DIVERSITY PATTERNS IN HIGH-LATITUDE GRASSLANDS

Running title: Diversity patterns in boreal grasslands

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ABSTRACT

Aim: Grasslands of varying land-use intensity and history were studied to describe and test species richness and compositional patterns and their relationships with the physical environment, land cover of the surrounding landscape, patch geometry, and grazing.

Location: The mainland of Norway

Methods: We utilized data from the Norwegian Monitoring Program for Agricultural Landscapes, which recorded vascular plants from 569 plots, placed within 97 monitoring squares systematically distributed throughout agricultural land on the Norwegian mainland. We identified four grassland types: (1) moderately fertilized, moist meadows; (2) overgrown agricultural land; (3) cultivated pastures and disturbed ground; (4) natural/unfertilized and outfield pastures.

Results: Soil moisture and grazing measures were found to be important in explaining species compositional variation in all grassland types. Richness patterns were best explained by complex and differing combinations of environmental indicators. Nevertheless, negative (nitrogen and light level) or unimodal (pH) responses were similar across grassland types. Vegetation plots adjacent to areas historically and/or currently dominated by mires, forests, or pastures, as well as abandoned and overgrown grasslands, had a slightly higher species richness. Larger grasslands surrounding the vegetation plots had slightly less species than smaller grasslands.

Conclusions: This study demonstrates that data from a national monitoring program on agricultural grasslands can be used for plant ecological research. The results indicate that climate-change related shifts along moisture and nutrient gradients (increases) may alter both species composition and species richness in the studied grasslands. It is likely that large and contiguous managed (grass)land might affect areas perceived as remnants, probably caused by the transformation to homogeneous (agri)cultural landscapes reducing edge-zones, which in turn may threaten the species pool and richness. The importance of land use and land-cover composition should be considered when planning management actions in extensively used high-latitude grasslands.

Keywords

Bayesian inference; Grassland monitoring; grazing; plant community composition; richness patterns; 3Q.

INTRODUCTION

Agricultural landscapes are undergoing continuous changes via human activity to meet the increased challenges of land-use efficiency. The accompanying rate of change in land-use regimes inevitably affects the patterns of species assemblages and diversity (EEA, 2011; Oppermann, Beaufoy, & Jones, 2012). In Europe, approximately 50% of all species are associated with agricultural habitats (Kristensen, 2003), and traditional farming and land management have created a mosaic of habitats which have promoted a diversity in several groups of organisms, e.g. plants, fungi, insects and birds (Stoate et al., 2009). In the range of agricultural habitats, secondary grasslands (including semi-natural grasslands; Dengler et al., 2020) and extensively grazed grasslands constitute a remarkably diverse ecosystem (Thomas, Jose, & Hirons, 1995; Wilson, Peet, Dengler, & Pärtel, 2012). Therefore, these grasslands are of considerable interest for landscape and nature conservation, not least because they harbour source pools of species for grassland restoration (Lindborg, 2006).

Semi-natural grasslands are a result of a long-term agricultural land use. This makes them particularly sensitive to changes in land-use regimes. In many countries over the past few decades, agricultural land use has been changing towards the extremes (so called ‘polarisation’; Ihse, 1996), i.e. land-use intensification (e.g. use of heavier and higher-efficiency machinery, increased inputs of fertilizers, use of agrochemicals, cultivation over larger and more homogenous areas; Tilman, 1999) or land abandonment (Dengler et al., 2020). Such processes are recognised to be a principal cause of habitat deterioration, loss, and fragmentation, which is threatening biodiversity in agricultural landscapes (Young et al., 2005; Saran et al. 2019).

Knowledge about past and present land-use practices are crucial to understanding patterns in land cover and vegetation, and the consequences these have for species diversity. This knowledge is essential for planning best management practices for the future (Kuussaari, 2009). However, quantitative information on land-use history is often difficult to obtain, and studies concerning the relationship between historical land use and current species diversity are rare (but see Gustavsson, Lennartsson, & Emanuelsson, 2007; Heubes, Retzer, Schmidtlein, & Beierkuhnlein, 2011).

In contrast to the negative effects of intensively used land, extensive land use (i.e. no ploughing, little or no input of fertilizers and chemicals) may contribute to more diverse grasslands, especially in landscapes where semi-natural grasslands are scarce (Lindborg, 2006). For instance, extensive grazing by domestic herbivores (e.g. grazing management based on low carrying capacity in areas with low agricultural productivity) may help to maintain open habitats and increase biodiversity (Rosenthal, Schrautzer, & Eichberg, 2012), although with varying effects across temporal and spatial scales (Dorrough, Ash, Bruce, & McIntyre, 2007; Reitalu et al., 2012). Grazing effects on species diversity may depend on, for instance, grazer type and weight, slope, grazing intensity and continuity (Zhang et al. 2018).

Taxonomic and functional diversity may be lower in grasslands grazed by sheep compared with cattle (Toth et al., 2018). Grazing may increase plant species richness in high altitude grasslands, whereas a decrease in number of species may be observed at lower altitudes (Speed, Austrheim, & Mysterud, 2013). However, the chronological duration of grazing management is also an important factor for species diversity, and grasslands grazed for longer (i.e. continuously grazed or grazed over several decades) have been found to have a higher richness than younger grasslands (Lindborg, 2006; Cousins, & Lindborg, 2008). In contrast, a reduced grazing influence and eventual abandonment will change the species assemblages and may introduce lasting effects on biodiversity at the landscape level, as open habitats are regrown by trees and shrubs (Young et al., 2005; Poniatowski et al., 2020). Continuing succession towards more closed canopies and shaded habitats will potentially exclude light demanding species (MacDonald et al., 2000).

Whilst the impact of the type and intensity of current land-use practices applied on grasslands may be assessed and managed, and thus potentially negative impacts on diversity mitigated, the more indirect impact of the surrounding landscape may be more difficult to influence. Species composition and richness of grasslands has been demonstrated to be dependent upon habitat continuity (e.g. Aavik, Jõgar, Liira, Tulva, & Zobel, 2008; Cousins, & Lindborg, 2008; Johansson et al., 2008; Waesch, & Becker, 2009; Radula et al., 2020), but the composition and the structure of the surrounding landscape (e.g. Cousins, & Aggemyr, 2008; Reitalu et al., 2012), as well as specific landscape characteristics (e.g. patch area and shape; e.g. Økland et al., 2006; Lomba et al., 2011; Saran et al., 2019) may also be important. For instance, a high proportion of arable fields surrounding semi-natural pastures have been found to have lower species richness when compared to pastures surrounded by more forests (Söderström, Svensson, Vessby, & Glimskär, 2001; Cousins, & Aggemyr, 2008). The effects of grassland patch shape complexity and size on species diversity in agricultural landscapes are, however, ambiguous and found to vary from having no significant effects (e.g. Cousins, & Aggemyr, 2008) to having significant effects (e.g. Økland et al., 2006).

By utilizing plant species data from the Norwegian Monitoring Program for Agricultural Landscapes (so called '3Q'), this research aims to increase our understanding of the extent to which observed patterns in vascular plant species richness and composition in high-latitude grasslands can be predicted by environmental and structural landscape features. Focusing on agricultural grasslands with varying land-use intensity and history, distributed systematically across bioclimatic regions of the whole of Norway (exceeding 13 degrees of latitude), we investigated whether historical and current land cover and grassland patch geometry affect vascular plant species richness. We also researched whether the observed patterns and relationships are consistent across regions with varying climate and geographical position. The knowledge gained is key information for designing biodiversity monitoring, management and conservation plans in these important habitats.

We specifically asked: (i) How important are grazing (type and intensity) and historical and current land cover for compositional and richness patterns? (ii) Are observed patterns in grassland vegetation influenced by the area and the shape of grasslands? (iii) Do correlation structures (relationships) detected vary with grassland type?

MATERIAL AND METHODS

Study area

The monitoring was established in 2004-2008 on agricultural grasslands across mainland Norway (57-70 °N, 0-32 °E) extending over ca. 13 degrees of latitude (Figure 1). Given the geographic position in the northern hemisphere and the impact of the North Atlantic Current (Gulfstream), the climate in Norway is relatively mild. Mean annual temperature is 5.8 °C, ranging from 6 °C to 8 °C in the southern coastal zones to -6 °C to -8 °C in the alpine Central and Southern Norway and continental Northern Norway (Figure 1). Similarly, geographic patterns vary for total annual precipitation, with minimum rates in the continental Southern and Northern Norway (<300 mm) and maximum rates along the south-western coastline (up to 4500 mm).

The bedrock in the study area mainly consists of granites and gneisses, but calcareous schists, limestones, sandstone and conglomerate do also occur (NGU, 2017). The dominant soil type is podzol. The studied grasslands are located at elevations between 1 m a.s.l. and 903 m a.s.l., covering lowland boreo-nemoral vegetation zones, southern and northern boreal zones (Northern Norway) and alpine (Northern Norway and continental South) vegetation zones.

The grasslands studied can be divided into outfields (outlying pastures with free-ranging domestic animals) and enclosed grassland covering the vegetation classes mesic, meso-xeric, and wet grasslands (Dengler et al., 2020), with areas varying from about 400 m^2 to 35 ha. They are dominated by forbs and graminoids (Appendix 2 Table S1). Trees and shrubs are least frequent.

Field sampling and data compilation

The grasslands can be classified as two major habitat types according to agricultural management practice: abandoned (unmanaged) grasslands and grazed (managed) grasslands. The ecological conditions of these grasslands were studied in 97 monitoring squares of 1 km x 1 km in size, drawn by a stratified random procedure from The Norwegian Monitoring Program for Agricultural Landscapes (Dramstad et al., 2002). Within each of these 97 monitoring squares, a defined maximum possible number of 16 sub-plots of 8 m x 8 m size have been established for data sampling using a 25 m raster grid dependant on specific criteria: a plot was established only if the centre of a selected raster grid point fell on grassland and if the selected plot had a minimum distance of 3 m to the border of a different land-cover type, in order to account for edge effects (Murcia, 1995). Following this protocol, in total for the 97 monitoring squares (with mean number of subplots = 6, maximum = 16, minimum = 1), 569 vegetation plots were selected for the analyses of vegetation and environmental conditions.

In the summer months of 2004 to 2008, vascular plants were recorded and species cover abundance of all species was estimated using Hult-Sernander's 5-grade abundance scale (1 = < 6.25% cover, 2 = 6.25–12.5%, 3 = 12.5–25%, 4 = 25–50%, and 5 = 50–100%; van der Maarel, & Franklin, 2013). The nomenclature follows Lid and Lid (2005).

We compiled a dataset of several spatial (landscape configuration, geographic position) and environmental (climate, land cover) variables that were deemed to be important predictors for species richness in grasslands: seasonal and annual mean air temperature, total seasonal and annual precipitation (climate normal 1961-1990; www.eklima.no), elevation (m above sea level), soil type (sand, peat, clay, humus rich, moraine), grazing intensity (categories from 1 = not grazed, 2 = lightly grazed and little loss of foliage, 3 = well grazed and some loss of foliage, 4 = heavily grazed and obvious loss of foliage, 5 = severely grazed and little foliage remaining) and grazer weight class (categories 0 = no grazing, 1 = light [sheep, goat], 2 =

heavy [cattle, horse]), as well as the shape, area, and circumference of the individual grassland in which a vegetation plot was located. Because data on environmental variables were uncomplete or lacking we used species indicator values (Landolt et al. 2010) to represent important environmental gradients (light, temperature, continentality, nitrogen, soil moisture, soil pH). However, soil moisture estimates from the field were available and used in addition to respective indicator values to compare and evaluate observed relationships. An overview over grazing intensity and grazer weight classes for all grassland types and grassland geometry statistics can be found in Appendix 1 (Tables S8, S9).

To study the potential effects of the surrounding landscape on species richness, we used data on current land use as interpreted from dominating land cover in the landscape (hereafter referred to as land cover) surrounding the grassland where a vegetation plot was located in. Data were compiled from the Norwegian high resolution land resource database ('AR5'; scale 1:5.000; Bjørdal & Bjørkelo, 2006). In this map, the minimum mappable units for land-cover types are: 0.05 ha (fully cultivated land, surface cultivated land, pasture, transport networks); 0.2 ha (forest, mire, open land) and 0.5 ha (built-up area) (Appendix 1 Table S1). Information on previous land cover was gathered from historical land resource maps (economic map series). Because of regional differences in map production, the reference years vary from 1958 to 1980, but land resources were primarily been mapped during the period 1963 to 1970. The historic land-cover type categories were matched with the categories used for current land-cover types (AR5 categories, described above) to enable the study of land-cover change effects on grassland vegetation.

