Trait-based responses to forestry and grazing modify long-term changes in biodiversity hot-spots of boreal forests

Konsta Happonen[1*], Lauralotta Muurinen[2], Risto Virtanen[2], Eero Kaakinen, John-Arvid Grytnes[3], Elina Kaarlejärvi[4], Philippe Parisot[5], Matias Wolff[2] & Tuija Maliniemi[3,5]

[1] Department of Geosciences and Geography, University of Helsinki, Finland

[2] Ecology and Genetics Research Unit, University of Oulu, Finland

[3] Department of Biological Sciences, University of Bergen, Norway

[4] Research Center for Ecological Change, University of Helsinki, Helsinki

[5] Geography Research Unit, University of Oulu, Finland

[*] Corresponding author

Contact information

Konsta Happonen, konsta.happonen@helsinki.fi, +358452591889

Abstract

Biodiversity decline is primarily caused by human land use, but its long-term effects on boreal forest understories remain unclear, even though the majority of boreal forests are under some type of management. Changes beyond trends in species richness are especially poorly understood. We resurveyed 245 vegetation plots in boreal herb-rich forest understories, originally sampled in 1968–1975, and investigated the effects of forest management and semi-domesticated reindeer herding on changes in seven community-level metrics: species richness, Shannon diversity, species evenness, vegetation height, leaf dry matter content (LDMC), specific leaf area (SLA), and temporal turnover. Some community properties changed, some remained unchanged, whereas the apparent stability of many community characteristics resulted from opposing trends in different parts of the study area cancelling each other out when viewed at a larger scale. For example, field layer communities outside the reindeer herding area had grown taller, whereas increased reindeer densities resulted in shorter communities within herding areas and consequently, community height remained unchanged at the scale of the whole study area. Changes in species evenness and Shannon diversity correlated negatively with shifts in community height, resulting in increased diversity inside the

reindeer herding area. Canopies in managed forests had higher cover in the long-term, which correlated with higher field-layer SLA and lower LDMC. Forest management intensity also correlated negatively with understory species richness trends. Compositional turnover was higher in managed forests, and lower inside the reindeer herding area. We conclude that even though the long-term effects of human land use on plant communities can be complex, complementing approaches based on species richness and dissimilarity metrics with functional trait-based perspectives has the potential to unearth mechanistic explanations for observed patterns, such as livestock grazing selectively affecting plants based on their height, and forest management filtering species based on their light-interception traits.

Keywords (6–10)

Temporal change, Community composition, Species diversity, Functional traits, Vegetation resurvey, Ungulate grazers, Large herbivores, Forest management, Diversity-productivity relationship

Introduction

Decreasing habitat quantity and quality are the lead drivers of biodiversity change in terrestrial ecosystems, caused primarily by human land use and land-use change (Butchart et al., 2010; Díaz et al., 2019; Sala et al., 2000). However, although species extinction rates are estimated to be high above background levels globally (Barnosky et al., 2011), several studies have shown that regional-to-local-scale diversity can actually remain stable or even increase with time (Sax and Gaines 2003; Dornelas et al. 2014; Vellend et al. 2013; McGill et al. 2015; Blowes et al. 2019; Steinbauer et al. 2018).

Plot-scale species richness is thought to be strongly controlled by regional species abundance distributions (Supp & Ernest, 2014). Furthermore, stability in species diversity does not mean absence of biodiversity change, since diversity trends can be unaffected by even complete temporal turnover of species (Supp & Ernest, 2014). Monitoring changes in species composition alongside changes in species diversity adds information about the consequences of global change (Hillebrand et al., 2018), which is helpful when the goal of the study is to capture processes that select against disappearing species.

Compositional change has often been studied using temporal dissimilarity metrics (Legendre & Legendre, 2012), which are informative about the rate of compositional turnover (Blowes et al., 2019). However, dissimilarity is a directionless metric that is at best indirectly informative about changing selection pressures on species affected by anthropogenic stressors such as land-use change.

One way to capture this information more directly is to monitor changes in the functional composition of communities. Indeed, functional traits have been suggested as one set of essential biodiversity variables needed for monitoring biodiversity change (Pereira et al., 2013), and have successfully been used in demonstrating the importance of historical management legacies on vegetation changes in temperate broadleaf forests (Perring et al., 2018).

In the case of vascular plants, the above-ground traits of species and communities vary on two independent axes that are important for different kinds of environmental constraints. Plant size determines competitive hierarchies in relation to light, while the leaf economics spectrum describes trait covariation related to e.g. survival-growth trade-offs (Bruelheide et al., 2018; Díaz et al., 2016). These global trait axes form a natural starting point for monitoring the biodiversity of vascular plants using functional traits. Unlike dissimilarity, changes in average functional traits are directly informative of changing selection pressures on vegetation (Violle et al., 2007), and resulting ecosystem consequences (Lavorel & Garnier, 2002). For example, increased light and nutrient availability due to recent forest cuttings should lead to understory communities composed of higher plants, since only taller species can reach the light in conditions of high resource availability (Blondeel et al., 2020), which would lead to higher food availability for grazers and browsers. Furthermore, trait-based results should be transferable between systems with different species pools, facilitating comparisons and meta-analyses that cross system borders (McGill et al., 2006). This last point is important, since identifying how community-level traits respond to land-use on these two trait axes could be important for management and conservation planning (Garnier et al., 2004; Keddy, 1992), and trait-based research could thus be used as the basis of conservation action outside the geographical range of the original study.

We demonstrate the usefulness of trait-based approaches by employing them in a study on vegetation changes in the biodiversity hot-spots of Finnish boreal forests. Boreal forests constitute almost a third of global forest cover, (Brandt et al., 2013), and most are managed for industrial wood production (Gauthier et al., 2015). Reported effects of management on community composition have been negligible in some dry sites (Nieppola, 1992), and lagged but detectable on more mesic sites, favoring some graminoids and pleurocarpous mosses against old-growth forest specialists (Muurinen et al., 2019). Additionally, Tonteri et al. (2016) found boreal forest understory species to have strong species-specific responses to cuttings that could not be predicted by growth forms, but by shade tolerance. Consequently, one would expect the average leaf economic traits in communities to change in response to altered light levels in managed forests, and more strongly in more productive forests. In Fennoscandian boreal forests, forest management has intensified manyfold from low intensity wood

harvesting to industrial-scale forestry after the 1950s (Löfman & Kouki, 2001; Rouvinen & Kuuluvainen, 2005), with detrimental effects on forest biodiversity (Hyvärinen et al., 2019).

In addition to forestry, humans also affect understories by controlling herbivore densities, for example by practicing animal husbandry. Since herbivores have strong effects on understory vegetation (Bråthen & Oksanen, 2001; Oldén et al., 2016), human-mediated changes in herbivore density can be regarded as land-use change with consequences for forest biodiversity that interact with the effects of forestry. One of the main large herbivore species in boreal forests is the reindeer (*Rangifer tarandus*), which in many parts of Eurasia are semi-domesticated free-ranging livestock. In Finland, reindeer occur only inside a designated reindeer herding area. Several local scale studies have shown reindeer herbivory to cause decreases in biomass and declines in favoured forage species such as herbs, deciduous shrubs, and lichens in the boreal coniferous heath forests and on tundra heaths (Bråthen & Oksanen, 2001; Olofsson et al., 2010; Sundqvist et al., 2019; Väre et al., 1995). However, there is limited evidence on whether these effects scale to larger geographical extents, and on how reindeer grazing influences vegetation in more productive forests (but see Maliniemi et al., 2019).

In this study, by employing diversity-, dissimilarity-, and functional trait -based approaches, we shed light on the poorly understood effects of land use on boreal forest understory vegetation change. Specifically, we ask four questions: 1) how have plot-scale species diversity, species composition, and functional composition changed in boreal herb-rich forests over 40–50 years, 2) how are the changes correlated with changes in canopy characteristics, and increases in semi-domesticated reindeer grazing pressure, 3) how does forest management affect understory communities directly, and indirectly via changes in the canopy, and 4) do spatial and temporal correlations in community properties agree, hinting at the existence of general processes that shape those properties?

We answer these questions with a vegetation resurvey study along gradients of management intensity and intensified grazing pressure in boreal herb-rich forests, using Bayesian regression modelling.

Materials and methods

Vegetation data and resampling

We conducted vegetation resurvey in boreal herb-rich forests in Northern Finland (Fig. 1). The resurveyed herb-rich forest sites were originally surveyed in 1968-75 by Eero Kaakinen (Kaakinen,

1971, 1974; Unpublished). The purpose of the original surveys was to identify phytosociological species associations in mature herb-rich forests. For this reason, the surveys were conducted in relatively undisturbed habitats. These forests harbour higher species richness than the surrounding less fertile and homogenous boreal forests. They occur typically as small patches and cover only a fraction of the forested area in northern Scandinavia, resulting primarily from the scattered distribution of calcareous bedrock and soil. The field layer of these forests is dominated by herbs such as *Geranium sylvaticum* and *Filipendula ulmaria*, ferns such as *Gymnocarpium dryopteris* and *Athyrium filix-femina*, and graminoids such as *Milium effusum* and *Elymus caninus*. Occasionally they also host species typically found in less fertile boreal forests, such as the dwarf-shrubs *Vaccinium myrtillus* and *Vaccinium vitis-idaea*. The three most abundant tree species *Picea abies*, *Alnus incana*, and *Betula pubescens* formed more than 80% of tree cover in our study plots, both during the original and resampling time periods.

Using detailed notes on the locations of the original sites, which in many cases included additional information on topographical position (elevation, aspect), we relocated and resurveyed the majority of the original 336 sites in 2013-14 and in 2019. Most surveys were done in teams of ≥2 investigators. We omitted sites with vague descriptions of location, and some sites that were located very far from other sites. The final number of plots, after applying exclusion criteria described below, was 245. Relocation error is inherent in vegetation resurveys, but was minimized as much as possible by the relocation help of the original surveyor and the patchy distribution of the studied vegetation types (Kapfer et al., 2017). This study thus applies all of the measures listed in Verheyen et al. (2018) for minimizing observer and relocation error. During both the original survey and the resurvey, species composition was estimated from 5 m x 5 m quadrats for the field layer and from 10 m x 10 m quadrats for shrub and canopy layers. The smaller quadrats were nested in the larger quadrats. The abundances of field and shrub-layer species were estimated as absolute percentage covers, and the covers of tree-layer species were estimated as relative covers. In addition, total canopy cover was estimated visually on a three-point ordinal scale (0–30%, 31–70%, 71–100%). In this study, we focus only on the vascular plants of the field and tree layers (see species list and trait values in Supplementary Table 1).

