Persistent land-use legacies increase small-scale diversity and strengthen vegetation–soil relationships on an unmanaged heathland

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Abstract

Land-use legacies are recognized determinants of vegetation dynamics and plant community assembly. The duration of these legacies and how they influence the structure of vegetation communities developing naturally in nutrient-poor ecosystems is not well understood. Here, we focus on the effects of increased nutrient availability from previous agricultural practices on multiple vegetation properties in a heathland where agriculture and domestic grazing ceased near 1870 and 1895, respectively. We compared diversity, compositional and functional properties of the vegetation responses to land-use legacies in the soil between areas with different agricultural histories (previously cultivated vs. uncultivated). Diversity measures were found to be higher in the previously cultivated soils. $\beta$-diversity was mainly driven by changes in species relative cover and increased with increasing nutrient availability in the cultivated area. Furthermore, functional traits related to nutrient acquisition (SLA and Leaf Nitrogen content) and the changes in vegetation composition were directly linked to soil properties only in the previously cultivated part of the heathland. Together these results revealed a shift to a deterministic control of the plant community, where increased nutrient availability leads to stronger associations between soil and vegetation properties. This suggests that as nutrients become available, niche differentiation and competitive interactions become the predominant underlying mechanisms structuring the community. Our study shows that land-use legacies of moderate intensity can alter the assembly mechanisms and diversity patterns in unmanaged vegetation that can be maintained after more than a century since cessation of agricultural practice. Identifying land-use legacies and understanding how they structure heathland communities can thus lead to management decisions adapted to the specific assembly mechanisms and result in a more effective management.

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Keywords: Beta diversity; Community assembly; Functional traits; Nutrient availability; Heathland conservation; Plant–soil feedback

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Introduction

Understanding how land-use legacies influence the development of ecological communities is necessary to reach more accurate predictions on how environmental change will affect future ecosystem structures, processes and functions (Perring et al. 2016). Land-use legacies can have long lasting effects on the chemical and physical structure of the soil and on multiple vegetation properties (McLauchlan 2006; Fichtner, von Oheimb, Härdtle, Wilken, & Gutknuecht 2014). The magnitude and the duration of agricultural legacies and their effect on the vegetation depend among other things, on the existing soil properties. On nutrient-limited habitats such as heathlands, fertilization from agricultural practices increases the nutrient content in the soil (von Oheimb et al. 2008) and can change species diversity and composition (Kleijn, Bekker, Bobbink, De Graaf, & Roelofs 2008; Kepfer-Rojas, Damgaard, Riis-Nielsen, & Schmidt 2017). Furthermore, tillage, ploughing and biomass removal from harvest, homogenize the top layers of the soil reducing the spatial heterogeneity of soil resources (Fraterrigo, Turner, Pearson, & Dixon 2005; McLauchlan 2006).

Increased nutrient availability and decreased soil heterogeneity can affect the structure and composition of heathland communities. First, increasing the amount of soil nutrients can lead to higher supply of limiting resources, releasing the community from the strong environmental filter that the original low nutrient and acidic conditions impose. Higher nutrient availability can improve the chance of establishment by a larger number of species from the regional species pool and thus increase the levels of α and β diversity (Chase 2003). Similarly, soil resource heterogeneity can affect different facets of diversity in plant communities. Niche-based ecological theory proposes that the number of species should increase in heterogeneous habitats because of an increase in the number of available niches, promoting species coexistence through resource partitioning (Tilman & Pacala 1993). However, in a thorough review Lundholm, Jeremy, and Lundholm (2009) found that although a positive heterogeneity-diversity relationship occurs often, non-positive or neutral relationships are also common (e.g. Baer, Blair, Collins, & Knapp 2004; Reynolds, Mittelbach, Darcy-Hall, Huseman, & Gross 2007).

Besides effects on biodiversity, land-use legacies can potentially affect the mechanisms behind community assembly by determining whether plant communities are deterministically or stochastically structured. Multiple studies have demonstrated that both types of mechanisms can operate simultaneously, but how and when the relative importance of these mechanisms change in relation to environmental gradients is not well understood (Weiher et al. 2011; Price, Gazol, Tamme, Hiiesalu, & Pärtel 2014). Community assembly theory predicts that the force behind the assembly mechanisms should change from stochastic to deterministic as resource availability increases either due to stronger biotic interactions or niche differentiation (Myers & Harms 2009; Conradi, Temperton, & Kollmann 2017). From this, it can be expected that higher nutrient levels can lead to stronger associations between vegetation and soil.