Statistical analyses

Species composition

TWINSPAN (Two-Way Indicator Species Analysis; Hill, 1979) and Non-metric multidimensional scaling (NMDS; Minchin 1987) were used to identify clusters of sampling units and depict variation in species composition in the grasslands studied in order to identify different grassland vegetation types. Species data were downweighted before ordination analysis in order to reduce the potential effects of rare taxa. Stress levels indicated that a three-dimensional NMDS was most appropriate (stress = 0.17) compared with two dimensions (stress = 0.27). Adding further dimensions reduced stress levels only marginally. Environmental variables were put onto the ordination space afterwards to support interpretation of the observed variation in grassland vegetation types. The environmental variables used were; elevation above sea level, grazing intensity (measurements/estimates in the field), and Landolt et al.'s (2010) indicator values (weighted averages for each plot) representing gradients of light, temperature, continentality, nitrogen, soil moisture, and soil reaction (pH).

To study if the observed variation in species composition is controlled by different spatial and environmental variables, Canonical Correspondence Analysis (CCA; ter Braak, 1986) was used as multivariate ordination and regression method. The explanatory factors used were grazing intensity and grazer weight class, historical and current land cover, and geometric variables in shape, area, and circumference of the grassland in which the vegetation plots were located. The latter three factors were log-transformed and centred to account for skewness in data distribution. To account for the nested sampling design of plots in monitoring squares, and the inherently correlated geographical and climatic information, we added the monitoring square association of plots as a variable to the model. Backward selection approach (R package 'vegan' function 'step') with evaluation of AIC and F-test was applied to identify the factors that significantly contributed to explaining the variation in species composition. In order to identify the most important variables which explained compositional patterns, we first ran models separately for the different variable groups (i.e.

spatial, environmental, and land cover) including group-internal interaction terms. Interaction terms across groups were further applied to test the vegetation type specific hypothesis, i.e. that grazing impacts are controlled by the environment (elevation, slope, moisture, grassland geometry). Only species occurring in more than five plots were considered in this multiple regression analysis, as setting a higher threshold than five species (e.g. 10, 15) did not influence the results.

Species richness

We applied Bayesian hierarchical inference (Gelman et al., 2004) as a mixed-effects model method to assess how species richness (α-diversity) is influenced by environmental factors (monitored directly and inferred by species composition) and the exploitation (management regime and history) of the grasslands studied. In the mixed-effect model we added an extra random-effect variable to account for broad-scale spatial structures, and we assumed an over-dispersed Poisson distribution. The over-dispersed Poisson outperformed a negative binomial distribution in terms of information criterion statistics.

The model specification followed the nested structure of the data. This allows two random effect contributions; a 1 km^2 monitoring square and a plot-specific contribution capturing the over-dispersion. The over-dispersion indicates a stronger difference between the observed richness than we anticipated from the assumed Poisson distribution alone. Finally, the models included fixed effects from a set of predictor variables. The continuous predictor variables were centred and scaled before analysis.

To test the credibility, or quality, of the relationships, all models were evaluated by (i) Watanabe-AIC (Waic; Watanabe, 2010), and (ii) the 95% credibility interval of the effects (indicating 'significance'). For model selection (best fit overall model) we applied both a forward selection on groups of monitored environmental variables, and a backward elimination of the inferred environmental variables (Harrel, 2001). The backward elimination started with all main terms, two-way interactions and second order polynomials. The main effects were only selected for elimination from the model if they were not in a credible polynomial term or in credible interaction with another environmental parameter. The Waic was used to compare different models and to test against a null-model (Hoeteker, 2007, McNally et al., 2017). Since the analyses were Bayesian they provide posterior distributions of the individual effects, rather than estimated and expected effect. Hence, the uncertainty is reported by the credibility intervals of the effects, which summarizes the posterior distribution; if 0 (null-effect) is not included, this indicates substantial evidence that the terms are different from 0, i.e. the effect is credible.

RESULTS

Variation in species composition

We identified four clusters of vegetation units through the TWINSPAN analysis (Figure 2). The variables that correlated best with NMDS axis 1 were soil pH (NMDS1 = 0.928***, r^2 = 0.7767) along with the highly correlated (r = 0.89***) variable nitrogen (NMDS1 = 0.892***, r^2 = 0.8760; Table 1). NMDS axis 2 correlated best with gradients light (NMDS2 = 0.983***, r^2 = 0.4635) and grazing intensity (NMDS2 = 0.949***, r^2 = 0.1929). Axis 3 correlated most with the soil moisture gradient (NMDS3 = 0.886***, r^2 = 0.6447). Species compositional distribution (Appendix 2 Figure S1) in the NMDS diagram indicates a productivity gradient along axis 1, with decreasing productivity towards negative values. Variation along NMDS axis 2 indicates a gradient from less open and less intensely grazed (negative end of axis) towards more open and more intensely grazed vegetation. Axis 3 suggests variation along the moisture gradient, with increasing moisture towards positive axis values. The grassland vegetation types represent: moderately fertilized pastures and moist meadows (n = 155); overgrown, former agricultural land (n = 105); cultivated pastures and disturbed grasslands (n = 196); natural (i.e. unfertilized) pastures and grazed outfields (n = 113; Figure 2). These types are characterized by: pasture species tolerating moderate fertilizing or common in natural nutritious damp/moist grasslands and upper salt marshes (fertilized pastures/wet meadows); nitrophilous species increasing in abundance in early regrowth stages of former manured agricultural land (cultivated pastures/disturbed ground); species common in cultivated grasslands (manured and with sown species), weeds and vegetation on trampled ground (abandoned land); species common in semi-natural pastures and grazed natural vegetation types like grazed woodland, coastal heath, semi-natural rich fens (natural/outfield pastures).

CCA found that soil moisture contributed significantly to determining variation in species composition in all grassland types. For cultivated pastures/disturbed ground, however, soil moisture was significant in interaction with grazer weight class, indicating that the effects of grazer weight class vary subject to moisture levels (Table 2). For abandoned land, a significant interaction term was found for grazing intensity, indicating that the effects of grazing intensity change with the size of the grassland area. Grazing-related variables and current land cover explained variation in species composition in more than two grassland types (Table 2). The soil type was significant for species composition in fertilized pastures/wet meadows. The total variance explained (i.e. constrained variables' share of total inertia; Table 2b) by the final models were: 7.79% (fertilized pastures/wet meadows), 10.13% (abandoned land), 10.04% (cultivated pastures/disturbed ground), and 12.00% (natural/outfield pastures). The share explained by conditional variables (i.e. regional variation, represented by monitoring square) was 50.54% (fertilized pastures/wet meadows), 63.51% (abandoned land), 53.96% (cultivated pastures/disturbed ground), and 50.09% (natural/outfield pastures). Hence, for all four types, between 58% (fertilized pastures/wet meadows) and 74% (abandoned land) could be explained by the sum of spatial (conditional) and environmental/ecological (unconditional) variables used in final models, while land-use related constrained variables explained the least.

Variation in species richness and explanatory variables of observed patterns

The accumulated numbers of species in the grassland types were 306 (fertilized pastures/wet meadows), 295 (abandoned land), 299 (cultivated pastures/disturbed ground) and 284 (natural/outfield pastures; Figure 3). The respective average species richness per plot (α-diversity) were 28.5 (SD = 9.9, fertilized pastures/wet meadows), 30.3 (SD = 11.3, abandoned land), 22.5 (SD = 8.2, cultivated pastures/disturbed ground) and 28.8 (SD 10.2, natural/outfield pastures). In cultivated pastures/disturbed ground, mean species richness was lowest (Welch two sample t-test, $p < 0.001$). Abandoned land had significantly higher richness than cultivated pastures/disturbed ground (30.3 species; Figure 3). The number of species unique for each grassland type was 42 (fertilized pastures/wet meadows), 37 (abandoned land), 41 (cultivated pastures/disturbed ground), and 48 (natural/outfield pastures), while 144 species were shared between all types.

Richness effects by environmental variables

The main contributors to species richness in the grasslands studied were the inferred environmental variables (weighted averaged indicator values), in particular nitrogen (negative) and pH (unimodal or positive linear), and to some extent also moisture (negative linear or unimodal; Table 3, Appendix 1 Table S3). Light values had consistently negative effects, especially in natural/outfield pastures, indicating lower species richness in grassland vegetation plots with higher light values. Continentality showed a consistent influence, but mainly via interaction with other variables (Table 3).

Environmental variables contributed most to explaining species richness in abandoned land and natural/outfield pastures (Table 3, Appendix 1 Table S3). The backward elimination demonstrated that almost all variables contributed significantly to the model, often in interaction with other variables. Most importantly, higher nitrogen values were negatively correlated with species richness in all grassland types, but only for abandoned land did it appear as part of an interaction with continentality, light and moisture (Table 3). Soil pH had a unimodal relationship with richness in fertilized pastures/wet meadows and abandoned land, otherwise the relationships were positive linear. Temperature had an inconsistent effect on richness as the result was weak negative (fertilized pastures/wet meadows and abandoned land), positive (cultivated pastures/disturbed ground), or no effect (natural/outfield pastures).

Soil moisture values were found to be relatively important in fertilized pastures/wet meadows and abandoned land (Table 3, Appendix 1 Table S3), with higher values predicting species-poorer communities. This negative relationship was also shown by the significant results on soil moisture from field estimates for abandoned land, indicating a strong decrease in species richness with increasing moisture levels (Appendix 1 Tables S2, S4).

Effects of land cover

Certain land-cover types had a relatively strong positive effect on richness in all grassland types, except for natural/outfield pastures (Table 4). The highest richness in fertilized pastures/wet meadows was found where land around the vegetation plot historically had been dominated by mires, even where mires no longer dominated the landscape. The second richest grasslands were in landscapes that historically and/or currently were dominated by forests (in all types except natural/outfield pastures). Significantly higher species richness was also predicted in vegetation plots that have been (abandoned land and cultivated pastures/disturbed ground) or that still were (all types except natural/outfield pastures) surrounded by pastures.

Effects of grassland geometry

The shape and area of the grassland the vegetation plot was located in contributed to the prediction of species richness in abandoned land (shape) and natural/outfield pastures (area; Appendix 1 Table S2). For area, the observed negative relationship indicates fewer species per plot (standardized size) with the increasing size of grassland area. More complex shape indicated higher richness. However, none of these effects were statistically significant.

Effects of grazing

For abandoned land, predictive models for grazing intensity (GI) and grazer weight class (GW) found positive relationships with species richness solely when the elevation variable was added (Appendix 1 Table S6). As the intercept for these models represents ‘no grazing’, richness increase was explained by higher elevation alone. Higher moisture levels were related to decreasing species richness. For cultivated pastures/disturbed ground, richness was slightly higher with steeper slopes. This positive relationship was strengthened in combination (interaction) with low and high GW. In natural/outfield pastures, intermediate GI (level 3) predicted significantly fewer species (Appendix 1 Tables S6, S7). This negative effect was marginally strengthened by an increasing grassland area (Appendix 1 Table S6). Increased area also contributed to a stronger decrease in richness when added to the model testing the effects of GW.

DISCUSSION

This research found that species composition and richness in Norwegian grasslands are primarily determined by the assessed environmental gradients. The influences of grazing, historical and current land cover, and grassland patch geometry explained diversity to a certain, but less important extent. Species composition and richness were only partly influenced by the same main drivers: nitrogen was found to be important for both, with richness being negatively impacted in all grassland types. Soil moisture was most important for species composition within each grassland type. For species richness, soil moisture was found to have negative effects, in particular in the wettest parts of overgrown areas.

The importance of the physical environment

In total, for all grasslands studied, species composition was determined by the gradients nitrogen, pH, and light. The importance of moisture conditions as co-driver indicates the vulnerability of grasslands to climate change, which in Norway is predicted to result in warmer and wetter conditions (Hanssen-Bauer et al. 2017.). For species richness, complex patterns were observed, with almost all environmental gradients being important predictors. The relative importance of each variable for richness varied with grassland type, and only few variables had clear positive or negative relationships with numbers of species.