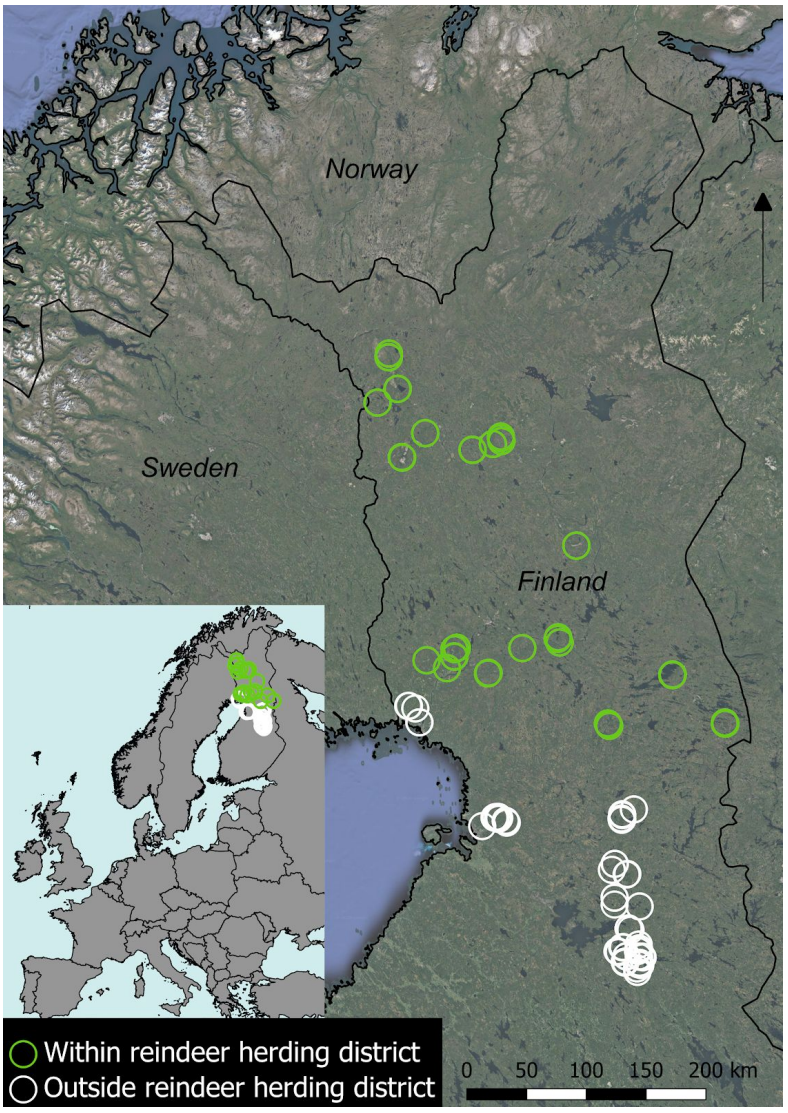


Fig. 1. Map of the study area.

Environmental changes

We estimated forest management intensity during the resurvey based on the protocol used for the assessment of threatened habitat types in Finland (Kouki et al., 2018, p. 180). The original protocol assigns sites on an ordinal scale of habitat quality ranging from zero to four. Here, we inverted the scale to describe management intensity. We also omitted the few sites that were destroyed by deforestation and land conversion to arrive at a management impact variable ranging from one to four. The management intensity assessment criteria include the structure of the canopy and vegetation layers, disturbance of the soil, and the amount of deadwood, and are described in Supplementary Table 2. These criteria are applied in a one-out-all-out manner, meaning that if any of the criteria for a more intensive management class were fulfilled, the site was assigned in that class even if it would have been a less intensively managed site based on all other criteria. The criteria are independent of

the other variables used in this study, meaning that species composition was not used as a measure of management intensity.

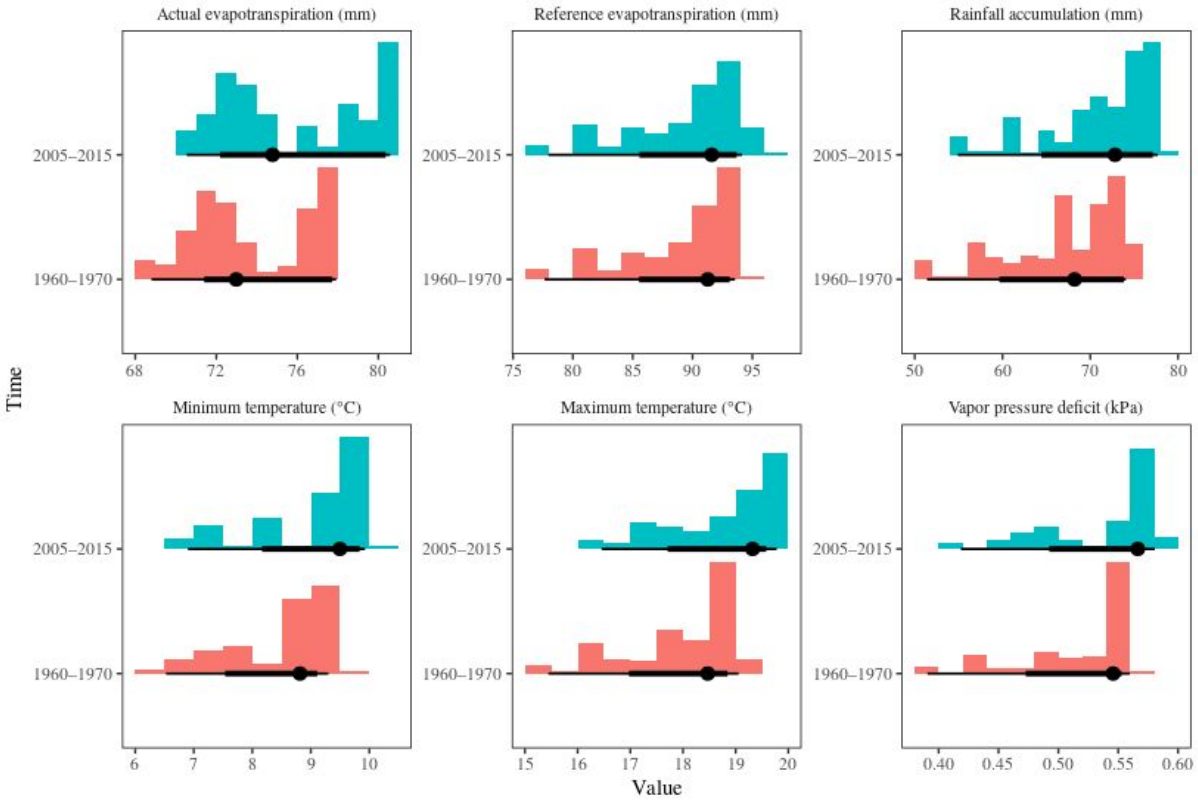
	Natural sites = 1	Semi-natural sites = 2	Managed sites = 3	Heavily managed sites = 4
MANAGEMENT INTENSITY	Not managed	Light management	Intensive management (but no ditching or mounding)	Very intensive management (incl. ditching, fertilization)
SOIL	Undisturbed	Disturbed, but enables prevalence of herb-rich forest species	Disturbed, declined conditions for herb-rich forest species prevalence	Severely disturbed, soil may have dried up or topsoil eroded, prevalence of herb-rich forest species endangered
VEGETATION LAYERS	All layers present	Layer variability declined	Layer variability clearly declined	Layers missing
STAND STRUCTURE	Natural variation, gap dynamic works	Variability declined, impacts of management visible in gap dynamics	Pronounced decline in variability	Even-aged stand, plantation
DEADWOOD	Varying aged and sized	Impacts of management visible in the amount of decaying wood	Scarce or invariable in age or size	Scarce or missing

Supplementary Table 2. The one-out-all-out criteria for inclusion in a management intensity class.

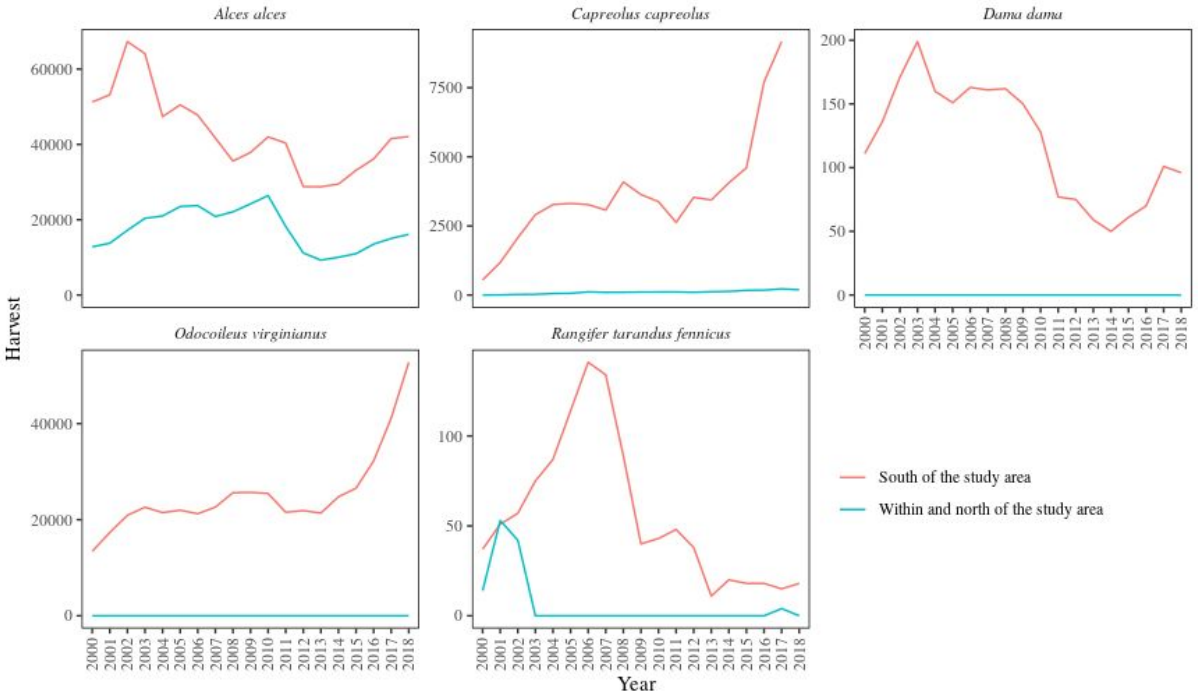
Reindeer are the major large grazer in our study area. Data on reindeer density trends in the different reindeer herding districts were provided by Jouko Kumpula from the Natural Resource Institute of Finland. The population sizes of other large herbivores in the study area, as inferred from hunting statistics, are negligible (Natural Resources Institute Finland, 2020, Supplementary Fig. 2), with the exception of the moose (*Alces alces*). Although the moose population in Finland has grown due to changes in forestry practices and hunting, the growth has been rather uniform across the country (Nygrén, 2009). Moreover, herbaceous field layer vegetation constitutes less than 5% of moose summer diets (Hjeljord et al., 1990). Thus, while moose density changes might have affected forest regeneration and shrub layer composition, the direct effects of increased moose densities should be rather small and uniform across the study area.

Because of our focus on land-use change, we intentionally left climate out of our models. On average, increases in minimum and maximum summer temperatures in our study plots have been 0.6℃ and 0.8℃, respectively (Supplementary Fig. 1). Since the changes experienced by the field layer are further buffered by the canopy layer (De Frenne et al., 2019; Lembrechts et al., 2020), and both canopies and understories have been shown to have small responses to climate change compared to land-use at decadal timescales (Danneyrolles et al., 2019; Tonteri et al., 2016), the direct effect of climate change was left out of the models.