Studies on community assembly usually focus on a few community properties which can limit our understanding of how vegetation communities are structured. Combining different facets of vegetation communities can aid in clarifying the underlying mechanisms behind community assembly. For instance, patterns in β-diversity can be insightful in distinguishing deterministic from stochastic processes of community organization (Chase & Myers 2011; Conradi et al. 2017). Similarly, analyses of functional traits of species can provide further insights as functional traits drive community assembly processes and can be directly linked to ecosystem functioning (Lavorel & Garnier 2002). An important consideration when using trait based approaches is the selection of appropriate traits that respond to or affect the ecological process of interest. Here, we focus on specific leaf area (SLA) and leaf nitrogen concentration (leaf N) as these traits are related to the uptake and conservation of nutrients and thus respond to and affect soil nutrient availability (Jager, Richardson, Bellingham, Clearwater, & Laughlin 2015). Analyses of taxonomical and functional vegetation properties can thus provide more nuanced insights into the mechanisms structuring ecological communities (Weiher et al. 2011).

In this study we focus on how land-use legacies affect the composition and small scale diversity patterns of an unmanaged heathland through its effects on the quantity and spatial distribution of soil resources. Although the agricultural intensity was only moderate and had ended more than a century ago, we expect the signature of past land-use still to be recognizable in both the soil and vegetation. More specifically, we hypothesize that increasing soil nutrient availability in the former cultivated soils will provide recruitment opportunities to a larger share of the regional species pool and thus lead to a higher α- and β-diversity. Furthermore, increasing nutrients are expected to lead to a more deterministic community structure where the composition of species responds more directly to the abiotic environment, leading to a selection of traits related to faster nutrient acquisition as the community is released from the strong environmental filter. In turn, the effects of these traits on the soil can contribute to the long-term maintenance of different vegetation properties on areas with different land-use. Finally, because of the nutrient-poor soil conditions in heathlands, we do not expect soil nutrient heterogeneity to be a strong determinant of vegetation properties.
Materials and methods

Study site and sampling

The heathland of Nørholm is a 350 ha Atlantic lowland heathland in the southwest of Denmark (E8°370, N55°410). This heathland is an important conservation and research area and has been the focus of several ecological studies including long-term vegetation development (Riis-Nielsen, Schmidt, Frandsen, & Binding 2005; Kepfer-Rojas, Schmidt, Ransijn, Riis-Nielsen, & Verheyen 2014; Ransijn, Kepfer-Rojas, Verheyen, Riis-Nielsen, & Schmidt 2015), determinants of tree colonization (Kepfer-Rojas, Verheyen, Johannsen, & Schmidt 2015) and species diversity (Kepfer-Rojas et al., 2017). Estimated atmospheric N-input increased to about 25 kg N ha\(^{-1}\) year\(^{-1}\) in 1970–1980 but current rates are 12–14 kg N ha\(^{-1}\) year\(^{-1}\). The area was under traditional agricultural practices until the end of the 19th century. As was common for heathland management, the area was divided into inflfields and outfields (Christiansen 2001) where inflfields were cultivated and outfields were used for grazing and for collection of heather and turf. The animals were at least seasonally stall-fed and during night placed in barns. Plant biomass, turf and manure were thus transferred from the outfield to the stable or midden and into the inflfields as a way of fertilization. Even after more than a century since abandonment, the effects of land-use legacies are evident in the vegetation between the two areas, with inflfields dominated by the dwarf-shrubs *Empetrum nigrum* and *Calluna vulgaris*, and inflfields co-dominated by the grasses *Deschampsia flexuosa* and *Molinia caerulea* and the same dwarf-shrub species (Riis-Nielsen et al., 2005). Since abandonment of agriculture, tree colonization has occurred at a remarkably slow pace, particularly in the previous cultivated areas, where competition with grasses mediated by increased nutrient availability has prevented colonization (Riis-Nielsen et al., 2005; Kepfer-Rojas et al., 2014; Kepfer-Rojas et al., 2015).