Nitrogen is a fundamental driver of changes in natural and semi-natural ecosystems, typically leading to reduced species richness at local, regional, and global scale (Humbert et al., 2016; Soons et al., 2017; Kleinebecker et al., 2018). This negative effect is confirmed by our study for areas with species indicating higher nitrogen availability, especially in abandoned land and natural/outfield pastures. Natural/outfield pastures are the systems in the dataset that are least influenced by agricultural management. Hence they may be expected to be highly sensitive to environmental changes involving nutrients. Increased nitrogen loads trigger species competition, the increase of biomass, and net primary productivity (Stevens et al., 2015) of a few strong, nutrient-demanding species in little or less competitive vegetation (e.g. outfields) and abandoned grasslands. Nitrogen availability is thus most likely the main driver of the predicted lower species richness in these particular grasslands.

In lowland Norway, species-rich semi-natural grasslands commonly occur in mosaics within forests and crop fields. In these regions, non-crop biotopes such as these grasslands may significantly increase botanical diversity in agricultural landscapes, locally providing more than 90% of flowering plants (Dramstad & Fry, 1995). The observed higher species richness in abandoned land at higher altitudes may be explained by the fact that with increasing elevation, the frequency of species-poor crop fields decrease, while natural and extensively used habitats (e.g. outfield mires, forests, mountain heaths) become more frequent. It is likely that such shifts in land-cover composition may locally increase the species pool and environmental heterogeneity (Cramer & Verboom, 2017) and thus, species richness, as more species are available to disperse from adjacent vegetation types. Since land abandonment is known to ultimately reduce species richness (Swacha et al., 2018), the observed higher richness may indicate a temporary state of succession with species still in the process of re-arranging (Måren et al., 2017).

Grassland species are typically more light-demanding, and management which keeps landscapes open is generally applied to support species diversity in semi-natural grasslands (Bele, Norderhaug & Sickel, 2018). In the vegetation of natural/outfield pastures studied here, we observed a somewhat surprising relationship: a negative relationship between more light-demanding vegetation and species richness. For outfield pastures at higher elevations (commonly related to upland farms since abandoned) lower species richness might result from the greater distance to edge zones featuring higher species richness (e.g., forest line; Burst et al., 2017). However, lower species richness may also be related to vegetation plots being placed in, or close to, species-poor vegetation types, which in Norway are commonly associated with outfield/natural pastures (e.g., dwarf-shrub/mountain/coastal heathlands). At the same time, abandoned grasslands at higher elevations had higher species richness than the similar grasslands at lower elevations, likely because the process of regrowth is slowed by the cooler climate.

Importance of grazing

Land use is a major driver of species richness in European grasslands and different management practices may have varying effects (Tälle et al., 2016). Grazing is commonly recommended to maintain species richness in semi-natural grasslands, while grazing cessation may decline species richness (Wehn et al., 2017). Our results show higher species richness in cultivated pastures/disturbed ground on grazed steeper slopes. These grasslands most likely benefit from either being protected from other human impacts (e.g. fertilizing) or fertilizers being off-washed more rapidly. This may be seen as strengthening the positive effect of the potential of grazing without additional management for grassland species diversity.

We found grazing intensity to significantly determine species composition, and thereby, in addition to soil pH and nitrogen, be potentially decisive for the maintenance of a particular ecosystem state (Zhang et al., 2018). In sum, for grazing-related predictors, correlations were rather weak, and neither grazer weight class nor grazing intensity could predict richness patterns satisfactorily, and overall, relationships were only significant for categories indicating no grazing. This may seem to indicate that grazing is unimportant for plant species richness in the grasslands studied. However, here, grazing category 1 means that grazing has recently ceased, and the vegetation likely indicates a temporary, unstable state, with ongoing succession, which especially in the first periods of abandonment, may be accompanied by a higher species richness (Poniatowski et al., 2020). Lower species richness in pastures may also be explained by regrowth-species suppression, or by certain grassland types which are, by nature, species-poor (e.g. dwarf-shrub heathland). This may explain the lower richness in the natural/outfield grasslands with vegetation which had clear signs of grazing (well grazed but not bare), representing an intermediate grazing intensity in our study system, and grazer weight class, when compared with no grazing. Moreover, grazing regimes may be highly variable in the grasslands studied, both within one grazing season and between years (grazing period and timing, stock size) making this factor difficult to map. Hence, the power of data may be limited due to uncertainties, or fragmentary knowledge, about local grazing management history. Not least, time-delayed responses of grassland communities to changes and inter-annual variation in grazing regimes may also explain the weak, or lacking, relationships (Allan et al., 2014). However, this is a theme warranting further investigation.

Importance of land-use history

Land-use history has been reported to explain a higher species richness than current land use (Le Provost et al., 2020). In our study, highest richness was observed in fertilized pastures/wet meadows that historically were located in mire-dominated landscapes. One explanation is that these grasslands have been created by draining mires, a practice known to provide good soil quality, well-suited for grass production and domestic animal grazing. However, rich mires are not especially common, and several species of such habitats are quite demanding in terms of particular soil nutrients and a higher pH. It is more likely that species richness in the respective grasslands is supported by remnant mire generalists (e.g. *Viola palustris*, *Carex nigra ssp. nigra*, *Epilobium palustre*) that persist in suitable habitat patches even after land-use change. Moreover, grasslands historically and/or currently surrounded by forest and pasture were species-richer, probably because of the larger species pool available when compared to other types (e.g. peat bog). Forests in the study area may be (or have been) heterogeneous, harbouring small 'islands' of different natural (e.g. mires and springs, moist broad-leaved forest, dry coniferous forest) and semi-natural habitats (e.g. grazed forests). With these islands featuring a specific species composition they could increase species richness for adjacent habitats through dispersal, which can be maintained for many years (even more than 50 years; Heubes et al., 2011; Kapfer & Popova 2021) after traditional land use has ceased. This time-delayed 'buffer' effect suggests that the distributional patterns might be in disequilibrium with the present habitat distribution, even after land abandonment (Eriksson, Cousins & Bruun, 2002; Allan et al., 2014). This is important, as it prolongs the time period available to adapt land management for species diversity conservation with the benefit of hindsight. In Norway, where recent trends are moving towards higher concentrations of grazing animals, the geographic distribution of pastures can be predicted to reduce dramatically. This may represent a threat for species diversity in the event of pasture abandonment and regrowth.

Patterns in current land cover were frequently similar to observed historical land cover, where the extent of forests and pastures in the surrounding landscape contributed to higher species richness. However, also the presence of the land-cover type 'open land' (i.e. natural and artificial land cover that may contain shrub-land and sparsely forested areas but also bare rock and mineral soil) contributed positively to species richness, possibly by open land facilitating increased dispersal of species between grasslands. It may also be explained by land-use related disturbance, thereby creating environmental heterogeneity through a variety of new (micro-)habitats for new species to establish, rather than being a local hot-spot of species richness enabling species to spread into grasslands from outside. However, it is impossible to disentangle which elements associated with the land-cover type 'open land' in fact are responsible for the positive relationship with species richness.

Species richness and patch geometry

Size and shape complexity of patches may significantly influence species richness (e.g. Game, 1980; Kunin, 1997; Økland et al., 2006; Heegaard et al., 2007). In Norwegian agricultural landscapes, the positive relationship between complexity and species richness (Heegaard et al., 2007) was explained by complex-shaped patches reducing distances to neighbouring, different land cover/vegetation types, as compared with same-sized simple-shaped (circular) patches. This complexity would increase the degree of interaction with the surrounding landscape such as seed dispersal and exchange rate between habitats (Game, 1980; Kunin, 1997). Similar edge-effects between patches were indicated by Cousins and Aggemyr (2008): although they found no clear relationship of shape and area with richness patterns in pastures (former arable fields), they did observe slightly increased species richness with decreasing distance from the patch edges to neighbouring patches. In our study, patterns of plot species richness were not consistently explained by the area or shape of the grassland polygons, although area did have some negative effect in abandoned land and natural/outfield pastures. In natural/outfield pastures, the observed lower richness with increasing grassland area may partly be explained by vegetation types in the outfields covering large areas which are species-poor by nature (e.g. dwarf-shrub heathland). However, in agricultural landscapes, it may also indicate negative effects connected with larger and more intensely managed meadows.

The lack of relationship between grassland shape and richness might be explained by the majority of grassland polygons in our study being regularly shaped (too little variation in complexity). Furthermore, the "mass-effect" (i.e., species dispersal into and establishment in patches where they are not self-maintaining; Shmida & Wilson, 1985) might be reduced in large grasslands, as the probability of plots being placed further away from species-richer edges increases with area, lowering the rate of species dispersal and establishment. This is partly documented by our study predicting species-poorer communities with increasing size of grassland area. Another explanation is the position of vegetation plots inside the grassland of varying size, with the larger area reducing the likelihood of covering all species present, when compared to smaller grasslands (e.g. Burst et al., 2017). However, the latter might be less important as the observed effect was rather marginal.

Conclusions

This research investigated patterns in vascular plant species richness and composition in high-latitude agricultural grasslands distributed over 13 degrees of latitude using data from a national monitoring program. Observed patterns were best predicted by a complex sum of environmental variables, whilst land-use related variables were less predictive. This highlights the importance of monitoring entire plant communities at the species level, and indicates the complex relationships caused by e.g. species competition. Species richness in more natural or abandoned grasslands suffered most in areas indicating higher nitrogen availability, especially in combination with higher moisture levels, suggesting that changes along these particular gradients will cause important vegetational changes with ongoing climate change.

Historical and current land cover with forests or mires dominating the landscape were found important, even where these habitats have disappeared. This implies that land-use history has a diversifying influence, and the proximity to other habitat types increases the local species pool and environmental heterogeneity, the positive effect of which may be visible decades after land-use change. Results suggest that larger and contiguous managed grasslands, the degradation of mires, and land abandonment, could threaten the species pool and hence species richness in (agri)cultural landscapes. The importance of land-cover composition, with regard to its potential role in defining species richness dynamics, should be taken into account when planning management actions in extensively used grasslands at high latitudes.

Author contributions: JK conceived the ideas and led the writing; JK and CP contributed and prepared the data; EH and JK performed statistical analyses. All authors contributed to interpretation and revising the text.

Data availability statement

All original data and datasets prepared as a part of this study and R codes are archived at the Norwegian Institute of Bioeconomy Research, Tromsø/Ås, and are available on request.

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Tables

Table 1. Results of environmental fitting on NMDS. Environmental variables are grazing intensity (field estimate categories), elevation (m a.s.l.), and weighted averaged site scores (indicator values for temperature, continentality, light, moisture, pH and nitrogen; Landolt et al., 2010). Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

Table 2. The results from CCA backward selection procedures with model evaluations based on the Akaike's Information Criterion (AIC) for each grassland type, and explained variation of the respective final models. Total inertia represents total amount of variation; condition(AREA) = area across Norway, i.e. the monitoring square in which vegetation plots are nested in; constrained = variation explained by significant variables of the final model; unconstrained = variation that is not explained by either constrained or conditional variables. GW = grazer weight class, GI = grazing intensity. Grazing effects were tested for interactions (:) with patch geometry, elevation, and slope. Only significant variables building the final models are shown.

Table 3. The effect of environment (as indicated by species composition) on species richness of the four grassland types. Orange = negative effects, and blue = positive effects. Light colours indicate that main effects are not significant, but variable is showing a significant second order (^) or interaction (:) term. Details on model statistics can be found in Appendix 1 Table S3.

Table 4. The effect of current (Cur) and historic (Hist) land cover on species richness associated with the different grassland types. Blue colour indicates a positive effect. FCL = fully cultivated land; SCL = surface cultivated land. Details on model statistics in Appendix 1 Table S5.

Figures

Figure 1: Temperature and precipitation (inlay) maps (normal climate data 1961-90) and distribution of the 97 vegetation monitoring squares á 1 km x 1 km in Norway containing in total 569 sampling plots of 8m x 8m size from which vegetation data was recorded. Species

numbers per monitoring square are averaged on all $64m^2$ plots sampled within a square. Tot ann prec = Total annual precipitation.