If any unincluded drivers have direct effects on field-layer vegetation, these will manifest as unexplained trends in our models.



Supplementary Fig. 1: Distributions of bioclimatic variables for the summer months in the study plots. The values are 10-year averages from the TerraClimate dataset (Abatzoglou et al., 2018), which has a nominal resolution of 1/24 degrees (~4km). The coloured bars are histograms, the points are medians, and the narrow and thick lines depict 95% and 50% quantile intervals, respectively.



Supplementary Fig. 2: Harvests of large herbivores in Finland 2000–2018, within and outside the study area. Data are from Natural Resources Institute Finland (2020).

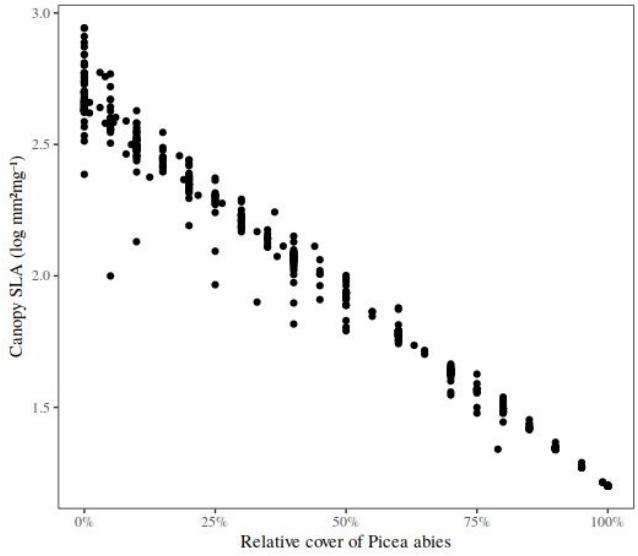
Community properties

All data processing and analyses were done in R (version 3.6.2 , R Core Team, 2019).

As species diversity measures, we calculated species richness, Shannon diversity, and species evenness. By Shannon diversity we mean the so-called true diversity of order 1, which is a unit conversion of the Shannon diversity index from entropy to species (Jost, 2006). As species evenness, we used Pielou's J, or the ratio of Shannon entropy to log-transformed species richness, which is a measure of relative evenness ranging from zero to one (Jost, 2010).

We calculated community weighted means (CWM) of log-transformed trait values for one size-structural trait and two leaf economic traits: vegetative height, specific leaf area (SLA), and leaf dry-matter content (LDMC). Trait values were log-transformed because generally, traits follow a log-normal distribution (A. D. Bjorkman & Myers-Smith, 2018). Species relative covers were used as weights. Trait values were retrieved from the TRY database (version 5, Kattge et al., 2011, 2020) and the LEDA database (Kleyer et al., 2008), and supplemented with our own measurements for common species that were not found from the databases. In four plots, some of the traits were available for less than 80% of total cover. These plots were excluded from analyses. In the remaining plots, trait cover was on average >99.5% for all traits.

We also calculated a CWM for the SLA of the canopy layer. SLA was not available for the non-native *Larix sibirica* (present on 1 site), for which we used the SLA of *Larix decidua* instead. SLA of the tree layer was highly negatively correlated with the relative cover of *Picea abies* (Supplementary Fig. 2), the main evergreen tree species in these forests.



Supplementary Fig. 2: The CWM of SLA in the tree layer is a function of the relative cover of Norway Spruce (*Picea abies*). SLA: specific leaf area.

Summary statistics of the studied properties during original sampling *ca.* 1970 are presented in Supplementary Tables 3 & 4, which help in interpreting the observed rates of change.

Variable	Unit	Mean	SD	Min.	Max.
D0	Species	21.97	5.99	8.00	44.00
D1	Species	8.24	3.49	1.77	28.89
E	Unitless	0.66	0.12	0.22	0.90
Height	Log cm	3.50	0.45	2.58	4.63
LDMC	Log proportion	-1.49	0.12	-1.81	-1.11
SLA	Log mm^2mg^{-1}	3.38	0.18	2.88	3.82
Canopy SLA	Log mm^2mg^{-1}	2.15	0.49	1.20	2.94

Supplementary Table 3: Summary statistics for continuous variables during the original survey (*ca.* 1970). D0: species richness, D1: Shannon diversity, E: species evenness, LDMC: leaf dry matter content, SLA: specific leaf area

Variable	Value	Proportion
Canopy cover class	1 (0–30%)	30%
	2 (31–70%)	53%
	3 (71–100%)	18%
Within reindeer herding area	No	62%
	Yes	38%

Supplementary Table 4: Summary statistics of categorical variables *ca.* 1970.

We subtracted the diversity measures and trait CWMs of the original sampling period from those of the resamples to get estimates of community change between the time-periods.

We used the R package *vegan* (version 2.5-6, Oksanen et al., 2019) to calculate temporal turnover in community composition using the version of Jaccard distance that takes into account species abundances. Plot-scale turnover was logit-transformed before analyses. We also calculated temporal turnover for the entire dataset.

Modelling

Models were built using the R package for Bayesian modelling *brms* (version 2.10.0, Bürkner, 2018), an interface to the probabilistic programming language Stan (Carpenter et al., 2017).

We used those sites for which we had the full set of response and predictor variables: changes in species richness, species diversity, species evenness, height, LDMC, SLA, canopy cover, and canopy SLA, location within the reindeer herding area, and management intensity. The final dataset thus consisted of 245 resampled sites.

We used two multivariate linear regression models to analyze plot-level changes in species diversity and composition. The first model tested average changes across the study area. It was an intercept-only model, with observed plot-level differences in species richness, species diversity, species evenness and functional composition, and turnover as the responses. We also modelled residual correlations among the variables. The second model tested the effects of canopy changes and increased herbivore density on the same seven community change metrics. In this second model, we added as predictors the observed changes in canopy cover and canopy SLA, and whether the plot belonged to the reindeer herding area. Since forest management can consist of varying practices e.g. ditching and other practices that have effects on soils, the residuals of this second model were further

studied in the different management intensity classes to see if management intensity had additional effects on community characteristics besides those mediated by changes in the canopy layer.

We built two additional models to study the effects of forest management on canopy characteristics. First, we modelled tree-layer canopy cover in the plots as a function of plot identity, sampling time, and management intensity. Since canopy cover was measured on an three-level ordinal scale, we used an ordinal regression model with a cumulative logit link (Bürkner & Vuorre, 2019). Plot identity was added as a group-level (random effect), and management intensity, sampling time, and their interaction were added as population-level (fixed) effects. Second, we modelled canopy SLA with the same predictors, but using ordinary linear regression with normally distributed errors.

We used the canopy models to predict the indirect effects of management intensity on community diversity and composition via changes in canopy characteristics. We made 4000 draws from the posterior distributions of the model parameters, and used them to acquire fitted values of canopy cover and canopy SLA in each management intensity class during original sampling and resampling. For the ordinal model, this was the probability of each of the canopy cover classes. We then used these fitted values to calculate the posterior probability of canopy cover transitions (canopy cover decreased, canopy cover stayed the same, canopy cover increased), and the posterior probability distribution of canopy SLA changes. We then used these posterior distributions of canopy change as predictors in the model of community change described above to infer the indirect effects of forest management intensity on community properties via effects on canopy characteristics.

We inspected whether temporal correlations resembled the spatial covariance between community properties. To quantify spatial correlations in community properties, we built a model explaining community diversity and functional composition with plot as a group-level (random) effect, time as a population-level (fixed) effect, and modelled residual correlations in the response variables.

In all models, priors were left as the *brms* defaults. All population-level effects were given a noninformative flat prior over the reals. The standard deviations of all group-level effects were given a half-t prior with 3 degrees of freedom, each prior was further scaled with a constant that equaled 10 standard deviations of the response. Correlations among responses were given a noninformative LKJ prior.

Results

Reindeer densities in the herding area had increased *ca.* 40% during the study period (Fig. 2 a). Signs of forestry were present in *ca.* 70% of the resurveyed plots, whereas the rest *ca.* 30% were deemed unmanaged (Fig. 2 b).

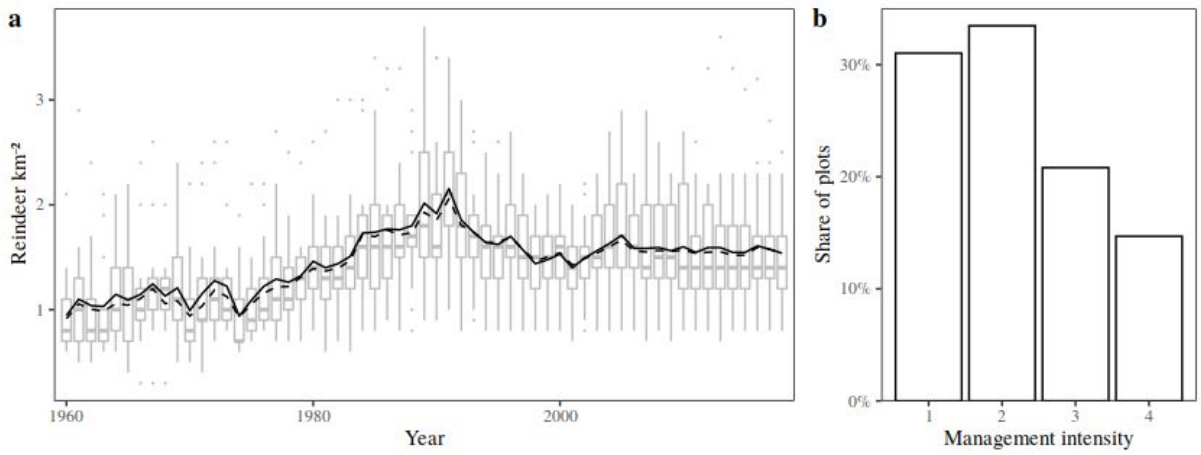


Fig. 2: Studied drivers of vegetation change. Panel a depicts changes in reindeer densities in the reindeer herding districts involved in this study. The boxplots show variation in densities among districts, the solid line is the average across those districts, and the dashed line is the weighted average that takes into account the plot frequencies within different herding districts. Panel b shows the percentage of resurveyed plots that belong to different management intensity classes (for inclusion criteria, see Supplementary Table 1).

There were no divergent transitions in any of the MCMC chains in any of our models, which would have indicated unreliable estimates of the parameter posterior distributions (Carpenter et al., 2017). In addition, all parameters converged to a stationary posterior distribution (R-hat < 1.01, Gelman & Rubin, 1992).

Across the study area, we detected no changes in species richness (Fig. 3 a), but observed increases in plot-level Shannon diversity (Fig. 3 b) and evenness (Fig. 3 c). There was no detectable change in average species height or SLA (Fig. 3 d,f), but average LDMC had increased, indicating slower leaf economics (Fig. 3 e). Average turnover (Fig. 3 g) between time periods was about 80%. For the full dataset (i.e. the relative abundances of all species across the study area), temporal Jaccard dissimilarity was 37%, which when divided over the average sampling interval (44 years) corresponds to a yearly turnover of 2.2%.