In the current study, transects were selected in areas distant from the edges of the heathland with similar topography, and where tree colonization had not occurred to minimize the effect of disturbance and colonization from external sources and to isolate the effect of soil properties. Ten 20-m transects were located on each of the two land-use types (i.e. inflfields and outfields). On each transect we used ten 1-m\(^2\) plots 1 m apart to record the visually estimated cover of all vascular species, mosses and lichens. All vascular species were identified to species level. Lichens and mosses were not recorded to species level and thus were not considered in statistical analysis of species numbers but were included in analysis of compositional differences.

Four soil samples were taken at each corner of the 1 m\(^2\) plot from the top of the mineral soil using a 3-cm diameter auger. The O-horizon (total organic layer, on top of the mineral soil) was characterized by measuring its depth (cm) using a ruler, and its biomass (g/cm\(^2\)) using Kopecky density rings of 22 cm\(^2\). This layer was missing from 8 plots from the cultivated area which were excluded prior to statistical analyses. The mineral soil was separated into two depths: 0–10 cm and 10–20 cm. The samples for each compartment were combined to a single sample per plot. Soil samples were dried for 48 h at 40°C before sieving over a 2 mm mesh. Samples were analyzed for pH-KCl by shaking a 1:5 ratio soil/KCl (1 M) mixture for 5 min and measuring with a pH meter Orion 920A with pH electrode model Ross sure-flow 8172 BNWP, Thermo Scientific Orion, USA. Total P was measured after complete destruction of the soil samples with HClO\(_4\) (65%), HNO\(_3\) (70%) and H\(_2\)SO\(_4\) (98%) in teflon bombs for 4 h at 150°C. P-concentrations were measured colorimetrically according to the malachite green procedure (Lajtha, Driscoll, Jarrell, & Elliot 1999). Bioavailable P which is available for plants within one growing season (Gilbert, Gowing, & Wallace 2009) was measured by extracting soil in NaHCO\(_3\) during 30 min (P-Olsen; according to ISO 11263:1994(E)) and colorimetric measurement according to the malachite green procedure (Lajtha et al. 1999). Exchangeable Ca\(^{2+}\) and Al\(^{3+}\) concentrations were measured by atomic absorption spectrophotometry (AA240FS, Fast Sequential AAS) after extraction in 0.1 M BaCl\(_2\) according to NEN-ISO 11260:2011. Finally, soil samples were analyzed for % C and N by combustion at 1200 °C by a CNS elemental analyzer (vario Macro Cube, Elementar, Germany).

Statistical analysis

We ordinated the vegetation data using non-metric multi-dimensional scaling (NMDS) of the Hellinger-transformed species’ cover and tested for differences between land-use classes using PERMANOVA (Anderson, Ellingsen, & McArdle 2006). We evaluated the effect of land-use legacies on soil properties using multivariate analyses. To obtain a combined value of soil properties we conducted a principal coordinate analysis (PCoA) on Euclidean distances of soil variables (Table 1). We used samples from the 0–10 cm depth and the depth and biomass ectorganic layer, because an O-horizon was absent from some plots on the cultivated area. Because the units of measurement of soil properties varied widely, variables were normalized between 0 and 1. We tested the effect of land-use history on soil heterogeneity using a test for homogeneity of multivariate dispersions (Anderson et al. 2006) on the distance to group centroids (i.e land-use category). Differences in distances to the centroid were tested with a permutation test with 999 permutations.

To test how well soil properties could explain plant community composition we used distance-based redundancy analysis (db-RDA). We conducted a separate db-RDA for each land-use class to compare the strength of the plant–soil association between land-use categories. To assess the contribution of edaphic factors we included the soil properties listed in Table 1 into the RDA, and to account for the spatial structure in the species’ distributions we incorporated...
Table 1. Soil and vegetation properties in previously cultivated and uncultivated areas. Soil properties were measured on the 0–10 cm layer, except for depth and biomass, which were measured in the organic horizon. Differences between land-use classes were tested with t-tests except for depth and biomass of the O-horizon which were tested with mixed effects models to account for missing observations. * = significant differences (P < 0.05); n.s. = not significant.

