Effects of abandonment on plant diversity in semi-natural grasslands along soil and climate gradients

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Abstract

Questions: What are the effects of abandonment on plant diversity in semi-natural grasslands? Do the effects of abandonment on taxonomic and functional diversity vary along environmental gradients of climate and soil?

Location: West and mid-Norway.

Methods: Plant composition was surveyed in 110 subplots of 4 m² in 14 sites across grazed and abandoned semi-natural grasslands. Climate data were extracted and soil composition analysed. To reduce the number of explanatory variables and deal with collinearity, we performed PCA. Data on the plant species vegetative height (H), leaf dry matter content (LDMC), specific leaf area (SLA), seed mass (SM) and number of seeds per plant (SNP) for 175 species were extracted from the LEDA database. Measures of plant diversity (species richness, CWM of functional traits and functional diversity (evenness and range)) were calculated for each subplot. To estimate the effects of abandonment on plant diversity and examine how these effects are moderated by gradients in soil and climate, we fitted mixed models to the data including site as a random effect.

Results: Species richness in the subplots was lower in abandoned semi-natural grasslands, especially on more calcareous soils. CWM H, LDMC and SM were higher in abandoned semi-natural grasslands. CWM LDMC was only higher in the driest subplots. The ranges in H, SLA and SM, as well as evenness in LDMC were also higher in abandoned semi-natural grasslands, but the range in LDMC was lower.

Conclusions: It is important to assess both taxonomic and functional diversity to understand ecosystem processes. The species pool in ecosystems influenced by a long history of intermediate grazing includes a high proportion of low stature, grazing-tolerant plant species. Abandonment of extensive land-use practices will cause a decline in taxonomic diversity (plant species richness) in such systems due to increased abundance of plants with high stature that outcompete the lower, grazing-tolerant plants. This process is predominant especially if moisture, soil fertility and pH are at intermediate levels. Changes in species communities due to abandonment will also influence ecosystem functioning, such as nutrient turnover and fodder production resilience.

Introduction

Landscapes in boreal ecosystems are mosaics of forest and open vegetation types. Most of the open vegetation types in Scandinavian boreal ecosystems are formed through centuries of agricultural management, and range from monospecific crops to species-rich semi-natural vegetation. Management has included extensive livestock grazing and land use associated with grazing quality improvement and fodder harvest. However, socioeconomic and technological changes in Europe have caused many farmers to abandon extensive land-use practices (Emanuelsson et al. 2009). As a result, the plant communities and soil conditions of these semi-natural ecosystems have, and will continue to change in new and different directions. Abandonment of extensive

grazing management is, therefore, one of the major land-use changes posing a threat to biodiversity in Northern Europe (Emanuelsson et al. 2009; Norderhaug & Johansen 2010).

The consequences of stopping management on plant species richness have been found vary (Prevosto et al. 2011). The main approach when studying influences of abandonment on plant diversity has been to assess the effects on plant richness only. Land use and thus also abandonment affects the functional characteristics of species assemblages (Mayfield et al. 2010). The consequences on biodiversity are not first and foremost a change in species number, but rather a change in which species are present and abundant. Functional traits can be used to describe characteristics and dynamics of plant communities and are morphological, phenological or physiological features that have an impact on a plant's fitness (Violle et al. 2007).

Five plant traits that reflect conditions in grasslands are vegetative plant height (H), seed mass (SM), seed output (seed number per plant: SNP), specific leaf area (SLA) and leaf dry matter content (LDMC; Westoby et al. 2002; Douma et al. 2012; Duru et al. 2012). H is related to competitive vigour (Westoby 1998), especially for light. Grazing disfavours plants with a high stature, and thus smaller plant species become more competitive. An expected consequence of relaxed grazing is therefore an increase in the abundance of tall plants (Douma et al. 2012). Increased H correlates with increased biomass but also with slower nutrient cycling (Pakeman 2011; Lavorel & Grigulis 2012).

Both LDMC and SLA are associated with the leaf economics spectrum and are strongly related to nutrient use (Diaz et al. 2004; Wright et al. 2004; Pakeman 2011). Through coevolution with herbivores, many plant species have adopted strategies such as tolerance and resistance to grazing, and thus enhanced fitness in grazed environments (Briske 1996). Both physical and chemical defence strategies are associated with high LDMC (Cornelissen et al. 2003). High SLA may also be associated with tolerance to herbivory (Westoby 1998). SLA is positively correlated with the photosynthetic rate and thus also growth rate (Chapin et al. 2011). A plant with high SLA might therefore be able to compensate for lost tissue even if grazed.