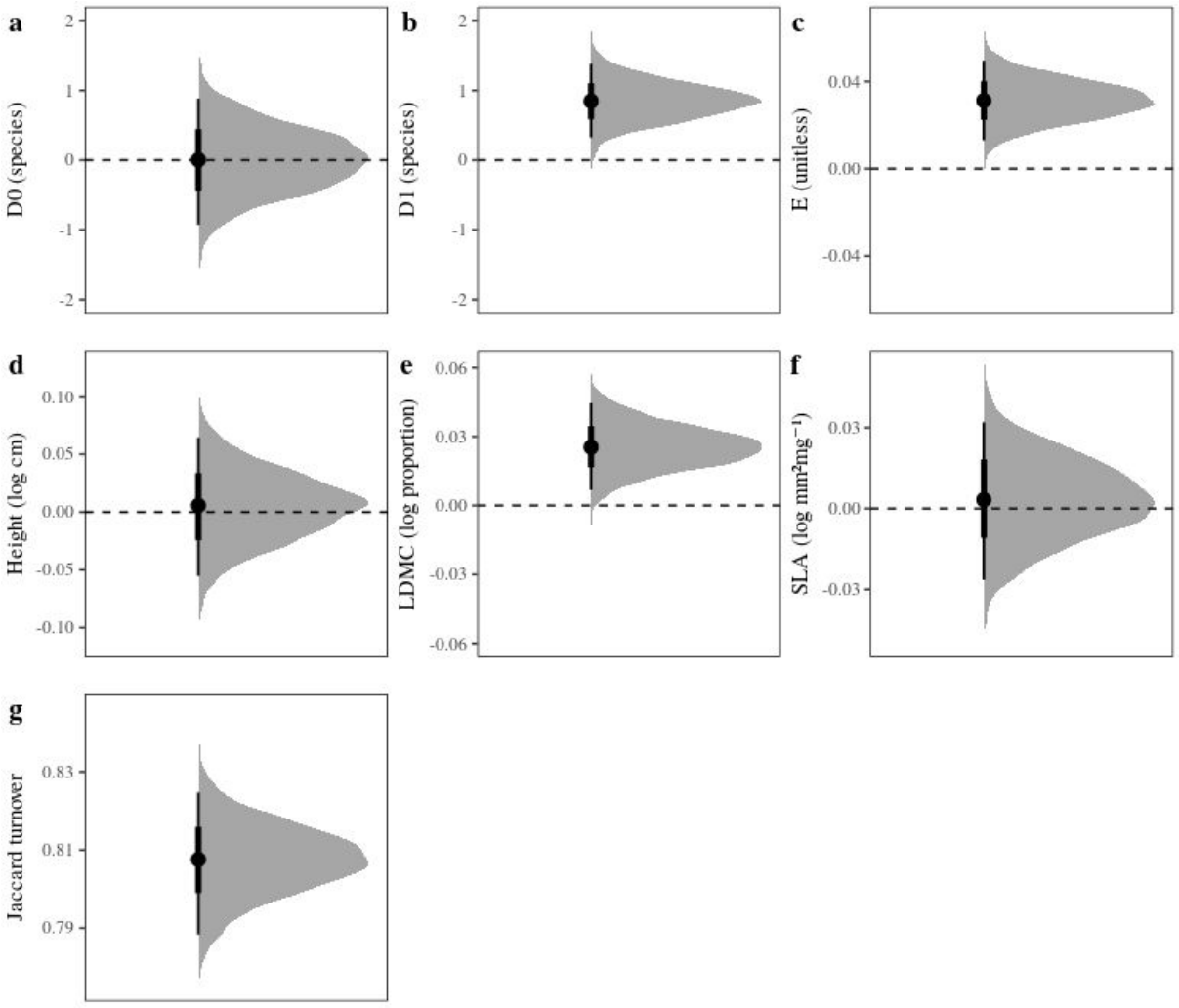


Fig. 3: Plot level average changes and their posterior distributions in species richness (D0, a), Shannon diversity (D1, b), species evenness (E, c), functional composition (d–f), and species composition (g), across the study area. The points are medians, the narrow and thick lines are 95% and 66% credible intervals, respectively, and the gray shading is a kernel density plot of the parameter's posterior distribution. LDMC = leaf dry matter content, SLA = specific leaf area.

Management intensity modulated changes in the canopy. In the three lowest management intensity classes, canopy SLA decreased, while in the highest management intensity class canopy SLA remained unchanged (Fig. 4 a). In all the management intensity classes, increasing canopy cover was always more probable than decreasing canopy cover (Fig. 4 b). In the highest and lowest management intensity classes, lack of canopy cover class transitions was the most probable outcome, while in the two middle classes increases in canopy cover were much more probable than other outcomes (Fig. 4 b).

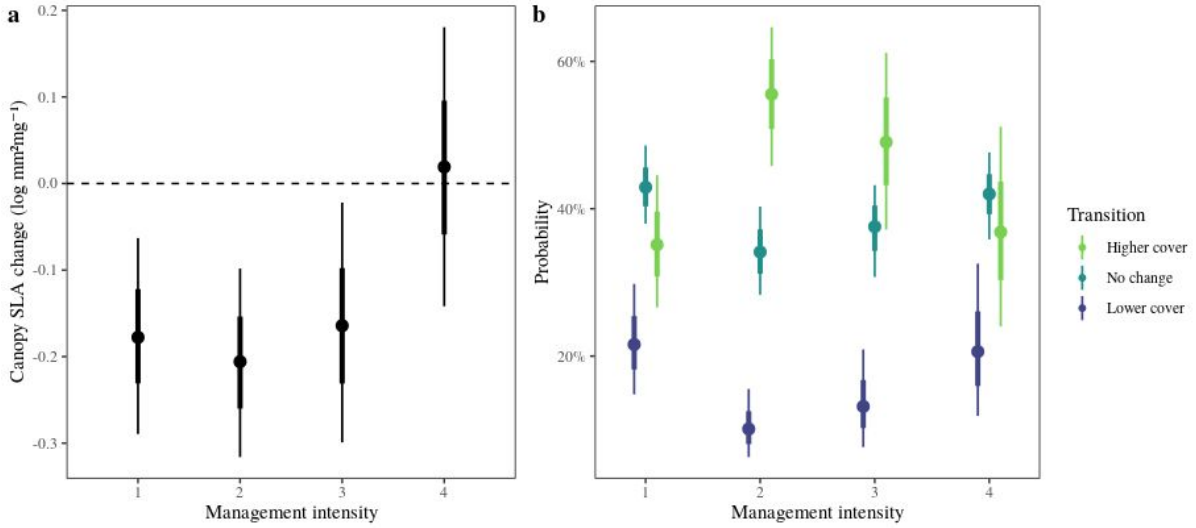


Fig. 4: Effects of management intensity on changes in canopy SLA (a), and on the probability of canopy cover transitions (b). The points represent medians, and the narrow and thick lines are 95% and 66% credible intervals, respectively.

Neither canopy changes nor location within the reindeer herding area had high probability of affecting species richness changes (Fig. 5 a). Increases in Shannon diversity and species evenness were both positively associated with the presence of reindeer (Fig. 5 b,c). Plots within the reindeer herding area were associated with a more negative trend in plant height (Fig. 5 d). Increased canopy cover was associated with increased SLA and decreased LDMC, while canopy SLA changes were positively correlated with LDMC changes and negatively correlated with changes in SLA (Fig. 5 d,e). Community turnover was higher in plots outside the reindeer herding area, and quite probably also in plots where canopy SLA had decreased (Fig. 5 g).

In addition to these explainable trends, we detected increasing trends in height and LDMC that were unassociated with our selected predictors (base change in Fig. 5 d & e).

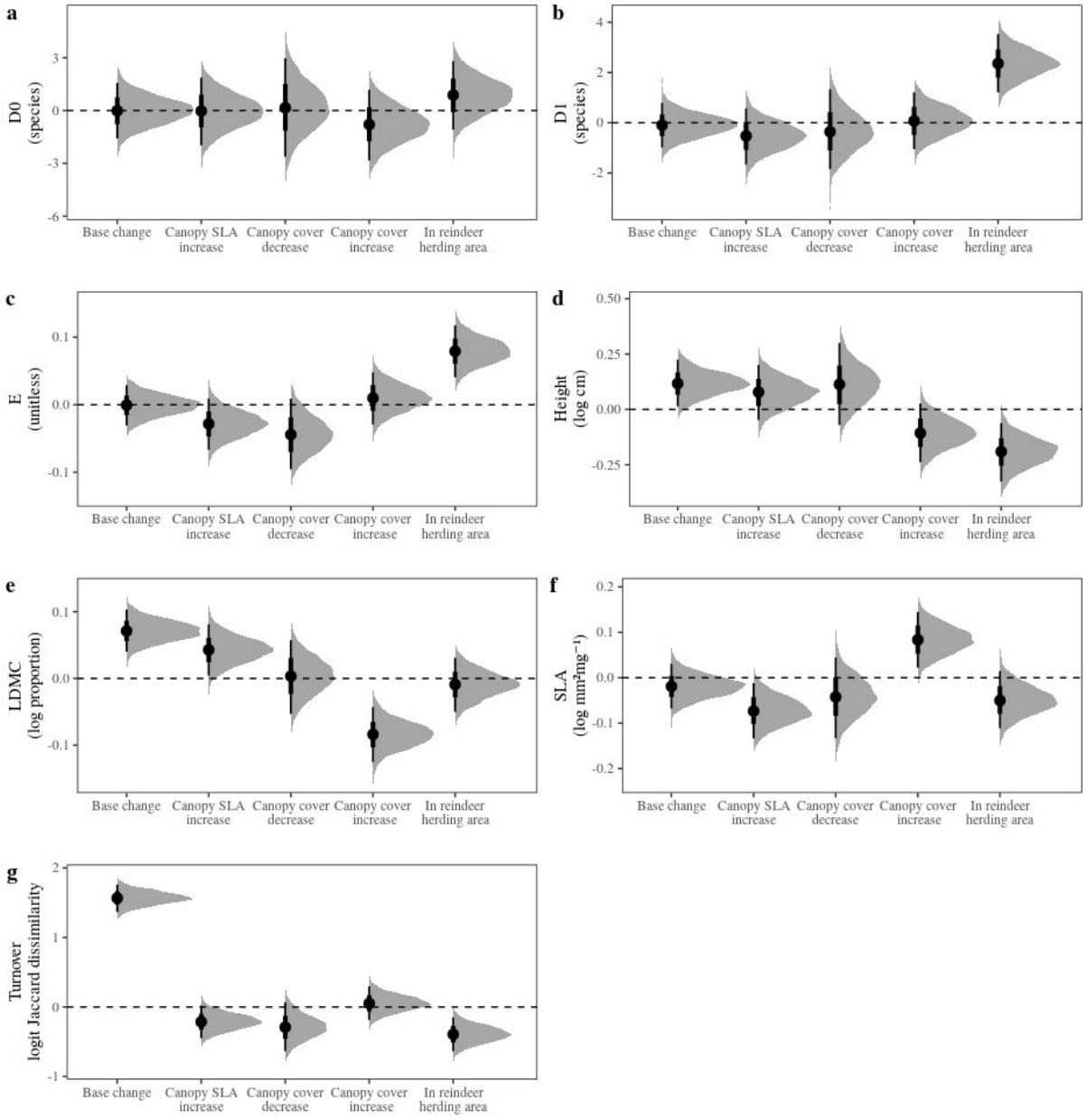


Fig. 5: Modulators of plot-level change. The effects of changes in canopy cover and canopy SLA, and location within the reindeer herding area on changes in species richness (D0, a), Shannon diversity (D1, b), species evenness (E, c), functional composition (d–f), and species composition (g). The points are medians, the narrow and thick lines are 95% and 66% credible intervals, respectively, and the gray shading is a kernel density plot of the parameter's posterior distribution. 'Base change' corresponds to the intercept of the model, and depicts changes in the absence of canopy changes and reindeer. 'Canopy SLA increase' depicts changes resulting from increasing log canopy SLA by 1.

