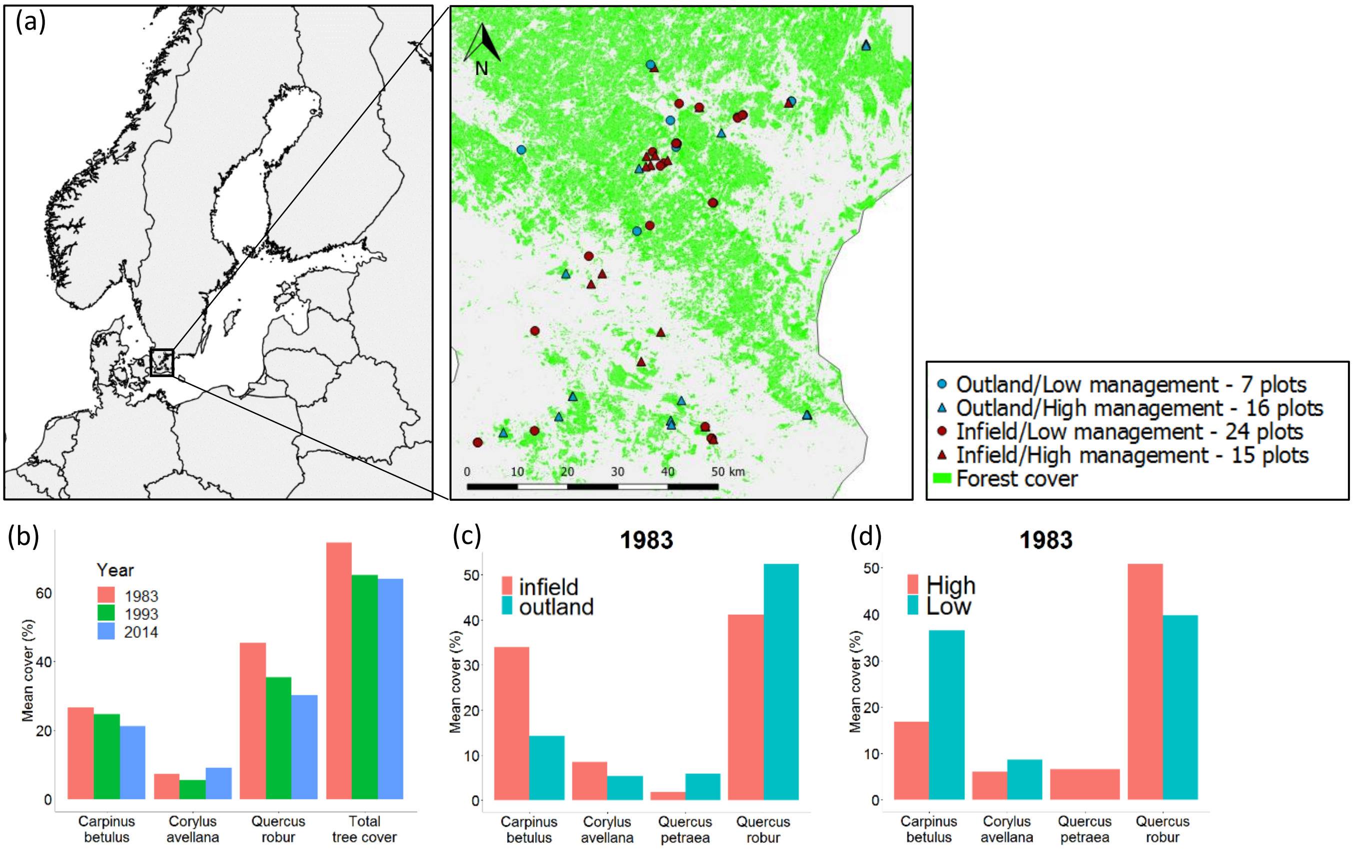

Figure 1 (a) Geographical location and distribution of the 62 study plots. The number of plots in each land use category, which is the combination of past land use and recent management intensity, is shown in the legend. (b) Mean cover (%) of the three most dominant tree species, as well as the total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