Seed mass (SM) and SNP are good predictors of dispersal and establishment success (Westoby et al. 2002). Small and numerous seeds enhance the chances of dispersal to suitable conditions for establishment (Baskin & Baskin 1998), such as small gaps of open soil. Trampling by domestic animals creates such patches, thus increasing germination opportunities, especially for small-seeded plants (Kahmen & Poschlod 2008). Larger seeds, on the other hand, incorporate more resources (Westoby 1998), and

high seed mass species are thus more tolerant of stress conditions (Westoby 1998; Cornelissen et al. 2003).

The kind, range and abundance of traits within a community are defined as functional diversity (Diaz et al. 2007) and offer a way to understand species responses in more detail. A commonly used approach to summarize the functional composition of single traits in a community is to calculate CWMs (Garnier et al. 2004). Functional diversity of certain traits is also considered a good indicator of plant strategy, community structure and ecosystem functioning, and can provide information on processes underlying community assembly (Villeger et al. 2008; Mouchet et al. 2010; Pakeman 2011). Measures that take abundances into account, such as functional evenness, enable detailed interpretation of relationships between functional diversity and environment (Mouchet et al. 2010). However, more is presently known about the effects of environmental shifts on the kind of functional traits that dominate a community (the functional identity) than on the range and evenness of functional trait values.

Objectives

The overall aim of this study was to investigate the effect of abandonment of management on plant diversity in boreal semi-natural grasslands and how these effects are modified by environmental factors. The questions asked in this study are: (1) what are the effects of abandonment on taxonomic and functional diversity in semi-natural grasslands; and (2) do the effects of abandonment on biodiversity vary along environmental gradients of climate and soil?

To address the research questions, we investigated if functional diversity of H, LDMC, SLA, SM and SNP differed in abandoned and managed semi-natural grasslands along soil and climate gradients. We then assessed whether community assemblages change as a consequence of reduced niche filtering, increased competition for light and altered dispersal and establishment success in abandoned compared to managed semi-natural grasslands. In abandoned semi-natural grasslands, we expected to find species with functional traits related to (1) higher ability to compete for light would increase, (2) grazing resistance and/or tolerance would decrease, and (3) dispersal and establishment would differ in abundance compared to those in managed semi-natural grasslands. We also expected that these differences would vary along environmental gradients as other environmental filters will interact with the effect of abandonment. Finally, as species characteristics of different communities vary, we also expected to see differences in functional range and evenness as well as in species richness.

Methods

Study design

The study took place in boreal ecosystems in west Norway (2012: 5°33′50″–7°21′18″E, 61°11′51″–61°33′50″N) and mid-Norway (2013: 10°16′35″–11°16′52″E, 63°09′24″–63°32′32″N)). The study uses a "space for time" design approach where plots including four subplots each were paired in 14 sites (Appendix S1). These subplots were used as units in the statistical models ($n = 110$).

In each site, one plot was established in a managed semi-natural grassland and one plot was established in an abandoned semi-natural grassland area. The semi-natural grasslands were not ploughed, reseeded or fertilized. The plots in the managed semi-natural grassland were within enclosures (2–88 ha) where sheep (15–620 animals) were left to graze in spring and/or autumn (28–90 d). Grazing densities ranged from 40 to 1892 sheep days ha^{-1}·yr^{-1}. In some of the managed semi-natural grasslands, shrubs and trees were cleared by the farmers to increase pasture quality. The abandoned semi-natural grasslands were at different successional stages, moving towards forest. Time since abandonment ranged from 5 to 70 yr. In each site, the two plots were located on either side of the enclosure fence, which was approximately perpendicular to the contour lines in the terrain. The maximum "vertical" lengths of the plots along the fences were 100 m, and each of the plots extended a maximum of 50 m away along the "horizontal" lines from the fences. Half of the subplots (which were 2 m × 2 m) were randomly located in the lower part of the plot, and the other half in the upper part. In the managed semi-natural grassland, locations of the subplots were rejected if <10 m from the fence to avoid shadow effects from the canopy in the abandoned plot.

Environmental variables

For each site, values of bioclimatic variables were extracted from the WorldClim database (http://www.worldclim.org/bioclim; Table S1a): annual mean temperature (MT), annual precipitation (AP), mean temperature of warmest quarter (MTWQ), precipitation of warmest quarter (PWQ) and elevation.