Simulating the indirect effects of management intensity on field layer diversity and composition via changes in canopy characteristics revealed that the indirect effects were the strongest in the two

middle classes of management intensity (Fig. 6). This was due to canopy cover changes being the most pronounced in these classes.

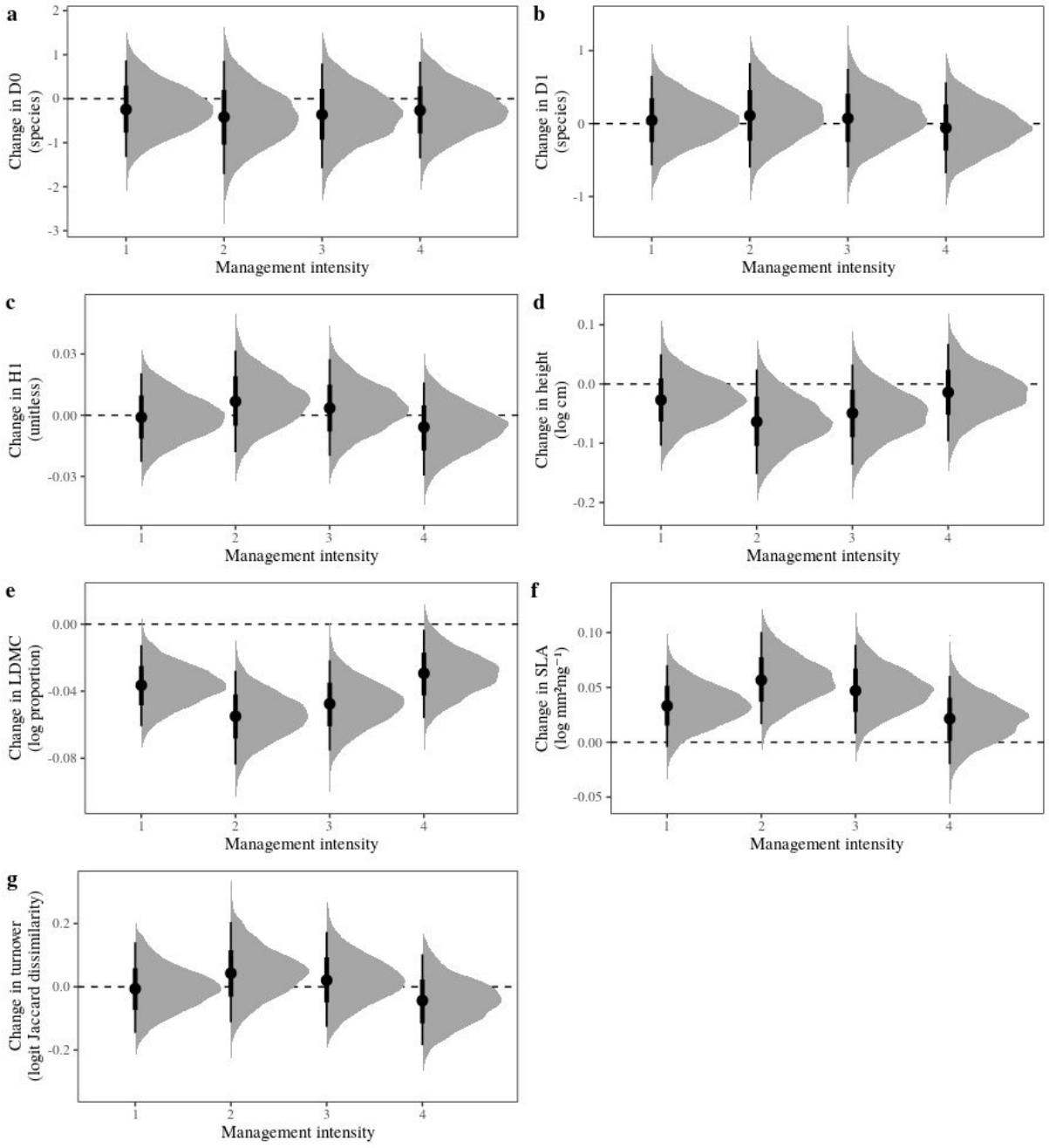


Fig. 6: The indirect effects of management intensity on community properties via changes in the canopy layer. The points are medians, the narrow and thick lines are 95% and 66% credible intervals, respectively, and the gray shading is a kernel density plot of the parameter's posterior distribution.

Examining the bias in the residuals of the model explaining changes in community properties with canopy changes and the reindeer reindeer herding area revealed that management intensity seemed to have additional direct effects on some variables in addition to effects modulated by canopy changes

(Fig. 7). Specifically, higher management intensity was associated with decreasing species richness (Fig. 7 a), increasing height (Fig. 7 d), decreasing SLA (in the highest management intensity class, Fig. 7 f), and increased turnover (Fig. 7 g).

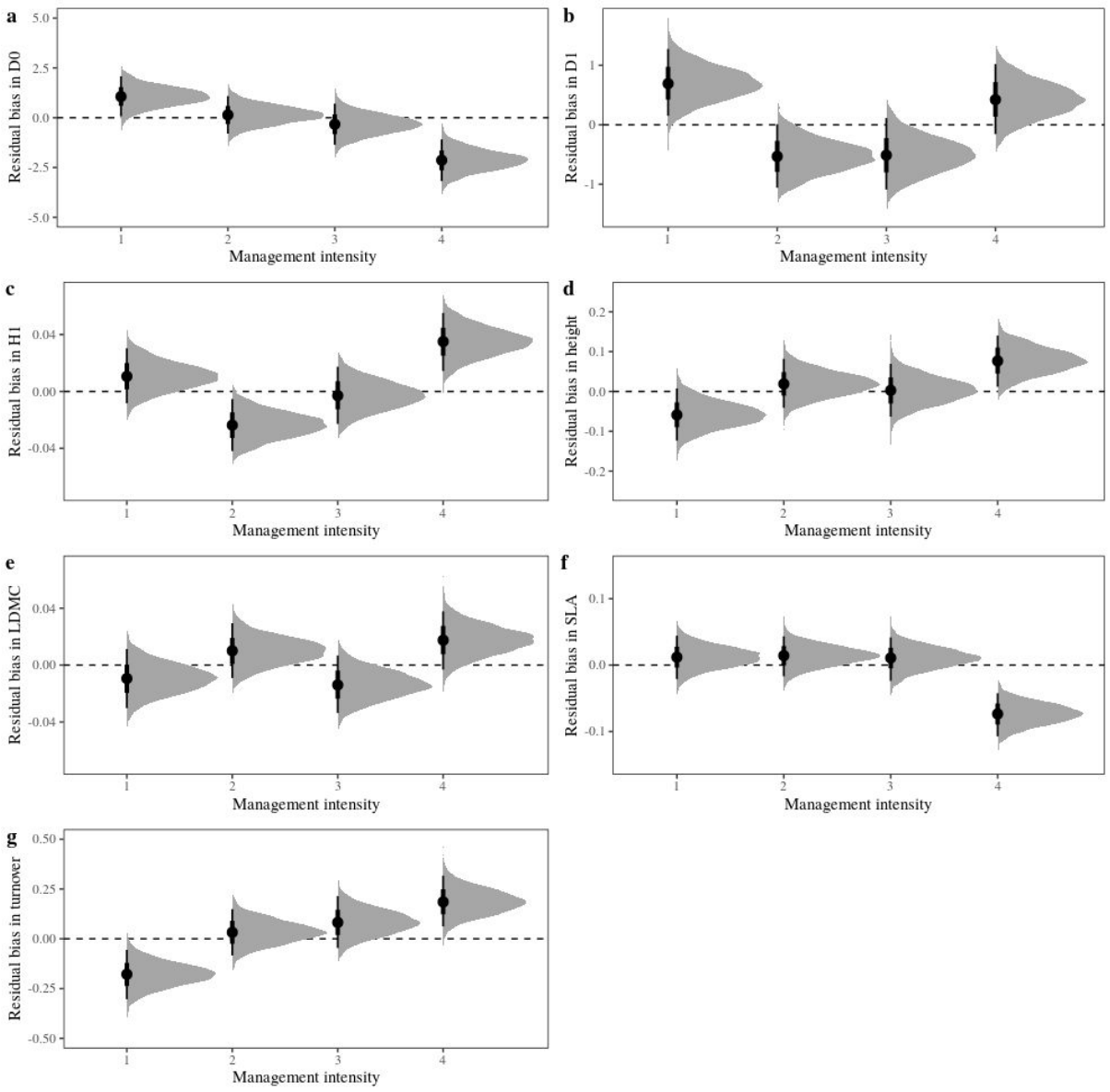


Fig. 7: The posterior distribution of residual bias in different management intensity classes from the model explaining changes in community properties with canopy changes and reindeer. The narrow and thick lines are 95% and 66% credible intervals, respectively, and the gray shading is a kernel density plot of the parameter's posterior distribution. D0: species richness, D1: Shannon diversity, E: species evenness, LDMC: leaf dry matter content, SLA: specific leaf area.

Spatial correlations and temporal covariance of community properties were highly similar (Fig. 8). Diversity and evenness measures correlated positively with each other, but negatively with height. LDMC had a positive correlation with height, but a negative correlation with SLA.