<table>
<thead>
<tr>
<th>Land-use history</th>
<th>Cultivated</th>
<th>Mean</th>
<th>SE</th>
<th>Uncultivated</th>
<th>Mean</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vegetation</td>
<td></td>
<td>Mean</td>
<td></td>
<td></td>
<td>Mean</td>
<td></td>
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<tr>
<td>Dwarf shrub cover (%)</td>
<td></td>
<td>63.51</td>
<td>(3.10)*</td>
<td>91.76</td>
<td>(1.43)</td>
<td></td>
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<tr>
<td>Grass cover (%)</td>
<td></td>
<td>33.37</td>
<td>(2.73)*</td>
<td>3.47</td>
<td>(0.50)</td>
<td></td>
</tr>
<tr>
<td>Forb cover (%)</td>
<td></td>
<td>10.42</td>
<td>(0.89)*</td>
<td>0.49</td>
<td>(0.14)</td>
<td></td>
</tr>
<tr>
<td>Moss cover (%)</td>
<td></td>
<td>16.83</td>
<td>(2.13)*</td>
<td>60.60</td>
<td>(2.10)</td>
<td></td>
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<tr>
<td>Number of species (plot)</td>
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<td>4.75</td>
<td>(0.10)*</td>
<td>3.27</td>
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<tr>
<td>Number of species (transect)</td>
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<td>7.6</td>
<td>(0.70)*</td>
<td>6.3</td>
<td>(0.58)</td>
<td></td>
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<tr>
<td>Total number of species</td>
<td></td>
<td>16</td>
<td></td>
<td></td>
<td>17</td>
<td></td>
</tr>
<tr>
<td>Soil</td>
<td></td>
<td>Mean</td>
<td></td>
<td></td>
<td>Mean</td>
<td></td>
</tr>
<tr>
<td>Olsen-P (mg/kg)</td>
<td></td>
<td>7.02</td>
<td>(0.19)*</td>
<td>2.41</td>
<td>(0.13)</td>
<td></td>
</tr>
<tr>
<td>Total P (mg/kg)</td>
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<td>194.44</td>
<td>(3.01)*</td>
<td>53.99</td>
<td>(1.92)</td>
<td></td>
</tr>
<tr>
<td>Al (mg/kg)</td>
<td></td>
<td>116.58</td>
<td>(2.90)*</td>
<td>60.73</td>
<td>(2.60)</td>
<td></td>
</tr>
<tr>
<td>Ca (mg/kg)</td>
<td></td>
<td>48.15</td>
<td>(3.55)*</td>
<td>54.47</td>
<td>(3.63)</td>
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<tr>
<td>C (%)</td>
<td></td>
<td>1.84</td>
<td>(0.05)*</td>
<td>2.51</td>
<td>(0.11)</td>
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<tr>
<td>N (%)</td>
<td></td>
<td>0.14</td>
<td>(0.00)*</td>
<td>0.11</td>
<td>(0.00)</td>
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</tr>
<tr>
<td>C:N ratio</td>
<td></td>
<td>13.06</td>
<td>(0.18)*</td>
<td>23.04</td>
<td>(0.56)</td>
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<tr>
<td>C:P ratio</td>
<td></td>
<td>96.61</td>
<td>(2.88)*</td>
<td>477.44</td>
<td>(16.42)</td>
<td></td>
</tr>
<tr>
<td>pH-KCl</td>
<td></td>
<td>3.42</td>
<td>(0.01)*</td>
<td>3.06</td>
<td>(0.01)</td>
<td></td>
</tr>
<tr>
<td>Depth</td>
<td></td>
<td>1.34</td>
<td>(0.13)*</td>
<td>5.38</td>
<td>(0.13)</td>
<td></td>
</tr>
<tr>
<td>O-horizon (cm)</td>
<td></td>
<td>0.53</td>
<td>(0.04)*</td>
<td>1.77</td>
<td>(0.08)</td>
<td></td>
</tr>
</tbody>
</table>

spatial variables derived from principal coordinates of neighborhood matrices (PCNM). This method allows modelling the spatial patterns in the vegetation at different spatial scales and effectively accounts for possible spatial autocorrelation (Dray, Legendre, & Peres-Neto 2006). Prior to inclusion in the final RDA we used forward selection to identify the soil properties that were more strongly associated with the community composition matrix. Similarly, we included only the spatial vectors that showed positive autocorrelation identified using Moran’s tests. With the final set of variables we used variance partitioning to disentangle the contribution of the soil and the spatial variables on the community composition for each land-use category.