Per subplot, we randomly collected five soil samples of 500 g (0–10 cm below the litter layer) with an auger (22-mm diameter). These were mixed to give one bulk soil sample per subplot. The soil samples were analysed by Eurofins Environment Testing Norway AS. The measured variables were pH, available P (P-Al), K (K-Al), Mg (Mg-Al), Ca (Ca-Al) and Na (Na-Al) (all in mg 100 g·soil^{-1} extracted using ammonium lactate (Al) in addition to organic matter (OM) measured by loss on ignition (g 100 g·dry matter^{-1}) and bulk density (density; kg·L^{-1};

Table S1b). Values below the detection threshold were assigned a zero value.

Botanical composition data

In each subplot all vascular plant species present were recorded and their abundance estimated in eight cover categories (0–1/64, 1/64–1/32, 1/32–1/16, 1/16–1/8, 1/8–1/4, 1/4–1/2, 1/2–1/1). These categories were transformed to relative percentage cover by taking the midpoint of each category divided by the total sum of the species cover in the subplots. 180 species were recorded in the study.

Trait data

For all plant species, we extracted values for the traits H, LDMC, SLA, SM and SNP from the LEDA database (Kleyer et al. 2008). 39 of the 175 species had at least one trait with missing values and the mean number of traits missing for these 39 species was 1.31 ± 0.69 (±SD). Instead of deleting species with missing data, we performed imputation methods which reduce bias in the estimated effects that are investigated (Donders et al. 2006). Missing trait values were estimated based on other traits with values present for that particular species using imputation methods as described in Taugourdeau et al. (2014). Pteridophytes were excluded for SM and SNP data.

Diversity

Based on the data obtained for botanical composition and traits, species richness (number of vascular plant species) and functional identity and diversity indices were calculated for each subplot. We calculated CWM, range and evenness of the functional traits using the FD package v 1.0-12 in R (Laliberte & Legendre 2010; R Foundation for Statistical Computing, Vienna, AT).

Analyses

To reduce the number of bioclimatic and soil variables in the analysis and deal with collinearity, PCAs (Janžekovič & Novak 2012) were performed first on the climatic variables and then on the soil variables. We then tested whether the first two principal component axes (PC1 and 2 of both climatic and soil analyses) were correlated using PCA. Since no correlations were detected, these four PCs were used as descriptors of climate and soil conditions in the following analyses. PCAs were performed by using the FactoMine R package (Lê et al. 2008).

The effect of ceasing sheep grazing management on species richness and CWM, range, and evenness of the five functional traits was estimated using LMEM. Sites were

included in all models as random intercepts, and we used the lme4 package v 1.1-12 (Bates et al. 2015) to estimate parameters of the models. For species richness, we used a generalized model with a Poisson distribution of the error term and a log-link function. For the functional identity and diversity indices, we used linear models but transformed the response variables to reduce problems with heteroscedasticity.

To test the effects of land use on the different response variables, we compared a model with land use as a fixed effect and a random effect of site to a model including only the latter effect. Then, to investigate whether the effect of abandonment varied with different climate and soil, we tested the interactions between land use and each of the four principal components by comparing models with each of the interactions to the model with only land use as fixed effect; site was included as a random effect in all instances. If at least two of the interactions were significant, we proceeded to test the three-way interaction of land use and two principal components. In such a way, we could establish if the varying effect of land use along one environmental gradient was influenced by another environmental gradient. The three-way interactions were tested by comparing the model with the three-way interaction to both the models including interactions between land use and each of the two principal components. The likelihood ratio of the models was evaluated using the Chi-square statistics and a P-value of 0.05 was used as the limit for a significant effect.

Shifts in CWM are mainly associated with the trait values of (sub)dominant species (Ricotta & Moretti 2011). However, to better interpret the results of the statistical analyses, abundance distributions were plotted within the functional space for each site. We constructed smoothed regression lines of the relative cover of the trait values in semi-natural and abandoned grasslands. In addition, we performed RLQ analysis to visually interpret relationships between the species abundances, the environmental characteristics and the species traits. In the RLQ analysis, partition of sites was taken into account (Wesuls et al. 2012) using the R ade4 package v 1.7-4.

All data analyses were performed using R 3.2.3 and all figures were made using ggplot2 v 2.1.0 (Wickham 2009).

Results

Environmental gradients

The first climate principal component (climate PC1) explained 57.3% of the total variation of the climate data set and the values along this first climate axis were positively related to levels of precipitation (correlation coefficients with annual precipitation = 0.98, precipitation of warmest quarter = 0.97; Fig. 1a). The second principal component climate axis explained 37.8% of the total variation and was negatively correlated with mean temperature of the warmest quarter ($r = -0.94$) and positively correlated with elevation ($r = 0.94$).