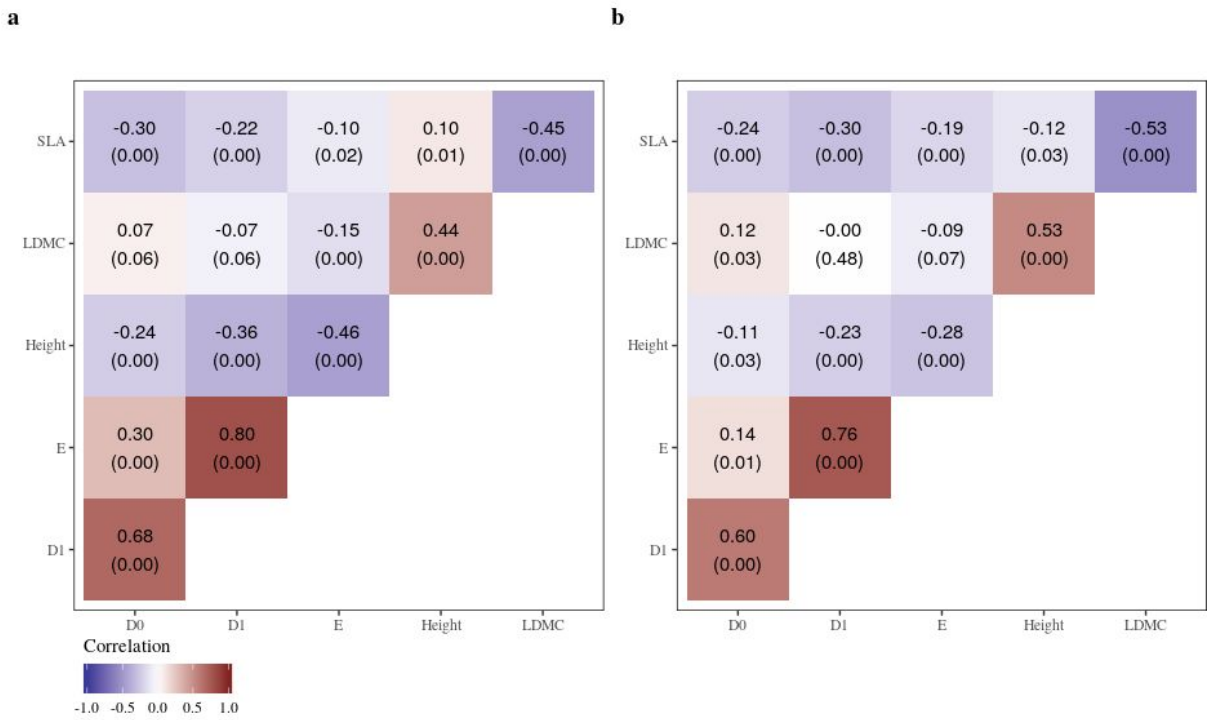


Fig. 8: Spatial (a) and temporal (b) correlations in field layer species richness (D0), Shannon diversity (D1), species evenness (E), height, SLA, and LDMC. The numbers in parentheses are type S error rates, i.e. how large proportion of the correlation coefficient's posterior distribution has an opposite sign compared to the point estimate.

The direct and indirect effects of land use and land-use change identified in this study are summarized in Fig. 9.

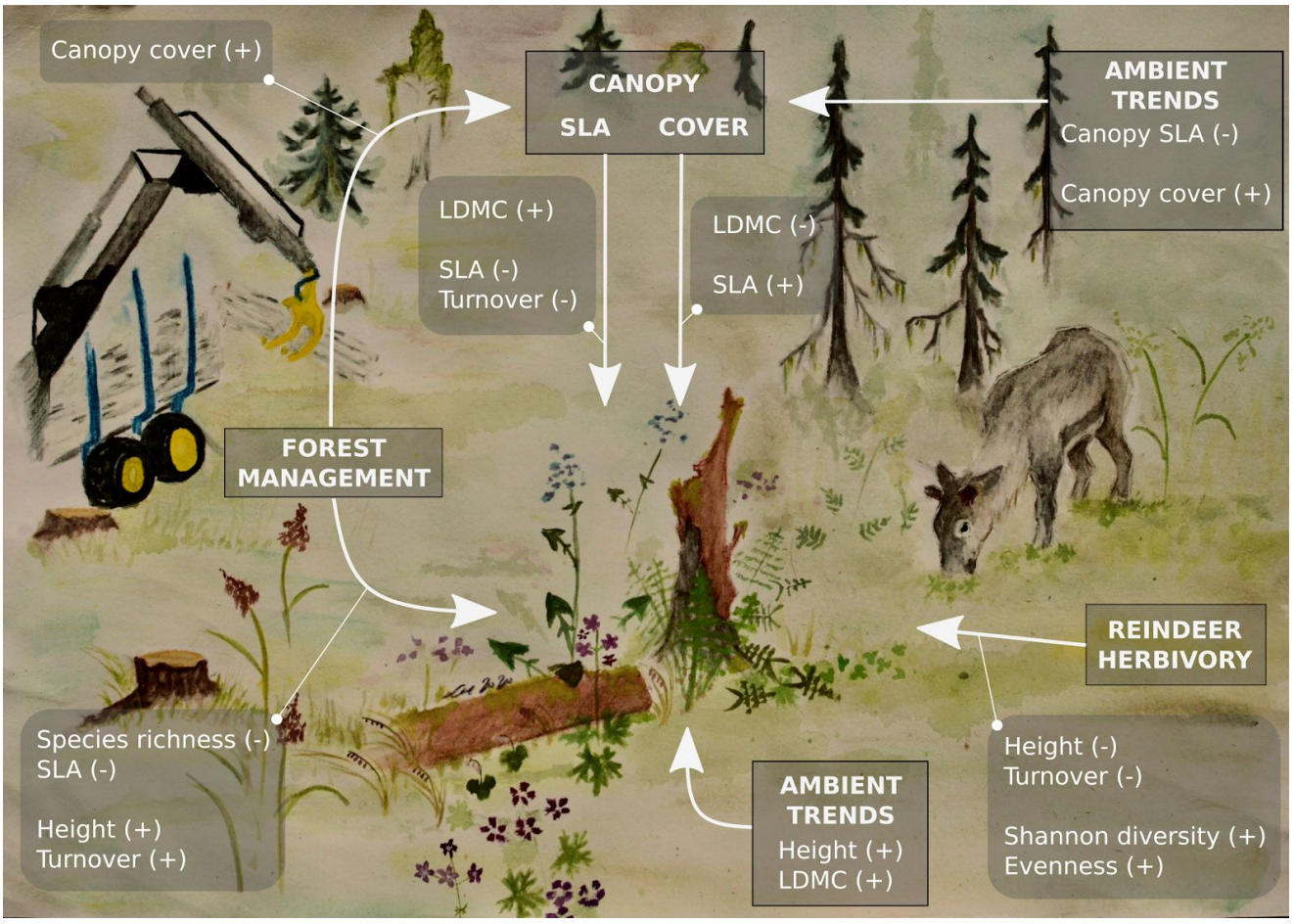


Fig. 9: Temporal changes in the diversity and composition of boreal herb-rich forest understory communities, and the long-term direct and indirect contributions of forest management and reindeer husbandry to those changes. This figure is a simplified summary of our key findings.

Discussion

Land use and land-use change have historically been the strongest drivers of biodiversity change (Butchart et al., 2010; Díaz et al., 2019), ones that should not be forgotten despite emerging threats from climate change, invasive species, and other more recent threats. Here, by using dissimilarity and trait-based approaches to account for changes in composition along with changes in diversity, we are able to show the functional footprint of human land-use in boreal forest biodiversity hotspots. Most observed changes in functional composition were directly linked to land-use in ways that are consistent with theory, highlighting the suitability of these metrics for biodiversity monitoring in the anthropocene (Pereira et al., 2013) and conservation planning (Keddy, 1992). As examples of trait-modulated effects, forest management increased canopy shading in the long-term, followed by shifts in leaf traits related to resource-use strategy and light interception, while increased grazer density decreased average plant size and, consequently, increased species evenness and species diversity.

Plot-scale species richness was very stable, as in a previous meta-analysis (Vellend et al., 2013), even though plot-scale species turnover was very high (*ca.* 80%). Our results are consistent with the hypothesis that local species richness is highly constrained by regional processes such as compensatory colonization-extinction dynamics (Supp & Ernest, 2014). Vegetation height and SLA were also stable, but Shannon diversity, species evenness and LDMC displayed trends when studied across the study area. However, further analysis revealed that many apparently static characteristics were actually changing differently within and outside the reindeer herding area, highlighting the need to consider regionally structured processes when studying temporal community changes.

We detected strong effects of the reindeer herding area on observed field-layer changes, consistent with reported experimental effects of grazing on plant communities in Scandinavian mountain forests (Sundqvist et al., 2019). That is, in the absence of canopy changes, plots within the reindeer herding area had decreasing or stable plant size, decreased SLA, and increased Shannon diversity compared to increasing plant size, stable SLA and stable diversity outside the area. SLA has been shown to correlate positively with nutrient concentrations (i.e. forage quality) in leaves (Díaz et al., 2016), while large plants have been shown to be more susceptible to mammalian herbivory (Díaz et al., 2007), suggesting that large size and high SLA could make species especially vulnerable to herbivory. Taken together with the fact that average reindeer densities in the area had grown by 40% during the study period, our results strongly suggest that human-regulated reindeer grazing is affecting the change-trajectory of field-layer vegetation in these diverse northern forests by selectively retarding the relative abundance of large plants with fast leaf economic traits.

Canopy changes are the product of both natural succession and succession modulated by forest management. In northern Finland, the late successional stages of herb-rich forests are naturally dominated by the evergreen *Picea abies*, which excludes deciduous tree species in competition during succession (Prach, 1985). In addition, forest management favors *Picea* over deciduous trees for its higher economic value. We observed decreased canopy SLA i.e. increased *Picea* dominance in all management intensity classes except the most intense management class, which included recent clearcuts where larger trees had been removed. This means that *Picea* dominance is increasing everywhere, even in the absence of management. Canopy cover had more often increased than decreased in all management intensity classes, but most prominently in the two intermediate management classes. This leads us to deduce two things. First, forest management decreases light availability at the forest floor in the long-term, meaning that the increases in light availability following harvesting (Tonteri et al., 2016) are transient and reversed in the following decades. The increase in canopy cover is most intense in those managed forests that have not been recently clearcut,

indicating that economic efficiency, perhaps related to even spacing of mature trees and lack of natural gap dynamics, decreases light availability in the field layer. Second, canopy cover seems to be increasing also in unmanaged, old-growth forests. Our study thus supports the aerial photograph-based observations of increasing canopy cover in Finnish and Canadian old-growth forests (Kulha et al., 2020). All in all, forest management seems to be changing canopy cover and canopy SLA in the same direction as other drivers such as natural succession, albeit for canopy cover the changes are much faster in managed forests.

Management also had direct effects on understory properties. Management intensity had clear negative effects on plot-scale species richness. These effects could be the result of concentrating resources to the tree-layer by practices such as ditching, which increase the growth of the tree-layer but decrease resource availability in the field layer. In addition, SLA had decreased in the highest management intensity class which included recent clearcuts, highlighting the fact that SLA is a key trait in light-availability -based species sorting (Dahlgren et al., 2006).

Canopy changes affected leaf traits in the field layer. Increased canopy cover led to increased SLA and decreased LDMC in the understory. SLA is a succession trait, which increases in response to shading (Dahlgren et al., 2006), whereas LDMC has probably decreased because of its negative covariance with SLA as part of the community-level leaf economics spectrum (Bruelheide et al., 2018). The negative correlation between canopy SLA and field layer SLA was surprising, since we would have expected canopy leaf traits to correlate positively with field layer leaf traits via litter decomposition-mediated resource availability effects (Maes et al., 2019). Low canopy SLA is an indicator of relative abundance of *Picea abies*, an evergreen species with long-lived leaves. It is possible that low canopy SLA is thus a further indicator of shady conditions, and that this shading effect is stronger than effects via decreased litter quality. There was also a reasonably high posterior probability that deeper canopy shading (increased canopy cover, decreased canopy SLA) leads to field-layer communities with shorter species. These results supplement results from previous studies, in which average height of field layer vegetation in response to less light either remained stable (Maes et al., 2019) or decreased (Blondeel et al., 2020). Decreasing plant height is an expected response if light is a limiting resource for plant growth, as is the case in forest understories (Blondeel et al., 2020), especially in the case of herbaceous plants which cannot annually increment their heights.