To gain more insights into how land-use legacies affect community structure and assembly mechanisms, we tested for effects of nutrient availability and nutrient heterogeneity on the small scale (i.e. within transects) diversity patterns (α- and β-diversity) and the community weighted means (CWM) of two functional traits. Alpha diversity was calculated as the number of vascular plants in each plot within each of the 20 transects. β-diversity was estimated for each transect using the partitioning methods of Baselga (2010) for abundance data and Bray-Curtis pairwise dissimilarities. This method allows decomposing β-diversity (βBC) into balanced (βbal) and gradient (βgra) components and provides a measure of β-diversity independent of differences in species richness. βbal is analogous to species replacement, where species are substituted by other species. βgra is analogous to nestedness in incidence-based measures, where the species in one site are a subset of another site (Baselga 2010). We used the mean pairwise dissimilarity of each plot to the other plots within each transect to represent the three components.

We used two functional traits: the specific leaf area (SLA) and leaf Nitrogen content (Leaf N), obtained from the TRY database (Kattge et al. 2011). We focus on these traits because they are important indicators of the leaf economic spectrum and are related to nutrient acquisition strategies (Jager et al. 2015). Community weighted means (CWM) for each trait were calculated for each plot.

The effects of nutrient availability and soil heterogeneity on diversity measures and functional traits were examined using linear mixed models with α, βBC, βbal, βgra, SLA and Leaf N as dependent variables. Nutrient availability was represented by the transect averages of the first axis scores of the soil PCoA and the mean distance from each plot to its transect’s centroid was used as a measure of soil heterogeneity. To test whether the effects of these factors were dependent on land-use, we included interaction terms with land-use class in the models. All models included transect as a random factor to account for the correlation between plots in the same transect. For all analyses we started with a model with both two-way interactions and conducted backward selection until only significant terms were left. Significance of the different terms was tested with likelihood ratio tests comparing a model with the term of interest with a model without that term. A Poisson error distribution was used to model alpha diversity, whereas a Gaussian distribution was used for all other variables.

All analyses were conducted in R version 3.4.3 (R Core Team 2017). Multivariate analysis of vegetation community (PERMANOVA, dbRDA, PCNM) were done with the “vegan” library (Oksanen et al. 2017). The “APE” library (Prasad, Claude, & Strimmer 2004) was used for the Moran’s test of autocorrelation. β-diversity decomposition was done with “betapart” (Baselga, Orme, Villeger, De Bortoli, & Leprieur 2017) and mixed models were done using the “lme4” library (Bates, Maechler, Bolker, & Walker 2015).

Results

The vegetation differed consistently between cultivated and non-cultivated fields (Table 1). Whereas cover of dwarf
shrubs and mosses was higher in the uncultivated areas, the formerly cultivated area had higher cover of grasses and forbs and higher α-diversity. The effect of land-use was also evident on soil properties. The thickness and biomass of the O-horizon were significantly higher on non-cultivated soils. The top layer (0–10 cm) in the cultivated soils had significantly higher pH values and nutrient contents except for Ca which was similar for both areas (Table 1).

Multivariate analysis of soil vegetation and soil showed clear differences between land-use classes (Fig. 1). Vegetation composition differed between land-use classes (PERMANOVA: Pseudo-F(1,198) = 81.09; P < 0.01), with higher multivariate dispersion (betadisper: Pseudo-F(1,198) = 43.59; P < 0.01) in the cultivated area (Fig. 1A). The vegetation was separated into two groups especially along the first ordination axis (Fig. 1A), which was correlated to the first axis of the soil PCoA (envfit: P < 0.01, R^2 = 0.64). In the soil PCoA, this axis explained 67% of the variation and revealed an increasing gradient of nutrient availability, being positively correlated to Olsen’s P, total P, pH, exchangeable Al and total N; and negatively correlated to total C, Ca, C:N, C:P, depth and biomass of the litter layer (Appendix A, Table 1 in Supplementary material). The second axis explained 15% and was only weakly correlated to soil properties. Soil heterogeneity was higher on uncultivated soils (betadisper: F(1,198) = 24.59, P < 0.01, Fig. 1B).