The first principal component soil axis explained 56.6% of the total variation in the soil data set and was positively related with soil fertility (correlation with organic matter = 0.94, bulk density = -0.91, available $P = 0.73$; Fig. 1b), while the second axis explained 24.0% of the variation and was positively related to increasing pH (correlation with available Ca = 0.94, pH = 0.82).
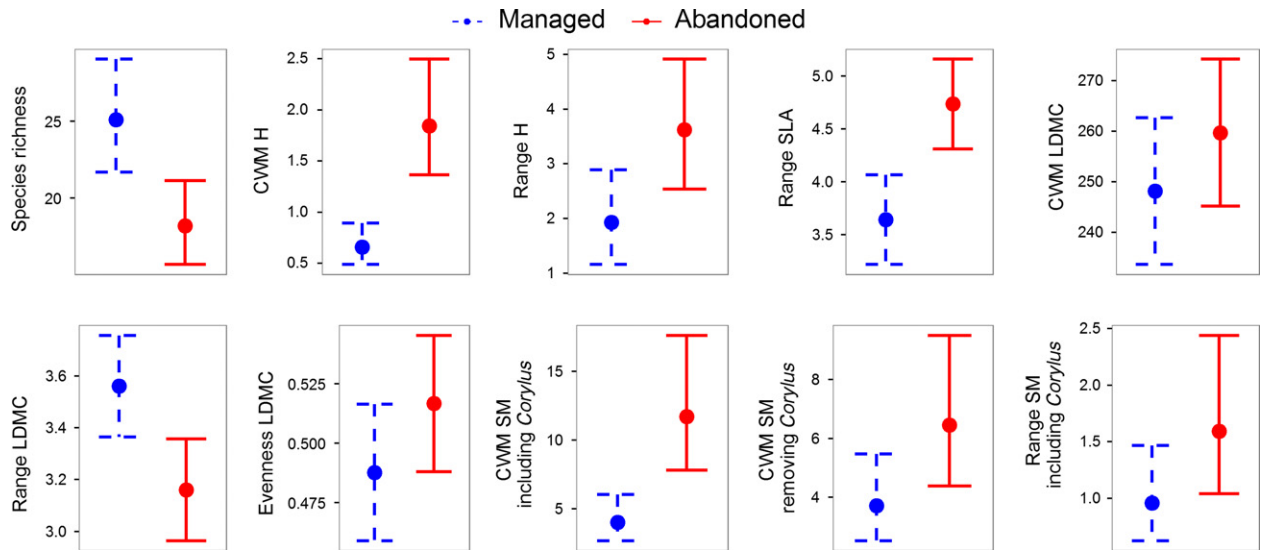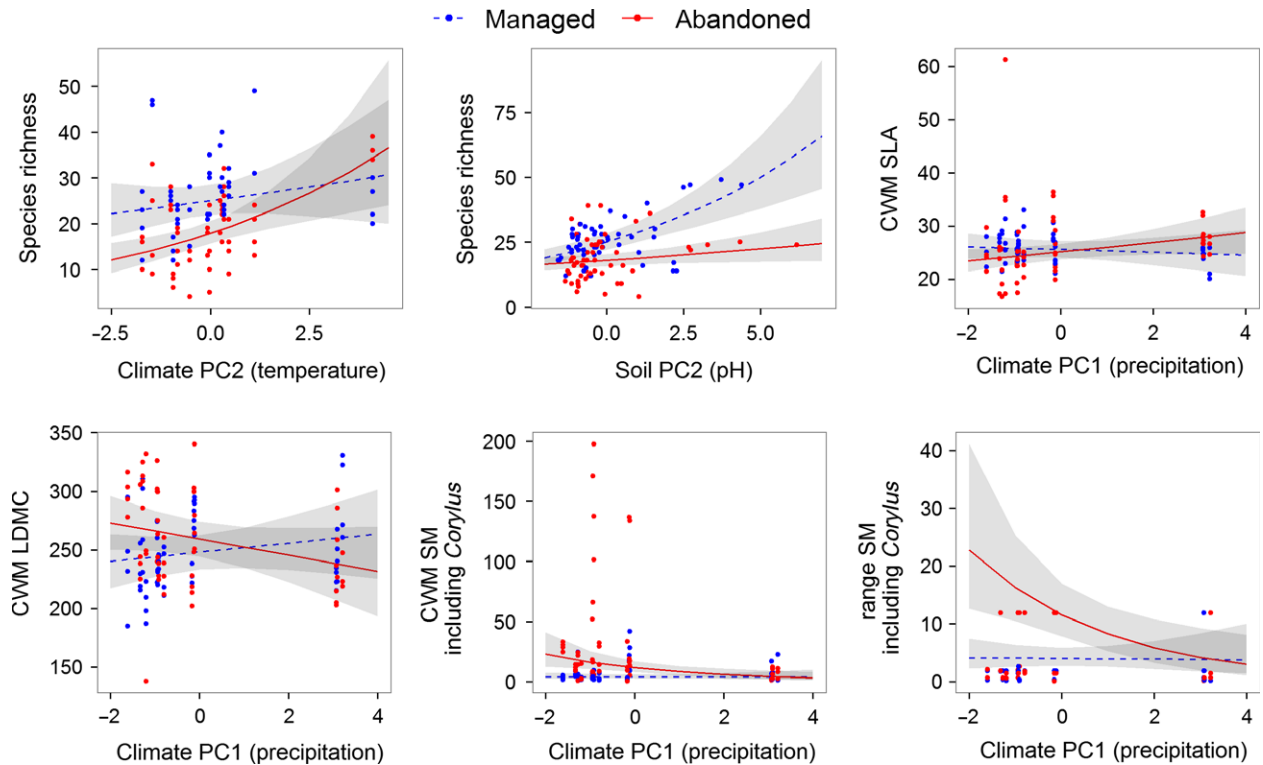
Biodiversity