Figure 2: NMDS diagram and correlated variables to identify different grassland types. Only the first two axes are shown. Cont = continentality, elev = elevation, GrazInt = grazing intensity, moist = moisture, nitro = nitrogen, temp = temperature. Respective species compositional patterns can be found in Appendix 2 Figure S1.

Figure 3: Box-plot on species richness per grassland type. Box-Whisker-plots: thick line = median, box = 50%, whisker = 90% of variation, points = outliers, notches are approximations of the 95% confidence interval of the median. N is the number of plots in each grassland type. Fertilized/wet = fertilized pastures/wet meadows; abandoned = abandoned land; cultivated/disturbed = cultivated pastures/disturbed ground; natural/outfield = natural/outfield pastures.

List of Appendices

APPENDIX 1

Table S1: Description of land-cover types from theNorwegian high resolution land resource database

Table S2: Additive model for test of significant relationships between all variables of interest with species richness.

Table S3: Relationships of environmental variables (weighted averaged indicator values) with species richness.

Table S4: Modelled species richness predictions of soil moisture.

Table S5: Model statistics of relationships between land cover and species richness.

Table S6: Grazing interaction models for different grassland types.

Table S7: Modelled richness relationships with grazing intensity and grazer weight class.

Table S8: Overview over number of plots in different grassland types with different levels of grazing intensity and grazer weight class.

Table S9: Summary of statistic of patch geometry of grassland polygons.

APPENDIX 2

Table S1: List of all vascular plant species and their occurrence in number of plots.

Figure S1: NMDS ordination plot of species composition.

Appendix S1: List of all taxa and full scientific names. Occ = occurrences in number of plots. Nomenclature follows Lid J. & Lid D. T. (2005) Norsk Flora. Det Norske Samlaget, Oslo.

Scientific name	**Occ**		**Scientific name**	**Occ**		**Scientific name**	**Occ**		**Scientific name**	**Occ**
Abies sp.	3		*Carex vaginata*	19		*Juncus triglumis*	1			
Abies alba	1		*Carex vesicaria*	6		*Juniperus communis*	72		*Rosa majalis*	7
Acer platanoides	15		*Carum carvi*	63		*Knautia arvensis*	47		*Rosa mollis*	8
Acer pseudoplatanus	3		*Centaurea jacea*	6		*Lapsana communis*	4		*Rosa subcanina*	1
Achillea millefolium	336		*Centaurea nigra*	2		*Lathyrus linifolius*	19		*Rubus sp.*	1
Achillea ptarmica	100		*Cerastium arvense*	8		*Lathyrus pratensis*	99		*Rubus arcticus*	4
Aconitum lycoctonum	8		*Cerastium fontanum*	210		*Lemna minor*	1		*Rubus idaeus*	120
Adoxa moschatellina	2		*Chamaepericlymenum suecicum*	17		*Leontodon autumnalis*	193		*Rubus nessensis*	5
Aegopodium podagraria	10		*Chamerion angustifolium*	86		*Lepidotheca suaveolens*	24		*Rubus plicatus*	1
Agrostis sp.	1		*Chenopodium album*	17		*Leucanthemum vulgare*	43		*Rubus saxatilis*	16

Agrostis canina	4		*Chrysosplenium alternifolium*	1		*Linaria vulgaris*	14		*Rumex sp.*	1
Agrostis capillaris	485		*Cicerbita alpina*	2		*Linnaea borealis*	3		*Rumex acetosa*	400
Agrostis gigantea	11		*Circaea alpina*	3		*Listera cordata*	1		*Rumex acetosella*	120
Agrostis mertensii	2		*Cirsium sp.*	1		*Listera ovata*	1		*Rumex crispus*	6
Agrostis stolonifera	18		*Cirsium arvense*	58		*Lolium multiflorum*	8		*Rumex longifolius*	209
Agrostis vinealis	1		*Cirsium heterophyllum*	36		*Lolium perenne*	32		*Rumex obtusifolius*	15
Aira praecox	2		*Cirsium palustre*	83		*Lonicera periclymenum*	1		*Sagina nodosa*	1
Ajuga pyramidalis	21		*Cirsium vulgare*	52		*Lotus corniculatus*	69		*Sagina procumbens*	24
Ajuga reptans	2		*Clinopodium vulgare*	3		*Lupinus polyphyllus*	3		*Salix sp.*	2
Alchemilla sp.	23		*Coeloglossum viride*	2		*Luzula campestris*	4		*Salix aurita*	13
Alchemilla Acutidens	3		*Comarum palustre*	29		*Luzula multiflora*	162		*Salix caprea*	60
Alchemilla alpina	18		*Conopodium majus*	24		*Luzula pilosa*	33		*Salix cinerea*	3
Alchemilla borealis	1		*Convallaria majalis*	2		*Lychnis flos cuculi*	10		*Salix glauca*	12
Alchemilla filicaulis	16		*Corylus avellana*	10		*Lycopodium clavatum*	1		*Salix hastata*	6

Alchemilla glabra	26		*Cotoneaster lucidus*	2		*Lysimachia thyrsiflora*	5		*Salix herbacea*	1
Alchemilla glaucescens	18		*Crepis paludosa*	15		*Lysimachia vulgaris*	9		*Salix lanata*	1
Alchemilla glomerulans	4		*Crepis praemorsa*	1		*Lythrum salicaria*	7		*Salix lapponum*	7
Alchemilla micans	48		*Dactylis glomerata*	142		*Maianthemum bifolium*	20		*Salix myrsinifolia*	38
Alchemilla monticola	44		*Dactylorhiza fuchsii*	3		*Malus sylvestris*	1		*Salix myrsinifolia x phylicifolia*	1
Alchemilla murbeckiana	2		*Dactylorhiza incarnata*	1		*Malus x domestica*	1		*Salix myrtilloides*	7
Alchemilla propinqua	2		*Dactylorhiza maculata*	3		*Matteuccia struthiopteris*	1		*Salix pentandra*	5
Alchemilla subcrenata	89		*Danthonia decumbens*	17		*Melampyrum pratense*	16		*Salix phylicifolia*	17
Alchemilla wichurae	51		*Deschampsia cespitosa*	389		*Melampyrum sylvaticum*	21		*Salix repens*	11
Alnus glutinosa	7		*Dianthus deltoides*	1		*Melica nutans*	10		*Sambucus nigra*	1

Alnus incana	25		*Digitalis purpurea*	16		*Menyanthes trifoliata*	1		*Sambucus racemosa*	12
Alopecurus geniculatus	49		*Drosera rotundifolia*	1		*Milium effusum*	8		*Saussurea alpina*	3
Alopecurus pratensis	53		*Dryopteris carthusiana*	25		*Moehringia trinervia*	1		*Saxifraga granulata*	3
Amelanchier spicata	2		*Dryopteris expansa*	7		*Molinia caerulea*	41		*Saxifraga stellaris*	1
Andromeda polifolia	1		*Dryopteris filix mas*	4		*Moneses uniflora*	1		*Schedonorus pratensis*	126
Anemone nemorosa	64		*Eleocharis mamillata*	1		*Montia fontana*	18		*Scirpus sylvaticus*	6
Angelica archangelica	4		*Elymus caninus*	5		*Myosotis arvensis*	26		*Scleranthus annuus*	4
Angelica sylvestris	67		*Elytrigia repens*	123		*Myosotis decumbens*	1		*Scrophularia nodosa*	1
Antennaria dioica	10		*Empetrum nigrum*	30		*Myrica gale*	6		*Sedum acre*	8
Anthoxanthum nipponicum	12		*Epilobium*	1		*Nardus stricta*	97		*Sedum album*	1

Anthoxanthum odoratum	255		*Epilobium alsinifolium*	1		*Narthecium ossifragum*	18		*Sedum anglicum*	7
Anthriscus sylvestris	194		*Epilobium anagallidifolium*	1		*Noccaea caerulescens*	12		*Sedum annuum*	2
Aquilegia vulgaris	1		*Epilobium ciliatum*	81		*Omalotheca norvegica*	6		*Sedum rupestre*	1
Arabis hirsuta	1		*Epilobium collinum*	1		*Omalotheca sylvatica*	12		*Selaginella selaginoides*	6
Arctium nemorosum	1		*Epilobium montanum*	28		*Oreopteris limbosperma*	4		*Senecio jacobaea*	6
Arenaria serpyllifolia	3		*Epilobium palustre*	36		*Origanum vulgare*	1		*Senecio sylvaticus*	1
Argentina anserina	11		*Equisetum arvense*	65		*Orthilia secunda*	2		*Senecio viscosus*	1
Armeria maritima	4		*Equisetum fluviatile*	10		*Oxalis acetosella*	58		*Senecio vulgaris*	1
Arrhenatherum elatius	3		*Equisetum palustre*	10		*Paris quadrifolia*	11		*Sibbaldia procumbens*	2
Artemisia vulgaris	29		*Equisetum pratense*	24		*Parnassia palustris*	5		*Silene dioica*	28
Athyrium filix femina	65		*Equisetum sylvaticum*	49		*Pedicularis palustris*	1		*Silene latifolia*	4

Atocion rupestre	2		*Erica tetralix*	17		*Pedicularis sylvatica*	8		*Silene vulgaris*	8
Atriplex littoralis	1		*Eriophorum angustifolium*	8		*Persicaria amphibia*	1		*Solanum dulcamara*	1
Atriplex patula	4		*Eriophorum vaginatum*	9		*Persicaria hydropiper*	11		*Solidago virgaurea*	59
Avena sativa	1		*Erodium cicutarium*	5		*Persicaria lapathifolia*	2		*Sonchus arvensis*	1
Avenella flexuosa	137		*Euphrasia sp.*	8		*Persicaria maculosa*	5		*Sonchus asper*	3
Avenula pratensis	1		*Euphrasia arctica*	1		*Petasites frigidus*	1		*Sorbus aucuparia*	100
Avenula pubescens	23		*Euphrasia stricta*	9		*Peucedanum palustre*	3		*Spergula arvensis*	10
Barbarea stricta	2		*Euphrasia wettsteinii*	1		*Phalaris arundinacea*	26		*Spergularia rubra*	3
Barbarea vulgaris	7		*Fallopia convolvulus*	4		*Phegopteris connectilis*	28		*Spergularia salina*	1
Berteroa incana	2		*Festuca ovina*	47		*Phleum alpinum*	32		*Stachys palustris*	5
Betula nana	3		*Festuca rubra*	322		*Phleum pratense*	220		*Stachys sylvatica*	5
Betula pendula	41		*Festuca vivipara*	38		*Phragmites australis*	3		*Stellaria alsine*	15
Betula pubescens	140		*Filaginella uliginosa*	10		*Picea abies*	54		*Stellaria borealis*	2

Bidens tripartita	3		*Filipendula ulmaria*	137		*Picea glauca*	1		*Stellaria crassifolia*	4
Bistorta vivipara	73		*Fragaria vesca*	31		*Picea sitchensis*	2		*Stellaria graminea*	245
Blechnum spicant	9		*Frangula alnus*	1		*Pimpinella saxifraga*	24		*Stellaria longifolia*	2
Botrychium lunaria	6		*Fraxinus excelsior*	10		*Pinguicula vulgaris*	3		*Stellaria media*	83
Brassica sp.	1		*Galeopsis sp.*	57		*Pinus sylvestris*	29		*Stellaria nemorum*	15
Briza media	1		*Galeopsis bifida*	57		*Plantago lanceolata*	23		*Succisa pratensis*	26
Bromopsis inermis	1		*Galeopsis tetrahit*	29		*Plantago major*	68		*Swida sericea*	2
Bromus hordeaceus	1		*Galium aparine*	8		*Plantago maritima*	3		*Syringa vulgaris*	1
Calamagrostis sp.	1		*Galium boreale*	34		*Plantago media*	9		*Tanacetum vulgare*	15
Calamagrostis arundinacea	3		*Galium elongatum*	7		*Platanthera sp.*	1		*Taraxacum Borea*	1
Calamagrostis canescens	11		*Galium mollugo*	59		*Platanthera bifolia*	2		*Taraxacum Ruderalia*	317
Calamagrostis neglecta	18		*Galium palustre*	20		*Platanthera chlorantha*	1		*Taraxacum Taraxacum*	1
Calamagrostis phragmitoides	30		*Galium saxatile*	47		*Poa sp.*	1		*Thalictrum alpinum*	2
Callitriche palustris	3		*Galium sterneri*	1		*Poa alpina*	6		*Thalictrum flavum*	2
Callitriche stagnalis	3		*Galium uliginosum*	35		*Poa annua*	122		*Tofieldia pusilla*	1