In the areas with different land-use history, separate dbRDA showed different responses of vegetation composition to soil properties. The soil and spatial components together significantly explained 37% and 16% of the variation in species composition in formerly cultivated and uncultivated areas of the heathland, respectively. In the cultivated area, plant–soil associations were stronger where soil variables alone explained 23% of the variation in vegetation while only 8% were explained in the uncultivated area. The forward selection showed that all soil variables except for Al and C were significantly related to the vegetation composition in the cultivated area, while only three variables (C:P, Olsen-P, and Al) appeared to be significant in the uncultivated area. The spatial variables explained a similar proportion of the variation in both areas (Fig. 2), but the proportion of the variation explained by the joint soil + space component was higher in the cultivated (8%) than in the uncultivated (1%) area.

The total number of vascular plants was similar between both areas (Table 1). Sixteen and 17 species were found on previously cultivated and uncultivated areas, respectively. α-diversity was higher at formerly cultivated soils but did not respond directly to nutrient availability or soil heterogeneity (Table 2, Fig. 3A). Overall small-scale composition dissimilarity (βBC) was higher on transects located on previously cultivated soils. Partitioning of βBC revealed that βbal accounted for 86% and 82% of the dissimilarity in cultivated...
Table 2. Summary of results of general and generalized mixed models for the effects of land-use legacies (LU) nutrient availability (NUT) and soil heterogeneity (HET) on small scale diversity and community-weighted means of functional traits. Test statistics obtained with likelihood ratio tests. In bold, significant effects. For an extended table with parameter estimates see Appendix A, Table 2 in Supplementary material.

<table>
<thead>
<tr>
<th></th>
<th>$\alpha$</th>
<th></th>
<th>$\beta_{uc}$</th>
<th>$\beta_{gra}$</th>
<th>$\beta_{bal}$</th>
<th>SLA</th>
<th>Leaf N</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>$X^2$</td>
<td>$P$</td>
<td>$X^2$</td>
<td>$P$</td>
<td>$X^2$</td>
<td>$P$</td>
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<tr>
<td>NUT</td>
<td>0.23</td>
<td>0.63</td>
<td>11.62</td>
<td>$&lt;$0.01</td>
<td>0.21</td>
<td>0.65</td>
<td>4.14</td>
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<tr>
<td>HET</td>
<td>0.95</td>
<td>0.33</td>
<td>0.88</td>
<td>0.35</td>
<td>0.01</td>
<td>0.92</td>
<td>1.51</td>
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<tr>
<td>LU</td>
<td>14.81</td>
<td>$&lt;$0.01</td>
<td>0.39</td>
<td>0.53</td>
<td>0.65</td>
<td>0.42</td>
<td>0.33</td>
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<tr>
<td>LU x NUT</td>
<td>2.21</td>
<td>0.14</td>
<td>2.81</td>
<td>0.09</td>
<td>0.33</td>
<td>0.57</td>
<td>4.10</td>
</tr>
<tr>
<td>LU x HET</td>
<td>0.08</td>
<td>0.78</td>
<td>0.03</td>
<td>0.87</td>
<td>0.04</td>
<td>0.85</td>
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</table>

Fig. 3. Effect of nutrient availability on $\alpha$-diversity (A) the balanced component of $\beta$-diversity (B) and the community weighted means of SLA (C) and Leaf N (D). Nutrient availability increases along the first axis of the PCoA ordination on soil variables (see text). Averaged transect values are presented with bars representing standard error of the mean. Circles = cultivated; triangles = uncultivated. Regression lines are shown for the different land-use categories. Solid lines = significant; dotted lines = not significant.

and uncultivated soils, respectively. The effect of nutrient availability was similar for the 3 components, increasing with nutrient availability in previously cultivated soils (Table 2, Fig. 3B). No effect of nutrient availability was found for uncultivated soil. Similarly, there was no overall effect of soil heterogeneity (Table 2). The same pattern was observed for the CWMs of SLA and Leaf N, where both traits increased with increasing nutrient availability only in cultivated soils; and soil heterogeneity did not have any effect (Table 2 and Fig. 3C and D).