Species richness

Overall, there were less vascular plant species per 4 m^2 in abandoned (estimated mean $\pm$ SE of number of vascular plant species per 4 m^2 = 18.20 $\pm$ 0.08) compared to managed (25.09 $\pm$ 0.07) semi-natural grasslands (Fig. 2; $\chi^2 = 62.112$, $P_{land\ use} < 0.001$), but the differences in richness varied with both temperature (climate PC2; $\chi^2 = 35.039$; $P_{interaction:\ land\ use\ -\ temperature} < 0.001$) and soil
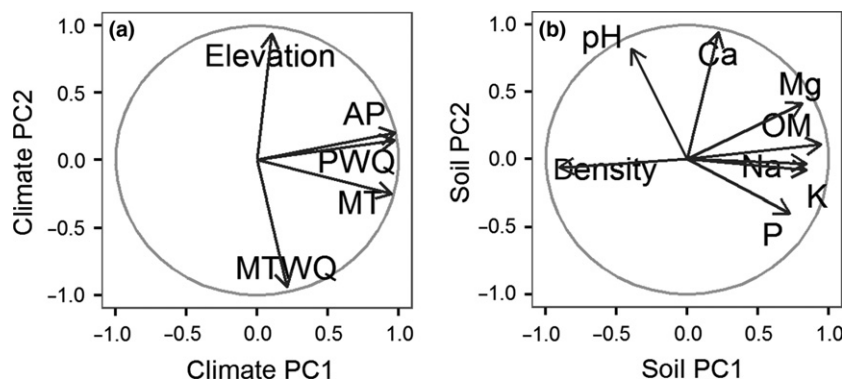
Fig. 1. Projection of (**a**) five climate variables and (**b**) eight soil variables along the first and second principal components (climate and soil PC). MT, annual mean temperature; AP, annual precipitation; MTWQ, mean temperature of warmest quarter; PWQ, precipitation of warmest quarter; P, available phosphorus, K, available potassium; Mg, available magnesium; Ca, available calcium; Na, available sodium; OM, organic matter; density, bulk density.

Fig. 2. Back-transformed estimated means and 95% CIs from LMM of plant diversity measures in managed and abandoned semi-natural grasslands. CWM, community-weighted mean, H, vegetative plant heights (m), SLA, specific leaf areas (mm^2·mg^{-1}), LDMC, leaf dry matter content (mg·g^{-1}), SM, seed mass (mg). [Colour figure can be viewed at wileyonlinelibrary.com]

Fig. 3. Plant diversity measures in semi-natural grasslands in two land-use categories along soil and climate gradients. Observed values, back-transformed estimated means and 95% CI from likelihood ratio Chi-squared tests of LMM of plant diversity measures in managed and abandoned semi-natural grasslands along temperature (warm–cold; Climate PC2), precipitation (dry–wet; climate PC1) and soil pH (acidic–calcareous; soil PC2) gradients. CWM, community-weighted mean; SLA, specific leaf areas (mm^2·mg^{-1}), LDMC, leaf dry matter content (mg·g^{-1}), SM, seed mass (mg). [Colour figure can be viewed at wileyonlinelibrary.com]

pH (soil PC2; $\chi^2 = 38.357$, $P_{\text{interaction: land use - soil pH}}$ < 0.001) gradients. Further, there was a three-way interaction between abandonment, temperature and soil pH (Fig. 3; $\chi^2_{\text{(climatePC2)}} = 29.857$, $\chi^2_{\text{(soilPC2)}} = 26.539$, $P_{\text{three-way interactions}}$ < 0.001 for both three-way interactions). The negative effect of abandonment on species richness was not found in sites at the colder end of the temperature gradient, whereas the negative effect was highest in more calcareous soils (Fig. 3). Subplots in one site showed much higher PC scores along the temperature gradient (Fig. 3). We therefore investigated whether the effect of abandonment varied along the gradient also if this site was removed from the analyses. This analysis showed no interaction between abandonment and temperature.