Calluna vulgaris	39		*Galium verum*	18		*Poa compressa*	5		*Tractema verna*	2
Caltha palustris	26		*Geranium pusillum*	1		*Poa nemoralis*	6		*Tragopogon pratensis*	3
Calystegia sepium	1		*Geranium robertianum*	3		*Poa palustris*	37		*Trichophorum cespitosum*	13
Campanula latifolia	7		*Geranium sylvaticum*	123		*Poa pratensis*	421		*Trientalis europaea*	95
Campanula persicifolia	2		*Geum rivale*	58		*Poa trivialis*	194		*Trifolium hybridum*	19
Campanula rotundifolia	117		*Geum urbanum*	30		*Polemonium caeruleum*	8		*Trifolium medium*	29
Capsella bursa pastoris	25		*Glaux maritima*	2		*Polygala serpyllifolia*	1		*Trifolium pratense*	154
Cardamine amara	2		*Glechoma hederacea*	16		*Polygala vulgaris*	2		*Trifolium repens*	325
Cardamine hirsuta	1		*Glyceria fluitans*	17		*Polygonatum verticillatum*	2		*Triglochin maritima*	2
Cardamine pratensis	37		*Gymnocarpium dryopteris*	26		*Polygonum aviculare*	36		*Triglochin palustris*	2
Carduus crispus	4		*Hepatica nobilis*	3		*Polypodium vulgare*	7		*Tripleurospermum inodorum*	25

Carex sp.	1		*Heracleum sp.*	1		*Populus tremula*	35		*Triticum aestivum*	2
Carex acuta	1		*Heracleum sibiricum*	19		*Potentilla argentea*	5		*Trollius europaeus*	17
Carex aquatilis	1		*Hieracium sp.*	2		*Potentilla crantzii*	8		*Tussilago farfara*	26
Carex binervis	2		*Hieracium Alpina*	1		*Potentilla erecta*	183		*Urtica dioica*	145
Carex brunnescens	12		*Hieracium Hieracium*	8		*Potentilla norvegica*	2		*Vaccinium myrtillus*	91
Carex canescens	29		*Hieracium lactucella*	44		*Potentilla thuringiaca*	6		*Vaccinium uliginosum*	39
Carex capillaris	1		*Hieracium peleteranum*	1		*Primula veris*	3		*Vaccinium vitis idaea*	52
Carex cespitosa	1		*Hieracium pilosella*	20		*Prunella vulgaris*	30		*Valeriana sambucifolia*	26
Carex cespitosa x nigra	1		*Hieracium Tridentata*	3		*Prunus sp.*	2		*Verbascum nigrum*	3
Carex demissa	6		*Hieracium umbellatum*	28		*Prunus avium*	4		*Verbascum thapsus*	1
Carex digitata	1		*Hieracium Vulgata*	28		*Prunus padus*	29		*Veronica agrestis*	1
Carex disticha	3		*Hippuris vulgaris*	1		*Pteridium aquilinum*	26		*Veronica arvensis*	4

Carex echinata	44		*Holcus lanatus*	109		*Puccinellia maritima*	1		*Veronica chamaedrys*	139
Carex elongata	1		*Holcus mollis*	17		*Pyrola media*	1		*Veronica longifolia*	1
Carex flava	2		*Huperzia selago*	1		*Pyrola minor*	8		*Veronica officinalis*	94
Carex hirta	1		*Hylotelephium maximum*	4		*Pyrola rotundifolia*	2		*Veronica scutellata*	1
Carex laxa	1		*Hypericum maculatum*	99		*Quercus robur*	8		*Veronica serpyllifolia*	97
Carex leporina	103		*Hypericum perforatum*	8		*Ranunculus acris*	357		*Viburnum opulus*	2
Carex mackenziei	1		*Hypochaeris maculata*	3		*Ranunculus auricomus*	44		*Vicia cracca*	173
Carex media	1		*Hypochaeris radicata*	15		*Ranunculus ficaria*	3		*Vicia sepium*	78
Carex muricata	3		*Impatiens glandulifera*	1		*Ranunculus flammula*	11		*Viola sp.*	2
Carex nigra	102		*Impatiens noli tangere*	4		*Ranunculus polyanthemos*	1		*Viola arvensis*	3
Carex pallescens	64		*Juncus articulatus*	18		*Ranunculus repens*	316		*Viola biflora*	8

Carex panicea	30		*Juncus bufonius*	13		*Ranunculus sceleratus*	1		*Viola canina*	49
Carex paupercula	2		*Juncus bulbosus*	11		*Rhamnus frangula*	1		*Viola epipsila*	3
Carex pilulifera	44		*Juncus conglomeratus*	51		*Rhinanthus minor*	32		*Viola palustris*	121
Carex pulicaris	1		*Juncus effusus*	56		*Rhododendron tomentosum*	1		*Viola riviniana*	22
Carex rostrata	12		*Juncus filiformis*	47		*Ribes spicatum*	12		*Viola tricolor*	36
Carex serotina	1		*Juncus gerardii*	1		*Ribes uva crispa*	4		*Viscaria vulgaris*	4
Carex spicata	1		*Juncus squarrosus*	15		*Rosa dumalis*	3			

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Appendix S2: Number of plots in different grassland vegetation types with different levels of grazing intensity (categories from 1 = not grazed, 2 = lightly grazed and little loss of foliage, 3 = well grazed and some loss of foliage, 4 = heavily grazed and obvious loss of foliage, 5 = severely grazed and little foliage remaining) and grazer weight class (categories 0 = no grazing, 1 = light [sheep, goat], 2 = heavy [cattle, horse]). Type 1 = fertilized pastures/wet meadows; type 2 = abandoned land; type 3 = cultivated pastures/disturbed ground; type 4 = natural/outfield pastures.

	Grazing intensity				
	1	2	3	4	5
type 1	111	14	19	10	1
type 2	71	21	10	2	1
type 3	68	36	57	22	13
type 4	35	41	32	3	2

	Grazer weight class		
	0	1	2
type 1	110	11	34
type 2	70	9	26
type 3	64	33	99
type 4	35	37	41

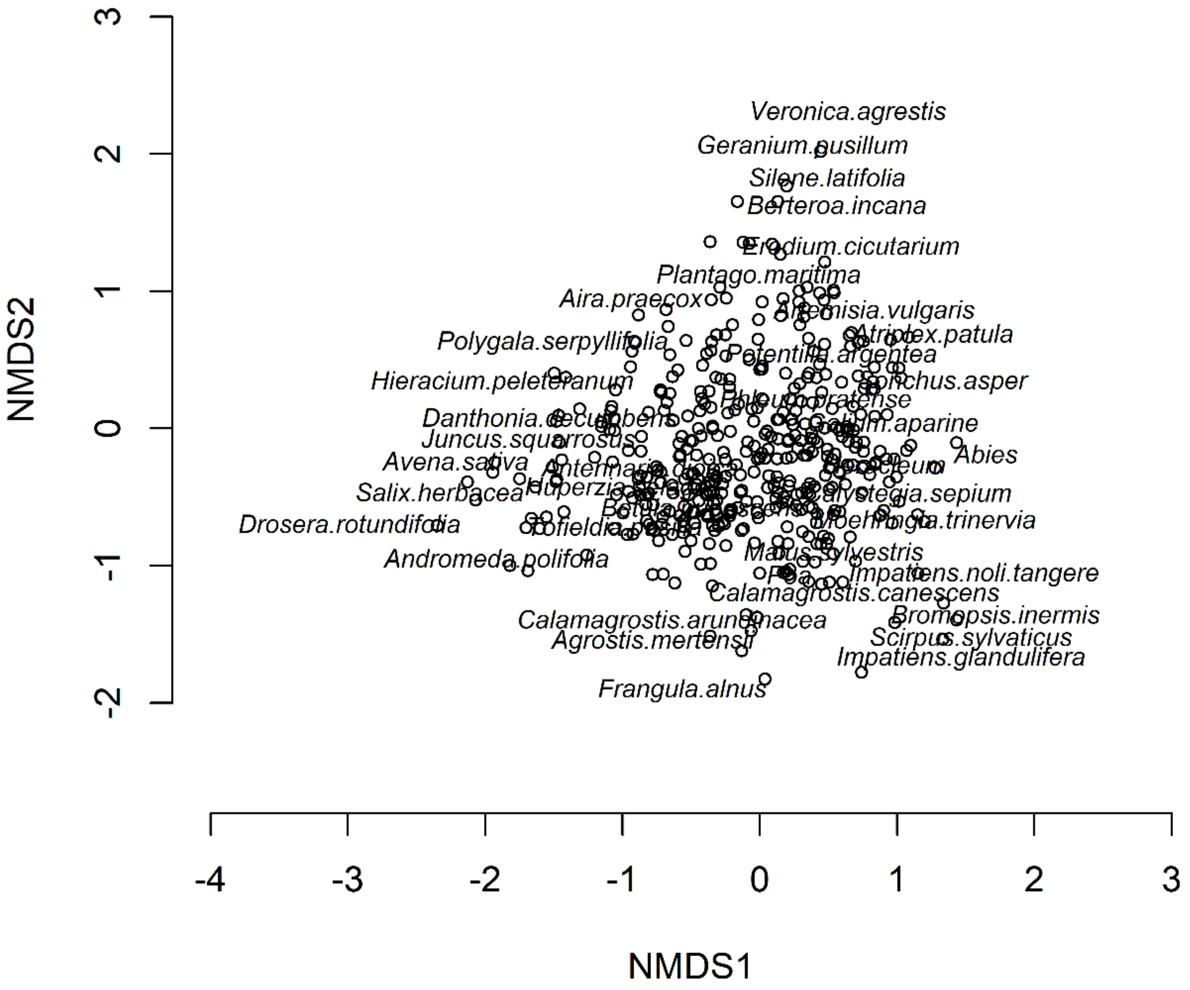
Appendix S3: Summary of statistics of patch geometry of the grasslands where a vegetation plot was located in. Shape is calculated by *shape = circumference/(2*sqrt(pi*area))*.

	Minimum	1st Quantile	Median	Mean	3rd Quantile	Maximum
Area [m^2]	392.2	5344.2	11436.6	25992.2	23441.3	364774.2
Circumference [m]	97.65	450.36	727.11	1151.95	1352.38	7232.2
Shape	1.074	1.509	1.931	2.281	2.667	7.196

Appendix S4. Main characteristics of the land cover types used as received from the classification system of the Norwegian high resolution land resource database.

21	Fully cultivated land (FCL)	Cultivated to normal ploughing depth. Can be used as field or pasture. Normally regenerated by ploughing.
22	Surface cultivated land (SCL)	Mostly used for pasture or grass production. Can be harvested with mechanical equipment.
23	Pasture	Can be used as pasture. Cannot be harvested with mechanical equipment. More than 50% of the area should be covered with grass or herbs that tolerate grazing.
30	Forest	Areas with >60 trees per hectare that are/can become >5m tall (>3m in North Norway). Trees should be distributed regularly throughout the area. Coniferous forest (>50% covered by coniferous trees). Deciduous forest (<20% covered by coniferous trees). Mixed forest (20-50% covered by coniferous trees).
50	Open land	Contains areas with mineral soils or bare rock, which do not qualify for the classes agricultural area, forest, built-up area, transport network or peat bog. Includes both natural and artificial land cover and can also contain shrub-land and sparsely forested areas.
60	Mire	Areas with peat soil of >30 cm depth. Includes forests on peat soil.

Appendix S5: NMDS ordination plot for species composition. Only the first two NMDS axes are shown.



Appendix S6: Relationships of environmental variables (as represented by weighted averaged indicator values for temperature (temp), continentality (cont), light, moisture, pH, nitrogen (nitro) with species richness. Both linear and unimodal models (^2) are tested, as well as interactions (:) between variables. Only significant variables after backward selection are shown. Significant effects (positive or negative) are printed in bold. The individual models represent the best fit of the indicator values, with the selection step before and after in a backward elimination listed in Table A2 as; Indi+1, Indi, Indi-1. Type 1 = moderately fertilized pastures/wet meadows; type 2 = abandoned land; type 3 = cultivated pastures/disturbed ground; type 4 = natural/outfield pastures.