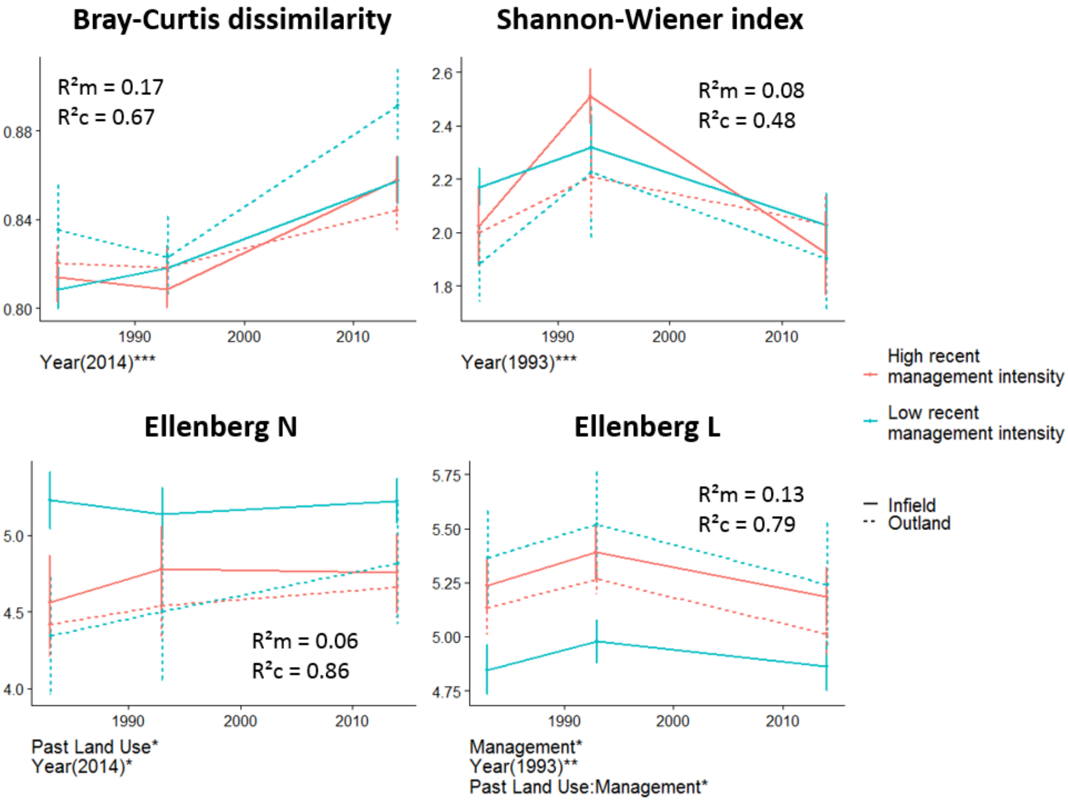

*Figure 2 Temporal changes in mean values (and standard errors) of the four response variables representing understorey diversity and composition. The level of recent disturbance by forest management is indicated by the line color (red = high; blue = low), while the past land use category is indicated by the line type (continuous = infield; dotted = outland). Below each graph, the significant predictors that were retained in the final model of the response variable are shown, with their level of significance ('***' for $p<0.001$; '**' for $p<0.01$; '*' for $p<0.0.5$). Interactions between predictors are indicated with ':'. The marginal and conditional R^2 (R^2m and R^2c respectively) for the final model of each response variable are also given. See Appendix S10 for the full model results.*