Vegetative plant heights

The CWM H and H range were higher in abandoned (CWM: 1.85 ± 1.65 m, range: 3.63 ± 0.03 m) compared to managed (CWM: 0.66 ± 1.65 m, range: 1.96 ± 0.03 m) semi-natural grasslands (Fig. 2; χ^2 = CWM: 23.538, range: 12.083, $P_{\text{land use}}$ CWM: <0.001, range: $P_{\text{land use}}$ < 0.001). Generally, taller species dominated in the abandoned semi-natural grasslands (Appendix S2) and the higher range of H in these grasslands was mainly due to these species.

Leaf traits

Both in the managed and abandoned semi-natural grasslands, LDMC of the dominant species were close to the mean value across all species (242 mg·g^{-1}; Appendix S2). Nonetheless, CWM LDMC was higher in the abandoned (259.71 ± 7.33 mg·g^{-1}) compared to the managed (248.12 ± 7.33 mg·g^{-1}) semi-natural grasslands (Fig. 2; $\chi^2 = 3.917$, $P_{\text{land use}} = 0.048$), except for in the sites with the most precipitation (Fig. 3; $\chi^2 = 10.286$, $P_{\text{interaction: land use - precipitation}} = 0.006$). LDMC range was lower and LDMC evenness higher in abandoned (3.16 ± 0.10 mg·g^{-1}, evenness: 0.52 ± 0.02) compared to managed (3.56 ± 0.10 mg·g^{-1}, evenness: 0.49 ± 0.02) semi-natural grasslands (Fig. 2; χ^2 = range: 9.657, evenness: 5.300, $P_{\text{land use}}$ = range: 0.002, evenness: 0.021).

The dominant species tended to have high SLA values in the managed and low SLA values in the abandoned semi-natural grasslands (Appendix S2). In spite of the difference in SLA of the dominant species in the managed and abandoned semi-natural grasslands, grazing abandonment did not make any significant difference to the overall effect on CWM SLA (overall CWM: 25.44 mm^2 mg^{-1}; $\chi^2 = 0.129$, $P_{\text{land use}} = 0.720$). Rather, the effect of abandonment on CWM SLA varied with precipitation (Fig. 3; $\chi^2 = 6.488$, $P_{\text{interaction: land use - precipitation}} = 0.039$) and SLA range differed between managed and abandoned semi-natural grasslands (Fig. 2; $\chi^2 = 22.717$, $P_{\text{land use}}$ < 0.001). In contrast to LDMC range, the SLA range was higher in the abandoned (4.74 ± 0.21 mm^2 mg^{-1}) compared to in the managed (3.64 ± 0.21 mm^2·mg^{-1}) semi-natural grasslands.

Dispersal and establishment

The RLQ analyses showed that *Corylus avellana* was an outlier for seed mass (SM) due to very high values (*C. avellana*: 805.65 mg; mean SM of the other species: 6.17 mg; Appendix S3), hence analyses were performed both when including and removing this species. When both including and removing *C. avellana*, CWM SM was higher in abandoned (including *C. avellana*: 11.72 ± 1.23 mg, removing *C. avellana*: 6.46 ± 1.22 mg) compared to in managed (including *C. avellana*: 4.00 ± 1.23 mg, removing *C. avellana*: 3.71 ± 1.22 mg) semi-natural grasslands (Fig. 2; χ^2 = including *C. avellana*: 24.483, removing *C. avellana*: 10.063, $P_{\text{land use}}$ including *C. avellana*: <0.001, removing *C. avellana*: = 0.002). The difference in SM was caused by a higher abundance of small-seeded species in grasslands with grazing (Appendix S2). The differences between CWM SM varied with precipitation (climate PC1), but only if *C. avellana* was included in the analyses (Fig. 3; $\chi^2 = 10.500$, $P_{\text{interaction: land use - precipitation}} = 0.005$). The largest differences in CWM SM between abandoned and managed semi-natural grasslands if *C. avellana* was included were found at the drier end of the precipitation gradient. Due to higher abundances of *C. avellana* in the abandoned semi-natural grasslands the range of SM values was higher in the abandoned (1.59 ± 1.24 mg) compared to the managed (0.96 ± 1.24 mg) semi-natural grasslands (Fig. 2; $\chi^2 = 5.217$, $P_{\text{land use}} = 0.022$), and the difference in SM range decreased along the precipitation gradient (Fig. 3; $\chi^2 = 6.727$, $P_{\text{interaction: land use - precipitation}} = 0.035$). Under wetter conditions, there seemed to be small or no difference in SM range even if *C. avellana* was included in the analyses (see estimates in Fig. 3).