TYPE	Effect	mean	sd	0.025quant	0.975quant
1	(Intercept)	**3.435**	0.036	3.364	3.504
	stemp	**-0.067**	0.027	-0.12	-0.015
	scont	0.01	0.026	-0.041	0.061
	slight	**-0.057**	0.024	-0.104	-0.008
	smoist	**-0.114**	0.027	-0.167	-0.061
	sph	**0.1**	0.03	0.042	0.158
	snitro	**-0.171**	0.029	-0.228	-0.114
	I(scont^2)	**-0.038**	0.011	-0.059	-0.016
	I(sph^2)	**-0.041**	0.015	-0.071	-0.012
	I(snitro^2)	**-0.071**	0.019	-0.109	-0.034
	slight:smoist	**0.04**	0.019	0.003	0.078
2	(Intercept)	**3.499**	0.046	3.409	3.589
	stemp	**-0.094**	0.033	-0.158	-0.03
	scont	**-0.105**	0.038	-0.178	-0.03
	slight	**-0.097**	0.029	-0.154	-0.039
	smoist	**-0.137**	0.037	-0.209	-0.063
	sph	**0.277**	0.045	0.189	0.364
	snitro	**-0.225**	0.05	-0.323	-0.128
	I(scont^2)	**-0.065**	0.032	-0.127	-0.002
	I(sph^2)	**-0.08**	0.028	-0.135	-0.025
	scont:sph	**0.154**	0.051	0.054	0.254
	scont:snitro	**-0.13**	0.049	-0.227	-0.034
	slight:sph	**-0.088**	0.04	-0.166	-0.01
	slight:snitro	**0.134**	0.04	0.054	0.213
	smoist:snitro	**-0.08**	0.038	-0.154	-0.007
3	(Intercept)	**3.221**	0.037	3.147	3.293
	stemp	**0.065**	0.029	0.008	0.121
	scont	-0.015	0.022	-0.059	0.028
	slight	**-0.061**	0.022	-0.105	-0.018
	sph	0.084	0.044	-0.002	0.171
	snitro	**-0.143**	0.041	-0.224	-0.062
	I(stemp^2)	**-0.03**	0.013	-0.056	-0.005

	I(slight^2)	**-0.037**	0.014	-0.064	-0.011
	I(snitro^2)	**-0.057**	0.017	-0.091	-0.025
	scont:slight	**0.075**	0.019	0.038	0.111
4	(Intercept)	**3.533**	0.048	3.439	3.626
	scont	-0.029	0.039	-0.105	0.048
	slight	**-0.155**	0.05	-0.254	-0.059
	smoist	0.056	0.04	-0.022	0.133
	sph	**0.214**	0.056	0.105	0.323
	snitro	**-0.219**	0.056	-0.33	-0.109
	I(slight^2)	**-0.119**	0.029	-0.175	-0.063
	I(smoist^2)	**-0.137**	0.031	-0.198	-0.075
	scont:slight	**-0.118**	0.028	-0.174	-0.063
	scont:smoist	**-0.089**	0.036	-0.161	-0.019
	slight:sph	**0.102**	0.031	0.041	0.163

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Appendix S7: Additive model for test of significant relationships between all variables of interest with species richness. Type 1 = moderately fertilized pastures/wet meadows; type 2 = abandoned land; type 3 = cultivated pastures/disturbed ground; type 4 = natural/outfield pastures. Effect = effect size of relationship; sd = standard deviation; 0.025 and 0.975 = quantiles of confidence interval. Mar = current land cover; Har = historic land cover; elev = elevation; Moist = soil moisture (field estimate); GrazI = grazing intensity; GrazVekt = grazer weight class. Indi = set of significant weighted averaged indicator values (Landolt et al. 2010). The Indi-models are fully reported in Table A3. Indi+1 = Indi with the residual variable with the strongest explanatory power added; Indi-1 = Indi with the in model-variable with least explanatory power removed. More detailed results (effect size, standard deviation and quantiles) for relationships of richness with land cover, grazing and indicator values are shown in Table 3 (land cover), Table A3 (indicator values), Table A4 (moisture), Table A7 (grazing).

TYPE	Model	DIC	wAIC	effect	sd	0.025	0.975
1	NULL	1007.08	1004.95				
	shape	1007.74	1005.1	0.18	6.63	-0.046	0.082
	area	1007.35	1005	-0.011	0.032	-0.074	0.051
	Mar5	**1006.77**	**1003.55**				
	Har5	**1005.44**	1005.46				
	elev	1007.6	1005.02	0.034	0.037	-0.038	0.107
	slope	1007.56	1005.14	-0.007	0.033	-0.071	0.057
	Moist	1008.07	1005.72				
	GrazI	1008.43	1005.75				
	GrazW	1007.68	1005.69				
	Indi+1	939.67	942.28				
	Indi	**939.06**	**941.76**				
	Indi-1	941.92	946.57				
2	NULL	685.27	694.51				
	shape	685.5	**691.1**	0.054	0.038	-0.021	0.13
	area	688.05	702.04	-0.049	0.037	-0.122	0.025

	Mar5	**683.53**	**686.7**				
	Har5	685.43	**692.83**				
	elev	**683**	**688.71**	0.139	0.045	0.049	0.227
	slope	**684.12**	**689.87**	0.069	0.039	-0.007	0.144
	Moist	**683.16**	**692.77**				
	GrazI	687.08	**692.93**				
	GrazW	**684.3**	**687.12**				
	Indi+1	654.04	652.9				
	Indi	**653.89**	**652.74**				
	Indi-1	654.43	653.57				
3	NULL	1228.76	1231.61				
	shape	1229.8	1234.65	-0.076	0.026	-0.127	-0.024
	area	1229.8	1234.65	0.057	0.025	0.007	0.107
	Mar5	**1225.78**	1234.79				
	Har5	**1226.16**	1239.23				
	elev	1229.25	1232.2	0.03	0.032	-0.033	0.093
	slope	**1226.57**	1233.21	0.062	0.027	0.008	0.116
	Moist	1230.16	1232.61				
	GrazI	1229.49	1232.35				
	GrazW	1229.82	1233.21				
	Indi+1	1213.72	1227.72				
	Indi	**1213.02**	**1226.24**				
	Indi-1	1213.62	1228.83				
4	NULL	741.94	739.72				
	shape	742.5	739.85	-0.023	0.033	-0.087	0.041
	area	**741.83**	**738.66**	-0.112	0.04	-0.19	-0.031
	Mar5	742.87	740.53				
	Har5	747.24	741.44				
	elev	742.5	740	0.031	0.04	-0.049	0.109
	slope	742.67	740.17	0.004	0.035	-0.065	0.072
	Moist	743.36	740.2				

GrazI	**739.85**	739.59
GrazW	742.1	739.8
Indi+1	737.2	739.49
Indi	**735.95**	**739.25**
Indi-1	737	740.39

Appendix S8: Modelled species richness predictions of soil moisture (field estimates) for each grassland type. Type 1 = moderately fertilized pastures/wet meadows; type 2 = abandoned land; type 3 = cultivated pastures/disturbed ground; type 4 = natural/outfield pastures. Significant effects (positive or negative) are printed in bold.

TYPE	Effect	mean	sd	0.025quant	0.975quant
1	(Intercept)2	3.309	0.077	3.156	3.461
	factor(Moist)3	-0.043	0.08	-0.199	0.115
	factor(Moist)4	-0.104	0.13	-0.361	0.152
2	(Intercept)2	3.546	0.08	3.388	3.702
	factor(Moist)3	-0.045	0.074	-0.188	0.103
	factor(Moist)4	**-0.349**	0.091	-0.528	-0.169
3	(Intercept)2	3.131	0.084	2.964	3.295
	factor(Moist)3	-0.032	0.085	-0.199	0.136
	factor(Moist)4	-0.124	0.129	-0.378	0.128
4	(Intercept)2	3.421	0.081	3.26	3.58
	factor(Moist)3	-0.055	0.089	-0.23	0.119
	factor(Moist)4	-0.062	0.107	-0.274	0.147

Appendix S9: Model statistics of relationships between land cover (current and historical) and species richness. Significant effects (positive or negative) are printed in bold. Land cover use categories: 21 = Fully cultivated land; 22 = Surface cultivated land; 23 = Pasture; 30 = Forest; 50 = Open land; 60 = Peat bog. Type 1 = moderately fertilized pastures/wet meadows; type 2 = abandoned land; type 3 = cultivated pastures/disturbed ground; type 4 = natural/outfield pastures. More details on land cover categories in Appendix 1 Table A1.

		Modern				Historic			
Type	Effects	mean	sd	0.025quant	0.975quant	mean	sd	0.025quant	0.975quant
1	(Intercept)21	**3.097**	0.066	2.965	3.226	**3.208**	0.051	3.106	3.306
	factor(ar5)22	0.208	0.129	-0.046	0.462	0.091	0.101	-0.109	0.288
	factor(ar5)23	**0.234**	0.085	0.069	0.402	0.088	0.069	-0.047	0.225
	factor(ar5)30	**0.306**	0.094	0.123	0.492	**0.223**	0.087	0.052	0.395
	factor(ar5)50	**0.176**	0.089	0	0.351	-0.138	0.13	-0.394	0.116
	factor(ar5)60					**0.452**	0.226	0.006	0.895
2	(Intercept)21	**3.26**	0.069	3.124	3.395	**3.263**	0.06	3.145	3.38
	factor(ar5)22	0.196	0.203	-0.192	0.609	-0.007	0.257	-0.49	0.527
	factor(ar5)23	**0.266**	0.079	0.113	0.422	**0.308**	0.071	0.169	0.449
	factor(ar5)30	**0.397**	0.122	0.16	0.64	**0.295**	0.099	0.103	0.493
	factor(ar5)50	0.006	0.137	-0.255	0.281	0.22	0.121	-0.019	0.459
	factor(ar5)60	-0.187	0.189	-0.562	0.182	-0.053	0.163	-0.378	0.262
3	(Intercept)21	**2.965**	0.045	2.876	3.053	**3.004**	0.043	2.918	3.088
	factor(ar5)22	0.124	0.1	-0.072	0.32	**0.211**	0.098	0.018	0.404
	factor(ar5)23	**0.216**	0.051	0.116	0.316	**0.159**	0.054	0.053	0.264
	factor(ar5)30	0.113	0.31	-0.518	0.699	**0.384**	0.092	0.201	0.563
	factor(ar5)50	**0.444**	0.128	0.193	0.694	0.167	0.101	-0.034	0.365
	factor(ar5)60	0.256	0.263	-0.271	0.766				
4	(Intercept)21	3.285	0.172	2.944	3.62	3.331	0.15	3.034	3.622
	factor(ar5)22	0.101	0.232	-0.354	0.557	-0.223	0.237	-0.68	0.248
	factor(ar5)23	0.033	0.177	-0.314	0.382	0.028	0.159	-0.282	0.342
	factor(ar5)30	0.261	0.188	-0.107	0.632	0.149	0.161	-0.167	0.466
	factor(ar5)50	0.132	0.188	-0.235	0.502	-0.111	0.173	-0.443	0.236
	factor(ar5)60	0.288	0.358	-0.426	0.981	-0.001	0.385	-0.763	0.749

Appendix S10: Grazing interaction models for type 2 (abandoned land), 3 (cultivated pastures/disturbed ground), and 4 (natural/outfield pastures) with respective variables significantly contributing to model improvement (evaluated using wAIC and DIC, results not shown). Richness in type 1 had no significant relationship with grazing. grasI = grazing intensities from 1 = no grazing to 5 = heavily grazed; GrazVekt = grazer weight classes: 1 = no grazer, 2 = light (sheep, goat), 3 = heavy (cattle, horse); ar = grassland patch area; sh = grassland patch shape; elev =elevation; moist = moisture (category from field estimate). ':' indicates significant interaction term. Variable statistics with significant effects are printed in bold.