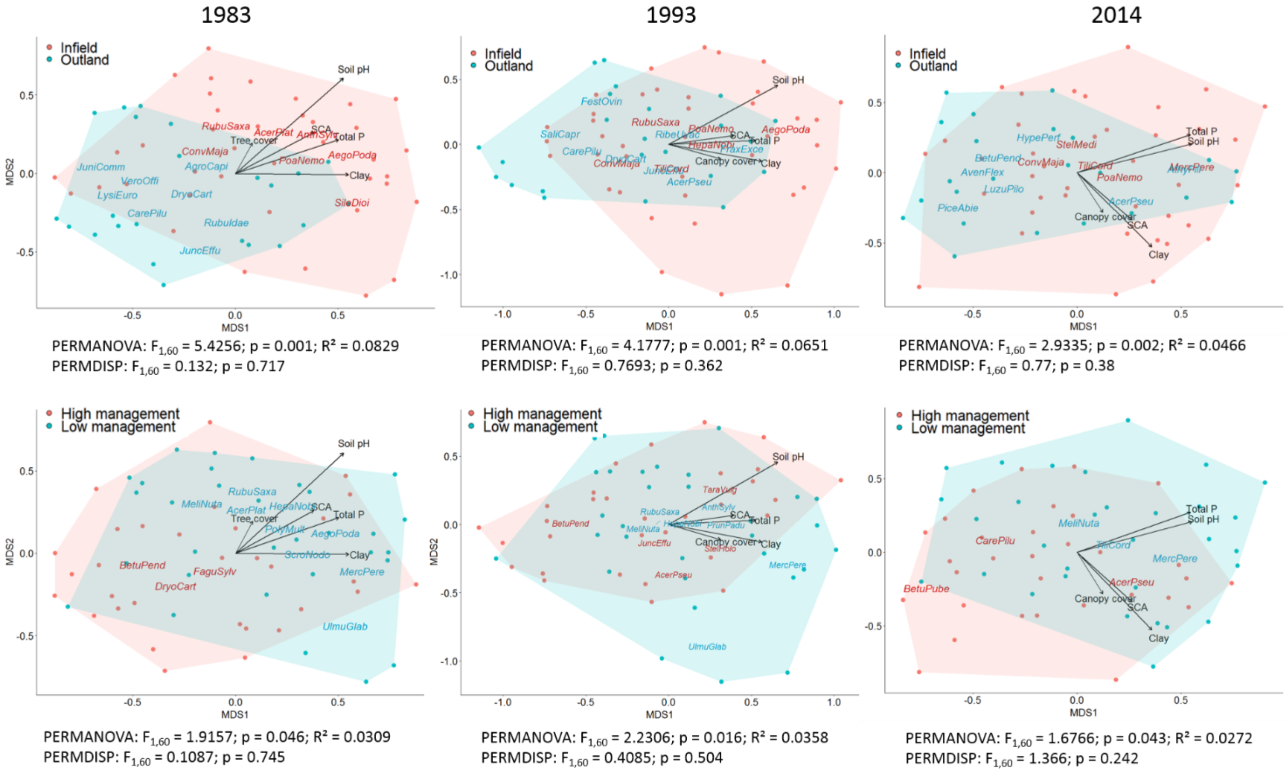

Figure 3 NMDS of understorey composition for each survey year. In the upper row, red dots represent former infield plots and the species in red are the indicator species of infield plots; blue dots represent former outland plots and the species in blue are the indicator species of outland plots. In the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

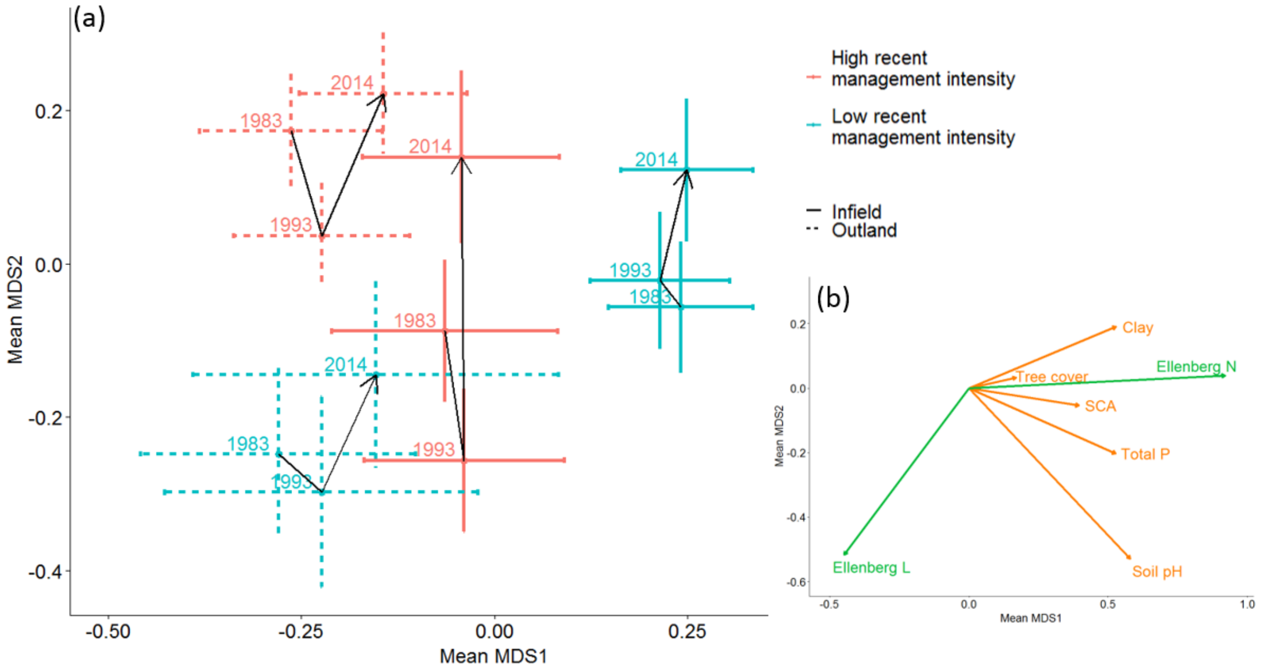

Figure 4 (a) Mean and standard error of the NMDS-coordinates for each survey year and for each plot category (resulting in 12 possible combinations of year, past land use and recent management level). The level of recent disturbance by forest management is indicated by the line colour (red = high; blue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

Supporting information

Appendix S1. Vegetation data manipulation

Appendix S2. Determining the level of recent management intensity for each plot

Appendix S3. Land-use and management classification for all 62 plots

Appendix S4. Details on soil sampling and analyses during our own sampling campaign in 2014

Appendix S5. Soil data for 1983 and 2014

Appendix S6. Shade-casting ability scores

Appendix S7. Shade-casting ability of the tree layer

Appendix S8. AIC model comparison results

Appendix S9. Backwards model selection for each year separately

Appendix S10. Details of linear mixed effect modelling results for the four response variables

Appendix S11. Indicator species analysis