Discussion

One of the main environmental filters of most plant communities is light (Crawley 1997), and an increased competition for light favours tall plants (Westoby et al. 2002). In pastures, competition for light is reduced by grazing and other management practices. Therefore, the obvious consequence of abandonment is increased abundance of light competitors (Prevosto et al. 2011), such as tall and broad-leaved plants (trees and tall herbs). Consequently, the main reason for the lower species richness per 4 m^2 in the

abandoned semi-natural grasslands in our study sites was competitive exclusion of many species caused by competition for light. Grasslands with a long history of grazing have developed plant communities including species adapted to herbivory and high light availability (Milchunas et al. 1988). If management changes and grazing intensity is reduced this may result in changes to the plant community and a reduction in the abundance of species specifically adapted to grazing.

High light availability in managed semi-natural grasslands enables high photosynthetic activity, which often correlates with high SLA (Westoby 1998). This is positively correlated with the capacity for tissue production, which makes plants more tolerant to tissue removal by grazing (Westoby 1998). We found a high abundance of species with high SLA in some of the managed semi-natural grasslands, indicating the dominance of grazing-tolerant species in those grasslands. As high SLA also leads to high evaporation and loss of nutrients (Wright et al. 2004), abandonment might favour species with lower values of SLA, as observed in our study.

Another consequence of grazing and the concomitant reduced competition for light and space seen in our study is the high abundance of species with smaller seeds in the managed semi-natural grasslands. This is in accordance with other studies (e.g. Pakeman et al. 2008). The frequency of gaps with bare soil in the vegetation can influence selection for seed size. Livestock trampling provides small patches where competition for light but also other resources is reduced. This increases opportunities for germination and seedling establishment, especially for small-seeded species (Kahmen & Poschlod 2008). In abandoned grasslands, the field layer is often quite dense, plant litter often accumulates at the soil surface, gaps with bare soil are less frequent than in managed grasslands and regeneration by seed is quite rare (Hamre et al. 2010; Johansen et al. 2016). Species with large seeds are expected to have an advantage compared to species with smaller seeds in abandoned grasslands as the former often produce seedlings with a better ability to penetrate the litter layer and establish under closed vegetation (Kahmen & Poschlod 2008).

The range of trait values in a community is often taken to reflect the diversity of plant strategies (Grime 1977; Crawley 1997). A low range indicates an environmental filtering process that causes only a narrow range of functional trait values to be selected (Botta-Dukát & Czúcz 2016). Environmental filtering (e.g. due to grazing management) can cause niche filtering and thus only species with shared traits can co-exist (Mouchet et al. 2010). In our study, this was noted by H-, SM- and SLA range being lower in the managed semi-natural grasslands, but LDMC range being higher in the same grasslands. The large range

in the values of LDMC in the managed semi-natural grasslands may indicate that these plant communities have a high resilience to drought and therefore provide relatively stable production of fodder over the years. Resilience is here understood as the capacity to recover from perturbations without large shifts in ecosystem functioning (Holling 1973). In grasslands, the resilience of above-ground biomass production in response to drought has been found to be positively related to functional diversity of LDMC (Pakeman 2014; Hallett et al. 2017).

The consequences of stopping management on plant species richness have been found to be variable (Prevosto et al. 2011), either increasing (Ford et al. 2012; Socher et al. 2013; Wanner et al. 2014), invariant (Vandvik & Birks 2004; Peco et al. 2006; Socher et al. 2013; Wanner et al. 2014) or decreasing (Janecek et al. 2013; Beilin et al. 2014; Wanner et al. 2014). The reasons for these varying results are due to different environmental impacts, as plant communities respond to other environmental factors in addition to management. This is pointed out by Milchunas et al. (1988) and shown in several studies (e.g. Bakker et al. 2006; Douma et al. 2012; Pardo et al. 2015). Moen et al. (1999) also states that the boreal vegetation is, in addition to light availability, filtered by temperature, precipitation and fertility conditions. In areas under intermediate levels of moisture, soil fertility and pH, low-intensity land-use practices such as grazing will have a positive effect on species richness (de Bello et al. 2006; Prevosto et al. 2011; Janecek et al. 2013). In harsh conditions, such as at low temperatures, grazing will decrease small-scale species richness (Vandvik & Birks 2004; Wanner et al. 2014). Our results support these predictions. We show that the effect of abandonment on species richness varies with temperature and pH: no effect in colder and more acidic environments, but increasingly negative effect with warmer temperatures and more calcareous soils. Species richness in semi-natural grasslands has been shown to correlate positively with pH (Vandvik & Birks 2004), this is in accordance with our results. The increasing difference in species richness between abandoned and managed semi-natural grasslands along the pH gradient also agrees with earlier studies (Janecek et al. 2013).