TYPE	Model	mean	sd	0.025quant	0.975quant
2	(Intercept)1	**3.400**	0.056	3.289	3.509
	grasI2	0.014	0.088	-0.158	0.187
	grasI3	0.142	0.111	-0.074	0.361
	grasI4	0.132	0.202	-0.264	0.534
	grasI5	-0.195	0.373	-0.936	0.533
	scale(ar2)	-0.06	0.040	-0.138	0.018
	(Intercept)1	**3.395**	0.054	3.290	3.501
	grasI2	0.017	0.089	-0.157	0.192
	grasI3	0.126	0.111	-0.091	0.344
	grasI4	0.066	0.212	-0.346	0.492
	grasI5	-0.223	0.361	-0.941	0.483
	scale(sh2)	0.058	0.039	-0.019	0.135
	(Intercept)1	**3.401**	0.052	3.300	3.504
	grasI2	0.005	0.087	-0.165	0.177
	grasI3	0.098	0.108	-0.115	0.311
	grasI4	0.069	0.206	-0.333	0.479
	grasI5	-0.02	0.356	-0.728	0.673
	scale(elev)	**0.135**	0.047	0.042	0.226
	(Intercept)1	**3.405**	0.053	3.300	3.509
	grasI2	-0.055	0.095	-0.240	0.132
	grasI3	0.078	0.112	-0.141	0.299
	grasI4	0.043	0.210	-0.365	0.463
	grasI5	-0.339	0.368	-1.069	0.381
	scale(slope)	0.082	0.042	-0.002	0.165
	(Intercept)	**3.554**	0.100	3.355	3.748
	grasI2	0.109	0.189	-0.266	0.478
	grasI3	-0.307	0.359	-1.021	0.391
	grasI4	0.089	0.210	-0.327	0.498
	grasI5	-0.174	22.361	-44.077	43.692
	Moist3	-0.006	0.093	-0.187	0.179
	Moist4	**-0.368**	0.111	-0.585	-0.149
	grasI2:Moist3	-0.275	0.200	-0.665	0.121

	grasl3:Moist3	0.332	0.371	-0.390	1.067
	grasl4:Moist3	-0.142	0.246	-0.629	0.339
	grasl5:Moist3	-0.174	22.361	-44.077	43.692
	grasl2:Moist4	-0.008	0.251	-0.500	0.486
	grasl3:Moist4	0.649	0.424	-0.182	1.485
	grasl4:Moist4	0	31.623	-62.086	62.034
	grasl5:Moist4	0	31.623	-62.086	62.034
	(Intercept)	**3.386**	0.057	3.272	3.499
	GrazVekt1	0.141	0.123	-0.095	0.387
	GrazVekt2	0.024	0.090	-0.154	0.202
	scale(ar2)	**-0.097**	0.047	-0.190	-0.004
	GrazVekt1:scale(ar2)	0.087	0.167	-0.239	0.418
	GrazVekt2:scale(ar2)	0.139	0.089	-0.037	0.313
	(Intercept)	**3.391**	0.052	3.288	3.495
	GrazVekt1	0.15	0.128	-0.098	0.405
	GrazVekt2	0	0.089	-0.173	0.175
	scale(sh2)	0.063	0.040	-0.016	0.141
	(Intercept)	**3.401**	0.051	3.300	3.502
	GrazVekt1	0.088	0.121	-0.147	0.330
	GrazVekt2	0.012	0.086	-0.156	0.182
	scale(elev)	**0.135**	0.046	0.044	0.225
	(Intercept)	**3.404**	0.053	3.299	3.508
	GrazVekt1	0.055	0.131	-0.199	0.315
	GrazVekt2	-0.040	0.091	-0.217	0.139
	scale(slope)	0.069	0.041	-0.013	0.150
	(Intercept)	**3.558**	0.090	3.377	3.733
	GrazVekt1	-0.026	0.111	-0.238	0.200
	GrazVekt2	-0.042	0.079	-0.198	0.114
	Moist3	-0.046	0.079	-0.197	0.113
	Moist4	**-0.357**	0.098	-0.547	-0.162
3	(Intercept)	**3.097**	0.049	2.999	3.193
	grasl2	-0.083	0.074	-0.231	0.062
	grasl3	0.028	0.063	-0.097	0.152
	grasl4	0.091	0.079	-0.064	0.245
	grasl5	-0.063	0.106	-0.272	0.143
	scale(slope)	**0.059**	0.028	0.004	0.113
	(Intercept)	**3.040**	0.053	2.934	3.143
	GrazVekt1	0.033	0.078	-0.123	0.185
	GrazVekt2	0.072	0.059	-0.045	0.188
	scale(slope)	-0.045	0.049	-0.142	0.051
	GrazVekt1:scale(slope)	**0.158**	0.078	0.005	0.310
	GrazVekt2:scale(slope)	**0.143**	0.059	0.028	0.258
4	(Intercept)	**3.387**	0.069	3.252	3.523
	grasl2	0.043	0.082	-0.119	0.203
	grasl3	**-0.199**	0.093	-0.382	-0.017
	grasl4	-0.328	0.203	-0.732	0.066
	grasl5	0.111	0.256	-0.397	0.611
	scale(ar2)	**-0.096**	0.041	-0.176	-0.014

(Intercept)	**3.453**	0.067	3.321	3.585
grasl2	-0.018	0.081	-0.179	0.142
grasl3	**-0.266**	0.093	-0.448	-0.084
grasl4	-0.370	0.212	-0.792	0.042
grasl5	0.063	0.271	-0.474	0.594
scale(sh2)	-0.002	0.032	-0.065	0.061
(Intercept)	**3.459**	0.065	3.331	3.587
grasl2	-0.024	0.080	-0.182	0.133
grasl3	**-0.271**	0.091	-0.449	-0.093
grasl4	-0.387	0.206	-0.798	0.013
grasl5	0.022	0.272	-0.518	0.557
scale(elev)	0.032	0.038	-0.045	0.107
(Intercept)	**3.45**	0.065	3.322	3.579
grasl2	-0.011	0.081	-0.171	0.148
grasl3	**-0.269**	0.091	-0.447	-0.090
grasl4	-0.386	0.207	-0.799	0.016
grasl5	0.062	0.268	-0.469	0.587
scale(slope)	-0.020	0.035	-0.088	0.048
(Intercept)	**3.473**	0.089	3.296	3.648
grasl2	-0.018	0.081	-0.177	0.140
grasl3	**-0.266**	0.091	-0.446	-0.087
grasl4	-0.366	0.210	-0.785	0.042
grasl5	0.068	0.272	-0.472	0.599
Moist3	-0.025	0.086	-0.194	0.143
Moist4	-0.036	0.102	-0.237	0.163
(Intercept)	**3.372**	0.074	3.227	3.519
GrazVekt1	-0.069	0.093	-0.253	0.112
GrazVekt2	0.001	0.094	-0.183	0.187
scale(ar2)	**-0.103**	0.044	-0.189	-0.015

Appendix S11: Modelled richness relationships with grazing intensity and grazer weight class for all grassland types. Intensity estimates from 1 (no grazing) to 5 (heavy grazing). Grazer weight class 1 = no grazer; category 2 = light (sheep, goat); category 3 = heavy (cattle, horse). Type 1 = fertilized pastures/wet meadows; type 2 = abandoned land; type 3 = cultivated pastures/disturbed ground; type 4 = natural/outfield pastures. Significant effects (positive or negative) are printed in bold.

		Grazing intensity				Grazer weight class			
TYPE	Effect	mean	sd	0.025quant	0.975quant	mean	sd	0.025quant	0.975quant
1	(Intercept)1	**3.256**	0.044	3.168	3.34	**3.246**	0.044	3.157	3.332
	factor(G)2	0	0.097	-0.192	0.189	0.055	0.118	-0.178	0.288
	factor(G)3	**0.174**	0.086	0.005	0.343	0.096	0.074	-0.05	0.241
	factor(G)4	-0.044	0.126	-0.292	0.204				
	factor(G)5	-0.034	0.336	-0.702	0.62				
2	(Intercept)1	**3.407**	0.055	3.297	3.515	**3.406**	0.054	3.298	3.513
	factor(G)2	0.011	0.088	-0.161	0.186	0.116	0.125	-0.125	0.366
	factor(G)3	0.116	0.11	-0.099	0.332	-0.002	0.089	-0.177	0.174
	factor(G)4	0.076	0.202	-0.318	0.483				
	factor(G)5	-0.201	0.372	-0.941	0.525				
3	(Intercept)1	**3.089**	0.049	2.992	3.184	**3.065**	0.051	2.964	3.164
	factor(G)2	-0.066	0.074	-0.213	0.079	0.042	0.078	-0.113	0.194
	factor(G)3	0.042	0.064	-0.084	0.167	0.05	0.059	-0.066	0.166
	factor(G)4	0.104	0.08	-0.053	0.26				
	factor(G)5	-0.081	0.107	-0.291	0.128				
4	(Intercept)1	**3.454**	0.065	3.326	3.583	**3.447**	0.07	3.31	3.584
	factor(G)2	-0.019	0.08	-0.176	0.137	-0.144	0.089	-0.32	0.03
	factor(G)3	**-0.268**	0.09	-0.446	-0.09	-0.063	0.093	-0.245	0.12
	factor(G)4	-0.372	0.205	-0.782	0.026				
	factor(G)5	0.062	0.269	-0.472	0.59				

Table 1. Results of environmental fitting on NMDS. Environmental variables are grazing intensity (field estimate categories), elevation (m a.s.l.), and weighted averaged site scores (indicator values for temperature, continentality, light, moisture, pH and nitrogen; Landolt et al., 2010). Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

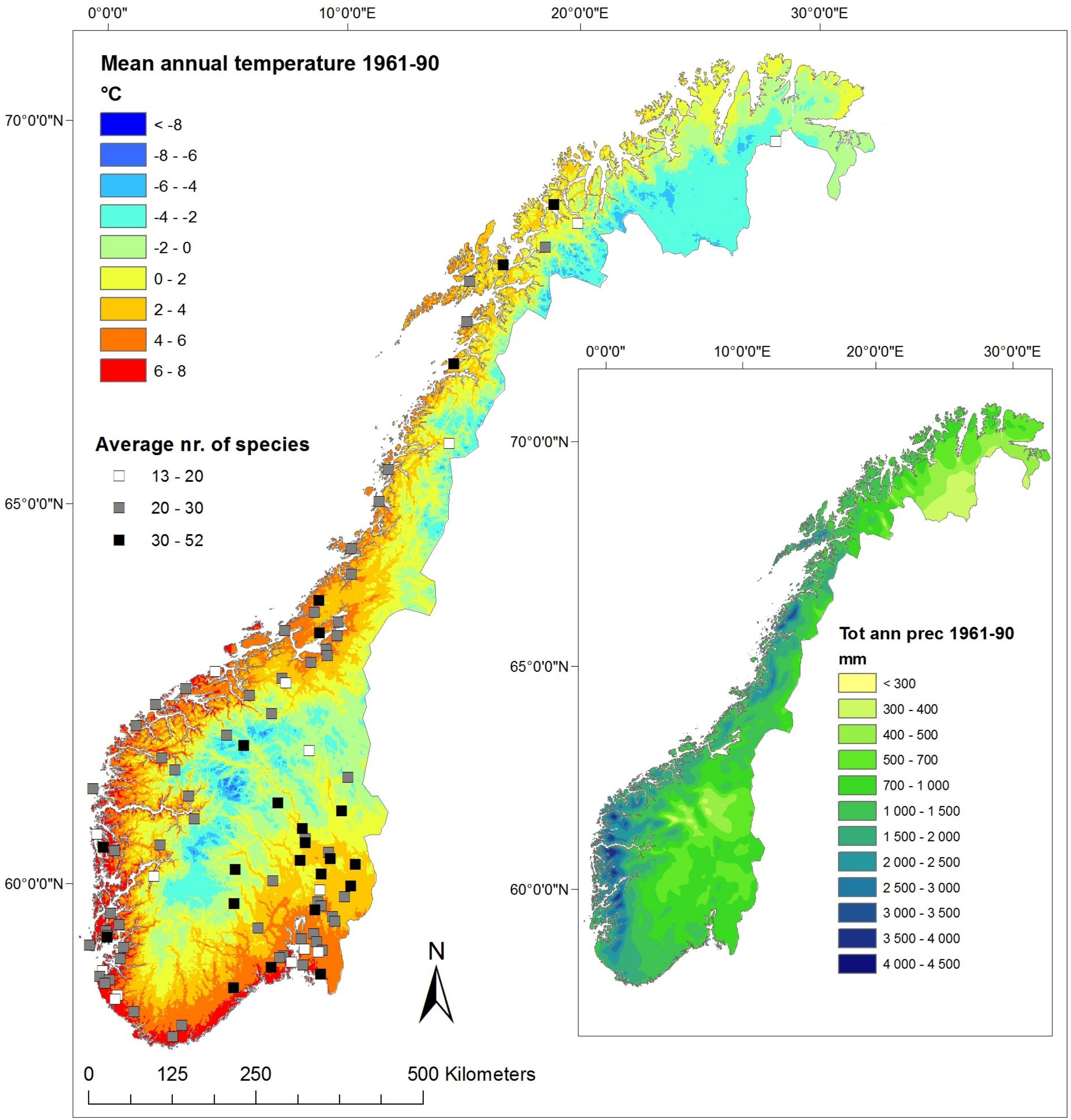
	NMDS1	NMDS2	NMDS3	r^2	Pr(>r)
Grazing intensity	-0.27684	0.94878	0.15223	0.1929	0.001 ***
Elevation	-0.26836	-0.73412	-0.62374	0.1164	0.001 ***
Temperature	0.88214	0.45783	-0.11059	0.3958	0.001 ***
Continentality	0.75822	0.13999	-0.63679	0.3223	0.001 ***
Light	-0.07691	0.98257	0.16923	0.4635	0.001 ***
Moisture	0.02684	-0.46250	0.88621	0.6447	0.001 ***
pH	0.92841	0.36955	0.03853	0.7767	0.001 ***
Nitrogen	0.89218	0.41219	0.18469	0.8760	0.001 ***