Discussion

We found evidence of persistent land-use legacies ca. 150 years after cessation of traditional agricultural practices with profound effects on the structure and the assembly mechanisms of this heathland community. Although outfield/infield systems were a common management practice in northern Europe (Diekmann 1994), few studies have investigated how these practices alter the mechanisms structuring heathland communities and the duration of these legacies after abandonment of agricultural practices. In this study, the most evident effects on the soil were the higher levels of nutrients and the reduced soil heterogeneity found on the previously cultivated parts of the heathland. Higher levels of bioavailable and total P, total N concentrations (despite lower total C concentrations) and higher pH values are expected in areas subjected to agriculture and likely resulted from fertilization (Dupouey, Dambrine, Laffite, & Moares 2002; De Schrijver et al. 2012). Another signature from agriculture are the lower C:N and C:P ratios and the less developed organic layer (i.e. low thickness and biomass), possibly as a result of a lower biomass input and faster mineralization during the agricultural period, and the change in community composition following abandonment of cultivation. The decreased heterogeneity observed in soil properties in the cultivated area can be related to ploughing which homogenizes the soil (Fraterriego et al. 2005).

Despite soil heterogeneity being higher for uncultivated soils, this did not translate into differences in the vegetation attributes measured in this study. Although, several field studies have demonstrated a positive correlation between soil heterogeneity and plant diversity, neutral or negative effects can be common (Lundholm et al. 2009), and have been reported in experimental studies in low nutrient ecosystems (Reynolds et al. 2007). The response of species diversity to heterogeneity could be constrained by recruitment limitation from the regional species pool (Mittelbach et al. 2001), competition with established vegetation (Gough, Osenberg, Gross, & Collins 2000) and clonality of dominant species (Reynolds et al. 2007). Some of these explanations are likely relevant in this case. First, the response of soil heterogeneity on diversity could be constrained due to limited recruitment from the species pool (Houseman & Gross 2006). In sites where environmental filtering is strong due to stressful conditions, community membership is limited only to those species with the necessary adaptations. In that case, the expected effect of increasing soil heterogeneity can be obscured by the overriding effect of the limited nutrient availability. Another consideration when analyzing environmental heterogeneity effects on diversity is the importance of the life history traits of dominant species. Experimental studies have demonstrated that clonal species may be able to exploit resources from different patch types limiting the effect of soil nutrient availability and heterogeneity (Eilts, Mittelbach, Reynolds, & Gross 2011). *E. nigrum* and *C. vulgaris* are the dominant dwarf-shrub species found in this area. These ericaceous species can reproduce clonally, and are typically associated with ericaceous mycorrhiza which allows them to access organic compounds in soil with low fertility (Cairney & Meharg 2003). These characteristics confer dwarf shrubs with the plasticity to occupy a larger portion of the nutrient gradient without directly responding to nutrient concentrations.

**α-diversity** was higher in the cultivated field, but did not show a direct relationship with nutrient availability. A possible explanation is that the moderately higher nutrient availability is sufficient to increase the average number of species that can coexist at smaller scales. However, the number of species does not capture the change in soil properties directly because the presence or absence of a species is also dependent on other processes such as dispersal, biotic interactions and stochastic processes. This is in agreement with studies demonstrating the limitation of species richness as an indicator of biodiversity change due to changing environmental conditions (Hillebrand et al. 2018). **β-diversity**, on the contrary, did increase with increased soil nutrients. This increase could be driven by the general increase in alpha diversity observed in the cultivated area of this heathland. However, the partitioning framework here showed that most of the differences in **β-diversity** where driven by the balanced turnover of species, i.e. that the cover of some species is being replaced by the cover of different species and not by species turnover. This suggests that nutrient availability has greater influence on compositional differences by affecting the relative cover of the different species, which supports the hypothesis of a shift in species dominance mediated by nutrient availability (Aerts et al. 1990).