In our study areas, soil fertility and moisture did not influence the effect of abandonment on species richness observed elsewhere (see above), but these factors have varying effects on functional identity and diversity. The results for CWM LDMC and CWM SLA between grazed and abandoned semi-natural grasslands vary along the precipitation gradient. Under drier conditions, CWM LDMC is higher in abandoned semi-natural grasslands but is lower under wetter conditions. CWM SLA showed the opposite results. In environments where soil moisture is a limited resource, high LDMC and low SLA is advantageous

as this decreases transpiration (Wright et al. 2004). In wetter environments, this is not such a problem, hence the observed lower CWM LDMC and higher CWM SLA. However, in the managed semi-natural grasslands, CWM LDMC is slightly higher and CWM SLA slightly lower under wetter conditions. This indicates that processes such as resistance to grazing and competition for soil nutrients are important in managed semi-natural grasslands. High LDMC is positively related to grazing resistance (Cornelissen et al. 2003) and slow nutrient turnover (Westoby et al. 2002; Wright et al. 2004). Whereas grazing usually decreases the competition for light in the sward, it can increase competition for soil nutrients (Niu et al. 2015). This is because of less nutrient input through litter and fewer trees and shrubs, which are known to increase *P* availability (Peco et al. 2006). Under drier conditions, plants suffer both from grazing and limited availability of soil moisture. As stated in Hilbert et al.'s (1981) growth-rate hypothesis, herbivore tolerance exists, especially in resource-poor conditions (e.g. drier environments). According to this hypothesis, plants in stressful environments grow slowly until they are defoliated, after which the plants accelerate their growth rate to compensate for tissue loss. This is only possible if the LDMC is at median values, which is generally the case for the most abundant species in our study.

The CWM SM is also influenced by the environment along the precipitation gradient, however only when *C. avellana* was included in the analyses. Where soil water resources are unlimited (wetter conditions), plants are able to allocate energy to higher seed mass even under the stress of grazing pressure. Under the most optimal water conditions, we recorded only small differences between CWM SM of the abandoned and managed semi-natural grasslands. It has been found that SM increases with temperature (Pakeman & Quested 2007; Kahmen & Poschlod 2008). Our results do not show this but, as Pakeman & Quested (2007) also pointed out, management such as sheep grazing might impact filtering by climatic conditions.

Conclusions

The pool of vascular plant species in ecosystems influenced by a long history of intermediate grazing pressure and low-intensity agricultural practices are rich in species adapted to grazing (such as grazing-tolerant plants) at the cost of reduced ability to compete for light (such as low stature plants) and space (plants with small seeds). The overall effect of abandonment of extensive land-use practices in such ecosystems are thus a decline in species richness, especially in areas under intermediate levels of moisture, soil fertility and pH. However, both land-use history as well as the environmental setting of ecosystems varies, in addition to the interplay between the effects of abandonment and other environmental factors.

In this study, we have illustrated how traits associated with ecosystem functioning, such as nutrient turnover and fodder production resilience, as well as species richness and grazing tolerance, respond to environmental change by investigating both taxonomic and functional diversity along environmental gradients. An assessment of both taxonomic and functional aspects along varying environmental conditions will contribute to better understanding of ecosystem processes and to knowledge-based conservation of biodiversity and ecosystem functioning, which are complementary goals.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Statistics of (a) climate variables and (b) soil variables included in climate and soil PCAs.

Appendix S2. Figures of (a) geographical position of the 14 study sites where (b) two plots including four subplots each were paired. One plot was located in a managed semi-natural grassland and the other in an abandoned semi-natural grassland area.

Appendix S3. Observed values (|) and relative cover (lines) of each plant species trait (H, LDMC, SLA, SM, and SNP) in each site (1–14).

Appendix S4. Results of the first two axis of RLQ where a partition of sites is taken into account. (a) All vascular plant species included in the analysis. (b) All vascular plant species except *Pteridophytes* included (*C. avellana* considered an outlier).