		Df	AIC	F	Pr(>F)		Total inertia
Fertilized pa	Grazer weight	2	751.82	1.31	0.050	*	
	+soil main type	4	751.71	1.23	0.045	*	
	+current land cover	4	752.38	1.32	0.020	*	4.31
	+moisture	1	752.76	2.03	0.005	**	
	+condition(AREA)	53	753.98				
Abandoned	GI:Area	1	488.59	1.45	0.045	*	
	+historic land cover	5	492.98	1.42	0.015	*	4.36
	+moisture	1	490.31	1.94	0.005	**	
	+condition(AREA)	44	511.76				
Cultivated p	GW:moisture	2	884.76	1.43	0.015	*	
	+shape	1	884.92	1.62	0.015	*	3.77
	+current land cover	5	887.26	1.49	0.015	*	
	+historic land cover	4	886.13	1.41	0.005	**	
	+condition(AREA)	68	903.82				
Natural/outf	Moisture	1	519.09	1.47	0.03	*	
	+slope	1	519.29	1.58	0.02	*	
	+current land cover	5	520.24	1.39	0.015	*	3.63
	+GW	2	519.42	1.41	0.01	**	
	+GI	1	519.69	1.81	0.005	**	
	+condition(AREA)	36	526.44				

Conditional	Constrained	Unconstrained
2.18	0.34	1.80
2.77	0.44	1.15
2.04	0.38	1.36
1.82	0.44	1.38

	Type 1	Type 2	Type 3	Type 4
Temperature (T)				
Continentality (C)				
Light (L)				
Moisture (M)				
Soil reaction (pH)				
Nitrogen (N)				
T^2				
C^2				
L^2				
M^2				
pH^2				
N^2				
C:L				
C:M				
C:pH				
C:N				
L:M				
L:pH				
L:N				
M:N				

	Type 1		Type 2		Type 3		Type 4	
	Mod	Hist	Mod	Hist	Mod	Hist	Mod	Hist
(Intercept)FCL								
SCL								
Pasture								
Forest								
Open land								
Peat bog								



Mean annual temperature 1961-90
°C
< -8
-8 - -6
-6 - -4
-4 - -2
-2 - 0
0 - 2
2 - 4
4 - 6
6 - 8
Average nr. of species
13 - 20
20 - 30
30 - 52
0°0'0"
10°0'0"E
20°0'0"E
30°0'0"E
70°0'0"N
65°0'0"N
60°0'0"N
N
0
125
250
500 Kilometers
Tot ann prec 1961-90
mm
< 300
300 - 400
400 - 500
500 - 700
700 - 1 000
1 000 - 1 500
1 500 - 2 000
2 000 - 2 500
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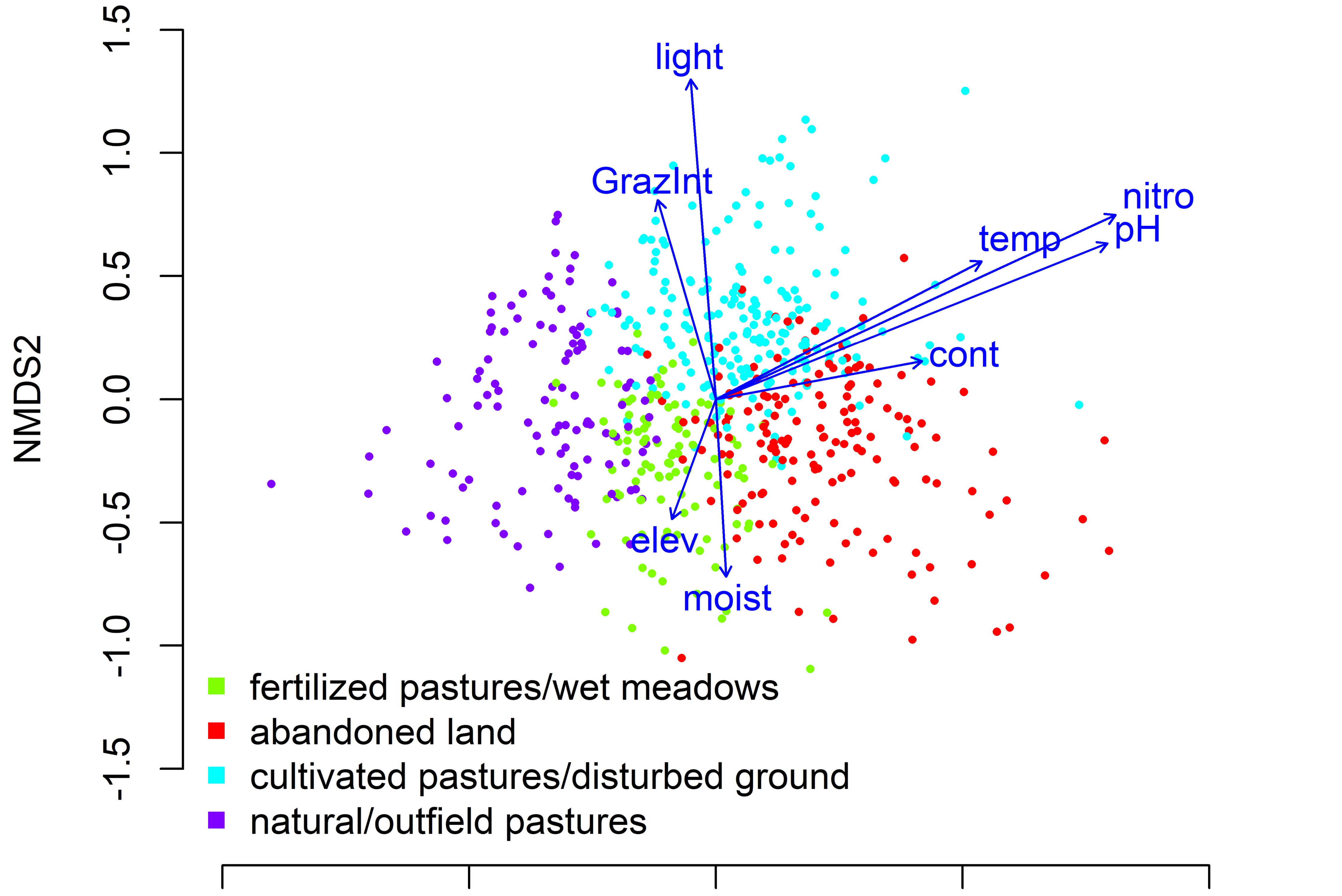
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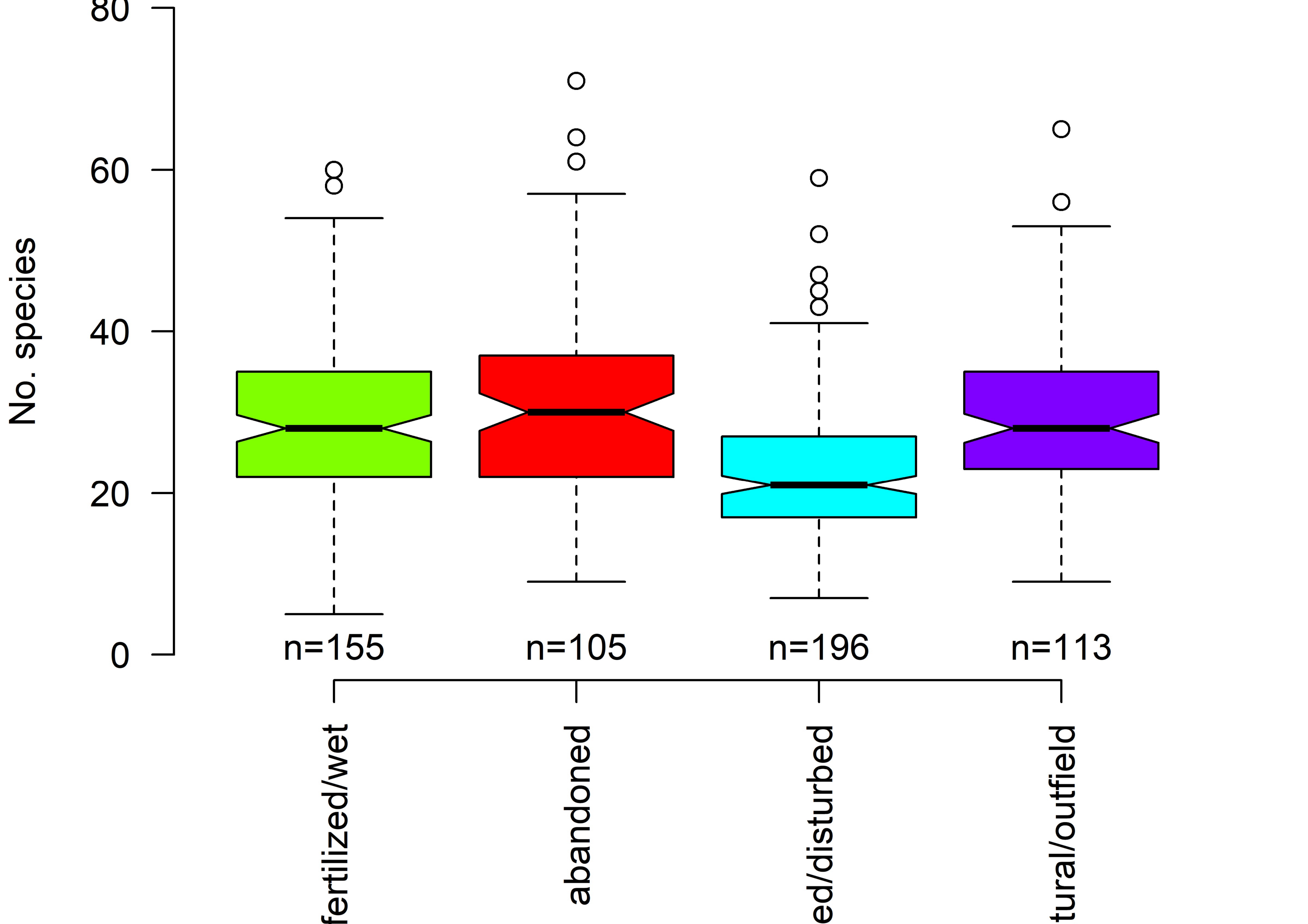
NMDS2
light
GrazInt
nitro
temp
pH
cont
elev
moist
fertilized pastures/wet meadows
abandoned land
cultivated pastures/disturbed ground
natural/outfield pastures


80
60
40
20
0
No. species
n=155
n=105
n=196
n=113
fertilized/wet
abandoned
ed/disturbed
tural/outfield