We found that species composition responded to nutrient availability but only on the previously cultivated soils, demonstrating that land-use legacies can alter the strength of the plant–soil interactions. The stronger correlation with soil properties suggests that species sorting or competitive interactions are possible assembly mechanisms on soils with higher nutrient availability (Conradi et al. 2017). This proposition has also been documented in other heathlands, where competitive interactions increase when nutrient availability is high (Aerts & Heil 1993) and is supported by the observed patterns in **β-diversity** in this heathland.

The spatial structure component that was not explained by soil properties accounted for similar proportions of the total explained variance in species composition on both land-use types. Typically, the spatial component of the variation in species composition is attributed to mechanisms that create spatial autocorrelation in the distribution of species; such as dispersal limitation, vegetative reproduction and clonality. Due to the small scale of our study and the long period without major disturbances, dispersal limitation is not considered to be of major importance (Horn et al. 2015), leaving vegetative reproduction and clonality as a more plausible explanation. The dominant species in this heathland is *E. nigrum*, being almost equally abundant in both areas (mean cover = 55% and 62% in the cultivated and uncultivated part,
respectively). This species reproduces mainly by rhizomatous clones which allows it to establish in different areas independently of nutrient availability or heterogeneity (Reynolds et al. 2007). Its wide tolerance to different nutrient availability and its predominantly vegetative reproduction can lead to a spatially structured distribution and explain why a similar amount of the variation is explained by space, independently from land-use history. On the other hand, we found a considerable part of the variation in species composition explained by the joint influence of soil and space on the cultivated soils whereas almost no variation was shared by the same components in the uncultivated part. This seems contradicting as the soil in the cultivated area of the heathland is more homogeneous due to the impact of agriculture. Such a pattern could emerge though due to biotic interactions mediated by nutrient availability (Horn et al. 2015). Another possibility is that a plant–soil feedback could lead to spatially correlated species distributions, and if the species have a direct effect on the soil properties, this could in turn lead to spatial autocorrelation.

The composition of the vegetation differed markedly depending on land-use history. Grass-encroachment resulting from increasing nutrient availability has been thoroughly documented and has been observed in many post-agricultural heathlands. The duration of this legacy on naturally developing community supports the idea of possible feedback mechanisms by which dwarf shrub and grass domination are maintained at the nutrient-poor and the enriched portions of the heathland, respectively. Selection of leaf functional traits related to faster nutrient content and higher decomposition rates could promote faster nutrient cycling in the cultivated area of the heathland in turn enhancing colonization by species with high nutrient acquisition rates such as grasses or related to higher soil P content such as several herbs (Hansen 1976). On the other hand, dwarf shrub species with functional traits related to slow nutrient acquisition have the advantage in nutrient poor soils (Aerts & Heil 1993). Because the same traits are related to slow decomposition rates, nutrient cycling is slower when these species are dominant (Jones & Power 2012). In this way, the conditions created by past agricultural practices are maintained and the vegetation remains in two different stable states even after nearly 150 years since abandonment of agriculture (Ransijn et al., 2015). The observed increase in SLA and Leaf N concentration support this hypothesis.

Our results have important implications for heathland conservation and management. First, previous studies have shown that long-lasting elevated nutrient availability can limit the recovery of heathland communities on ex-arable lands. Walker et al. (2007) found that despite re-establishment of soil conditions favorable for heathland species, competition with nutrient-demanding species constrains the success of restoration in post-agricultural sites. In this study we found that although significantly different, pH and bioavailable P on both land-use types are well within the typical range of heathland ecosystems (Schelfhout et al. 2015). Despite that, the observed differences in vegetation and in the structuring mechanisms demonstrate that even these small changes can be sufficient to push the system towards a different state which can be maintained long after abandonment of agriculture.

However, we found that typical heathland species composition can be maintained in the absence of management even in areas where nutrients have been added through agriculture and where regional nitrogen deposition has been high. So far this heathland has been self-maintained as a mosaic of patches of grasses and dwarf shrubs which seem to remain in stable states (Ransijn et al., 2015). This mosaic creates heterogeneous and diverse vegetation which can provide different niches to heathland-associated species and ultimately increase the diversity at the landscape level. Similarly, a more heterogeneous vegetation composition can contribute to the multi-functionality of heathlands and therefore, it should be considered when assessing the importance of these areas for conservation purposes or provisioning of ecosystem services.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.baae.2018.10.004.

References


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