In addition, plots had increased field-layer LDMC in the absence of canopy changes, indicating slower leaf economics. This unexplained change could be an effect of some global change driver we did not include in the models. Since warmer climates are generally associated with faster leaf

economics (Anne D. Bjorkman et al., 2018; Wieczynski et al., 2019), which would correspond with lower LDMC, climate change is not a likely driver for this trend. Further research is thus needed on the causes of this trend.

Temporal and spatial covariation of community properties was extremely similar, hinting that the diversity and functional composition of these forest understory communities are not independent of each other, but are controlled by some mechanistic constraints. Unsurprisingly, leaf traits seemed to covary according to the leaf economics spectrum (Wright et al., 2004). However, many of the strongest correlations involved average height; plots with higher vegetation had lower Shannon diversity and species evenness, and higher LDMC. This suggests that the diversity-biomass relationship is behind many of the observed patterns. Communities composed of larger species might have fewer plant individuals and exhibit decreased evenness due to the dominance of large plants (Oksanen, 1996). Reindeer grazing effects are most likely a result of this coordination: tall species are being eaten (Kaarlejärvi et al., 2017; Sundqvist et al., 2019) and dominance thus reduced, which increases diversity (Grime, 1973).

For the full dataset, temporal turnover was of the same magnitude as average turnover in terrestrial ecosystems in a recent meta-analysis (2% year^{-1}, Blowes et al., 2019). Plot-scale community turnover was much higher, which was unsurprising because of high species diversity, long sampling intervals, and inherent but minimized relocation error. However, we still detected effects of the reindeer herding area and management intensity on plot.scale turnover. Turnover was greater in more intensively managed forests, agreeing with previous studies that have reported that human disturbance accelerates biodiversity change (Barlow et al., 2016; Lake et al., 2000). However, we also found that turnover was lower within the reindeer herding area, which is seemingly in conflict with our findings that reindeer have strong effects on field layer vegetation. Since the reindeer herding area is generally in higher latitudes than areas outside it, it is possible that the observed effect is due to forests in colder climates having slower growth, smaller species pool, and thus slower community dynamics. Such differences in turnover rates between fertile and less diverse infertile sites have previously been reported for boreal forests (Maliniemi et al., 2019). A further explanation could be that changes induced by increased reindeer densities are counteracting changes unrelated to them. We found this to be the case with plant size — vegetation height increased outside the reindeer herding area, but was stable or decreased within it. These types of effects have previously been reported in the tundra, where reindeer and other large herbivores have been found to inhibit shrubification, tree-line creep, and associated ecosystem changes (Olofsson et al., 2009; Olofsson & Post, 2018; Post & Pedersen, 2008). Our study thus suggests that the buffering effect of large herbivores against vegetation changes

extends from the tundra to forest understories as well. Increasing herbivore densities has been suggested as a way to protect permafrost in the boreal and tundra biomes from warming temperatures (Beer et al., 2020), our study suggests that large herbivores could potentially be useful in protecting plant communities beyond permafrost areas as well.

Conclusions

In the long-term, forest management decreases light availability in the understories of boreal herb-rich forests, leading to field-layer communities with "fast" leaf economic traits indicating prioritisation of growth over survival, such as high SLA. In addition, forest management decreases plot-scale diversity and increases compositional turnover. In the absence of herbivory or canopy changes, we found that field-layer vegetation had grown in height. However, this trend was reverted or even reversed within the reindeer herding area, where the human-controlled density of grazing ungulates had increased during the sampling interval. Reindeer husbandry thus seems to reduce plot-scale turnover and dominance, and increase diversity. Land-use can have complex effects on plant communities, but our study demonstrates that functional trait -based approaches are highly useful in connecting vegetation changes to local- and regional-scale mechanisms that drive them in a globally applicable way.

Acknowledgments

We acknowledge funding from Societas Pro Fauna et Flora Fennica, Societas Biologica Fennica Vanamo , Societas Amicorum Naturae Ouluensis , Academy of Finland (project #259072), Finnish Cultural Foundation, The Finnish Society of Forest Science and Jane & Aatos Erkko Foundation.

We thank Anu Skog and Niilo Tenkanen for help in field work.

References

Abatzoglou, J. T., Dobrowski, S. Z., Parks, S. A., & Hegewisch, K. C. (2018). TerraClimate, a high-resolution global dataset of monthly climate and climatic water balance from 1958-2015. *Scientific Data*, *5*, 170191. https://doi.org/10.1038/sdata.2017.191

Barlow, J., Lennox, G. D., Ferreira, J., Berenguer, E., Lees, A. C., Mac Nally, R., Thomson, J. R., Ferraz, S. F. de B., Louzada, J., Oliveira, V. H. F., Parry, L., Solar, R. R. de C., Vieira, I. C. G., Aragão, L. E. O. C., Begotti, R. A., Braga, R. F., Cardoso, T. M., de Oliveira, R. C., Jr, Souza, C. M., Jr, … Gardner, T. A. (2016). Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature*, *535*(7610), 144–147. https://doi.org/10.1038/nature18326

Beer, C., Zimov, N., Olofsson, J., Porada, P., & Zimov, S. (2020). Protection of Permafrost Soils from Thawing by Increasing Herbivore Density. *Scientific Reports*, *10*(1), 4170. https://doi.org/10.1038/s41598-020-60938-y

Bjorkman, A. D., & Myers‐Smith, I. H. (2018). Tundra Trait Team: A database of plant traits spanning the tundra biome. *Global Ecology and*. https://onlinelibrary.wiley.com/doi/abs/10.1111/geb.12821

Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Rüger, N., Beck, P. S. A., Blach-Overgaard, A., Blok, D., Cornelissen, J. H. C., Forbes, B. C., Georges, D., Goetz, S. J., Guay, K. C., Henry, G. H. R., HilleRisLambers, J., Hollister, R. D., Karger, D. N., Kattge, J., Manning, P., … Weiher, E. (2018). Plant functional trait change across a warming tundra biome. *Nature*, *562*, 57–62. https://doi.org/10.1038/s41586-018-0563-7

Blondeel, H., Perring, M. P., Depauw, L., Lombaerde, E. D., Landuyt, D., Frenne, P. D., & Verheyen, K. (2020). Light and warming drive forest understorey community development in different environments. *Global Change Biology*, *26*(3), 1681–1696. https://doi.org/10.1111/gcb.14955

Blowes, S. A., Supp, S. R., Antão, L. H., Bates, A., Bruelheide, H., Chase, J. M., Moyes, F., Magurran, A., McGill, B., Myers-Smith, I. H., Winter, M., Bjorkman, A. D., Bowler, D. E., Byrnes, J. E. K., Gonzalez, A., Hines, J., Isbell, F., Jones, H. P., Navarro, L. M., … Dornelas, M. (2019). The geography of biodiversity change in marine and terrestrial assemblages. *Science*, *366*(6463), 339–345. https://doi.org/10.1126/science.aaw1620

Brandt, J. P., Flannigan, M. D., Maynard, D. G., Thompson, I. D., & Volney, W. J. A. (2013). An introduction to Canada's boreal zone: ecosystem processes, health, sustainability, and environmental issues. *Environmental Reviews*, *21*(4), 207–226. https://www.nrcresearchpress.com/doi/abs/10.1139/er-2013-0040

Bråthen, K. A., & Oksanen, J. (2001). Reindeer reduce biomass of preferred plant species. *Journal of Vegetation Science*, *12*(4), 473–480. https://doi.org/10.2307/3236999

Bruelheide, H., Dengler, J., Purschke, O., Lenoir, J., Jiménez-Alfaro, B., Hennekens, S. M., Botta-Dukát, Z., Chytrý, M., Field, R., Jansen, F., Kattge, J., Pillar, V. D., Schrodt, F., Mahecha, M. D., Peet, R. K., Sandel, B., van Bodegom, P., Altman, J., Alvarez-Dávila, E., … Jandt, U. (2018). Global trait-environment relationships of plant communities. *Nature Ecology & Evolution*, *2*(12), 1906–1917. https://doi.org/10.1038/s41559-018-0699-8

Bürkner, P.-C. (2018). Advanced Bayesian Multilevel Modeling with the R Package brms. *The R Journal*, *10*(1),

395–411. https://journal.r-project.org/archive/2018/RJ-2018-017/index.html

Bürkner, P.-C., & Vuorre, M. (2019). Ordinal Regression Models in Psychology: A Tutorial. *Advances in Methods and Practices in Psychological Science*, *2*(1), 77–101. https://doi.org/10.1177/2515245918823199

Butchart, S. H. M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J. P. W., Almond, R. E. A., Baillie, J. E. M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K. E., Carr, G. M., Chanson, J., Chenery, A. M., Csirke, J., Davidson, N. C., Dentener, F., Foster, M., Galli, A., … Watson, R. (2010). Global biodiversity: indicators of recent declines. *Science*, *328*(5982), 1164–1168. https://doi.org/10.1126/science.1187512

Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P., & Riddell, A. (2017). Stan: A Probabilistic Programming Language. *Journal of Statistical Software*, *76*(1), 1–32. https://doi.org/10.18637/jss.v076.i01

Dahlgren, J. P., Eriksson, O., Bolmgren, K., Strindell, M., & Ehrlén, J. (2006). Specific leaf area as a superior predictor of changes in field layer abundance during forest succession. *Journal of Vegetation Science: Official Organ of the International Association for Vegetation Science*, *17*(5), 577–582. https://doi.org/10.1111/j.1654-1103.2006.tb02481.x

Danneyrolles, V., Dupuis, S., Fortin, G., Leroyer, M., de Römer, A., Terrail, R., Vellend, M., Boucher, Y., Laflamme, J., Bergeron, Y., & Arseneault, D. (2019). Stronger influence of anthropogenic disturbance than climate change on century-scale compositional changes in northern forests. *Nature Communications*, *10*(1), 1265. https://doi.org/10.1038/s41467-019-09265-z

De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B. R., Hylander, K., Luoto, M., Vellend, M., Verheyen, K., & Lenoir, J. (2019). Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution*, *3*(5), 744–749. https://doi.org/10.1038/s41559-019-0842-1

Díaz, S., J., S., Brondízio, E. S., Ngo, H. T., Guèze, M., Agard, J., Arneth, A., Balvanera, P., Brauman, K. A., Butchart, S. H. M., Chan, K. M. A., Garibaldi, L. A., Ichii, K., Liu, J., Subramanian, S. M., Midgley, G. F., Miloslavich, P., Molnár, Z., Obura, D., … Zayas, C. N. (2019). *Summary for Policymakers of the Global Assessment Report on Biodiversity and Ecosystem Services*. IPBES secretariat.

Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Prentice, I. C., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A. T., Dickie, J., Gillison, A. N., Zanne, A. E., … Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, *529*(7585), 167–171. https://doi.org/10.1038/nature16489

Díaz, S., Lavorel, S., McINTYRE, S. U. E., Falczuk, V., Casanoves, F., Milchunas, D. G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W., Clark, H., & Campbell, B. D. (2007). Plant trait responses to grazing — a global synthesis. *Global Change Biology*, *13*(2), 313–341. https://doi.org/10.1111/j.1365-2486.2006.01288.x

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., & Toussaint, J.-P. (2004). Plant Functional Markers Capture Ecosystem Properties During Secondary Succession. *Ecology*, *85*(9), 2630–2637. https://doi.org/10.1890/03-0799

Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A. Z., & Schepaschenko, D. G. (2015). Boreal forest health and global change. *Science*, *349*(6250), 819–822. https://doi.org/10.1126/science.aaa9092

Gelman, A., & Rubin, D. B. (1992). Inference from Iterative Simulation Using Multiple Sequences. *Statistical Science: A Review Journal of the Institute of Mathematical Statistics*, *7*(4), 457–472. http://www.jstor.org/stable/2246093

Grime, J. P. (1973). Competitive Exclusion in Herbaceous Vegetation. *Nature*, *242*(5396), 344–347. https://doi.org/10.1038/242344a0

Hillebrand, H., Blasius, B., Borer, E. T., Chase, J. M., Downing, J. A., Eriksson, B. K., Filstrup, C. T., Harpole, W. S., Hodapp, D., Larsen, S., Lewandowska, A. M., Seabloom, E. W., Van de Waal, D. B., & Ryabov, A. B. (2018). Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring. *The Journal of Applied Ecology*, *55*(1), 169–184. https://doi.org/10.1111/1365-2664.12959

Hjeljord, O., Hovik, N., & Pedersen, H. B. (1990). Choice of feeding sites by moose during summer, the influence of forest structure and plant phenology. *Ecography*, *13*(4), 281–292. https://doi.org/10.1111/j.1600-0587.1990.tb00620.x

Hyvärinen, E., Juslén, A., Kemppainen, E., Uddström, A., & Liukko, U.-M. (2019). *The 2019 Red List of Finnish species*. Finnish Ministry of the Environment & Finnish Environment Institute. http://hdl.handle.net/10138/299501

Jost, L. (2006). Entropy and diversity. *Oikos* , *113*(2), 363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x

Jost, L. (2010). The Relation between Evenness and Diversity. *Diversity*, *2*(2), 207–232. https://doi.org/10.3390/d2020207

Kaakinen, E. (1971). *Tutkimuksia Kainuun lehtokasvillisuudesta* [Master's Thesis]. University of Oulu.

Kaakinen, E. (1974). *Kainuun ja Kuusamon lehtokasvillisuudesta* [Licenciate's thesis]. University of Oulu.

Kaarlejärvi, E., Eskelinen, A., & Olofsson, J. (2017). Herbivores rescue diversity in warming tundra by modulating trait-dependent species losses and gains. *Nature Communications*, *8*(1), 419. https://doi.org/10.1038/s41467-017-00554-z

Kapfer, J., Hédl, R., & Jurasinski, G. (2017). Resurveying historical vegetation data–opportunities and challenges. *Applied Vegetation Science*. https://onlinelibrary.wiley.com/doi/abs/10.1111/avsc.12269

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., Abedi, M., Acosta, A. T. R., Adamidis, G. C., Adamson, K., Aiba, M., Albert, C. H., Alcántara, J. M., Alcázar C, C., Aleixo, I., Ali, H., … Wirth, C. (2020). TRY plant trait database - enhanced coverage and open access. *Global Change Biology*, *26*(1), 119–188. https://doi.org/10.1111/gcb.14904

Kattge, J., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P. B., Wright, I. J., Cornelissen, J. H. C., Violle, C., Harrison, S. P., Van BODEGOM, P. M., Reichstein, M., Enquist, B. J., Soudzilovskaia, N. A., Ackerly, D. D., Anand, M., … Wirth, C. (2011). TRY - a global database of plant traits. *Global Change Biology*, *17*(9), 2905–2935. https://doi.org/10.1111/j.1365-2486.2011.02451.x

Keddy, P. A. (1992). A Pragmatic Approach to Functional Ecology. *Functional Ecology*, *6*(6), 621–626. https://doi.org/10.2307/2389954

Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P., Thompson, K., Sonnenschein, M., Poschlod, P., van Groenendael, J. M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G. M., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., … Peco, B. (2008). The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *The Journal of Ecology*, *96*(6), 1266–1274. https://doi.org/10.1111/j.1365-2745.2008.01430.x

Kouki, J., Junninen, K., Mäkela, K., Hokkonen, M., Aakala, T., Hallikainen, V., Kari, Kuuluvainen Korhonen, Loiskekoski, M., Mattila, O., Matveinen, K., Punttila, P., Ruokanen, I., Valkonen, S., & Virkkala, R. (2018). 5.5: Metsät. In T. Kontula & A. Raunio (Eds.), *Suomen luontotyyppien uhanalaisuus 2018 : Luontotyyppien punainen kirja. Osa 1: Tulokset ja arvioinnin perusteet* (pp. 171–202). Ympäristöministeriö.

Kulha, N., Pasanen, L., Holmström, L., De Grandpré, L., Gauthier, S., Kuuluvainen, T., & Aakala, T. (2020). The structure of boreal old-growth forests changes at multiple spatial scales over decades. *Landscape*

Ecology. https://doi.org/10.1007/s10980-020-00979-w

Lake, P. S., Palmer, M. A., Biro, P., Cole, J., Covich, A. P., Dahm, C., Gibert, J., Goedkoop, W., Martens, K., & Verhoeven, J. (2000). Global Change and the Biodiversity of Freshwater Ecosystems: Impacts on Linkages between Above-Sediment and Sediment BiotaAll forms of anthropogenic disturbance—changes in land use, biogeochemical processes, or biotic addition or loss—not only damage the biota of freshwater sediments but also disrupt the linkages between above-sediment and sediment-dwelling biota. *Bioscience*, *50*(12), 1099–1107. https://doi.org/10.1641/0006-3568(2000)050[1099:GCATBO]2.0.CO;2

Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, *16*(5), 545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Legendre, P., & Legendre, L. F. J. (2012). *Numerical Ecology*. Elsevier Science.

Lembrechts, J. J., Aalto, J., Ashcroft, M. B., De Frenne, P., Kopecký, M., Lenoir, J., Luoto, M., Maclean, I. M. D., Roupsard, O., Fuentes-Lillo, E., García, R. A., Pellissier, L., Pitteloud, C., Alatalo, J. M., Smith, S. W., Björk, R. G., Muffler, L., Cesarz, S., Gottschall, F., … Nijs, I. (2020). SoilTemp: a global database of near-surface temperature. *Global Change Biology*. https://doi.org/10.1111/gcb.15123

Löfman, S., & Kouki, J. (2001). Fifty Years of Landscape Transformation in Managed Forests of Southern Finland. *Scandinavian Journal of Forest Research / Issued Bimonthly by the Nordic Forest Research Cooperation Committee* , *16*(1), 44–53. https://doi.org/10.1080/028275801300004406

Maes, S. L., Perring, M. P., Depauw, L., Bernhardt-Römermann, M., Blondeel, H., Brūmelis, G., Brunet, J., Decocq, G., den Ouden, J., Govaert, S., Härdtle, W., Hédl, R., Heinken, T., Heinrichs, S., Hertzog, L., Jaroszewicz, B., Kirby, K., Kopecký, M., Landuyt, D., … Verheyen, K. (2019). Plant functional trait response to environmental drivers across European temperate forest understorey communities. *Plant Biology* , *n/a*(n/a). https://doi.org/10.1111/plb.13082

Maliniemi, T., Happonen, K., & Virtanen, R. (2019). Site fertility drives temporal turnover of vegetation at high latitudes. *Ecology and Evolution*, *9*(23), 13255–13266. https://doi.org/10.1002/ece3.5778

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, *21*(4), 178–185. https://doi.org/10.1016/j.tree.2006.02.002

Muurinen, L., Oksanen, J., Vanha-Majamaa, I., & Virtanen, R. (2019). Legacy effects of logging on boreal forest understorey vegetation communities in decadal time scales in northern Finland. *Forest Ecology and*

Management, *436*, 11–20. https://doi.org/10.1016/j.foreco.2018.12.048

Natural Resources Institute Finland. (2020). *Suomen Virallinen TIlasto (SVT): Metsästys, Riistasaalis (kpl)*. https://statdb.luke.fi/PXWeb/pxweb/fi/LUKE/LUKE__06%20Kala%20ja%20riista__02%20Rakenne%20ja%20tuotanto__16%20Metsastys/5_Mets_saalis.px/?rxid=cf553b1b-570e-4211-bd97-f8906bc8278f

Nieppola, J. (1992). Long-term vegetation changes in stands of Pinus sylvestris in southern Finland. *Journal of Vegetation Science: Official Organ of the International Association for Vegetation Science*, *3*(4), 475–484. https://doi.org/10.2307/3235804

Nygrén, T. (2009). *Suomen hirvikannan säätely : biologiaa ja luonnonvarapolitiikkaa* [PhD thesis, University of Joensuu]. http://epublications.uef.fi/pub/urn_isbn_978-952-219-314-8/urn_isbn_978-952-219-314-8.pdf

Oksanen, J. (1996). Is the Humped Relationship between species Richness and Biomass an Artefact due to Plot Size? *The Journal of Ecology*, *84*(2), 293–295. https://doi.org/10.2307/2261364

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2019). *vegan: Community Ecology Package* (Version 2.5-6) [Computer software]. https://CRAN.R-project.org/package=vegan

Oldén, A., Raatikainen, K. J., Tervonen, K., & Halme, P. (2016). Grazing and soil pH are biodiversity drivers of vascular plants and bryophytes in boreal wood-pastures. In *Agriculture, Ecosystems & Environment* (Vol. 222, pp. 171–184). https://doi.org/10.1016/j.agee.2016.02.018

Olofsson, J., Moen, J., & Östlund, L. (2010). Effects of reindeer on boreal forest floor vegetation: Does grazing cause vegetation state transitions? *Basic and Applied Ecology*, *11*(6), 550–557. https://doi.org/10.1016/j.baae.2010.03.004

Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P. E., Oksanen, T., & Suominen, O. (2009). Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology*, *15*(11), 2681–2693. https://doi.org/10.1111/j.1365-2486.2009.01935.x

Olofsson, J., & Post, E. (2018). Effects of large herbivores on tundra vegetation in a changing climate, and implications for rewilding. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *373*(1761). https://doi.org/10.1098/rstb.2017.0437

Pereira, H. M., Ferrier, S., Walters, M., Geller, G. N., Jongman, R. H. G., Scholes, R. J., Bruford, M. W., Brummitt, N., Butchart, S. H. M., Cardoso, A. C., Coops, N. C., Dulloo, E., Faith, D. P., Freyhof, J., Gregory, R. D., Heip, C., Höft, R., Hurtt, G., Jetz, W., … Wegmann, M. (2013). Essential biodiversity

variables. *Science*, *339*(6117), 277–278. https://doi.org/10.1126/science.1229931

Perring, M. P., Bernhardt-Römermann, M., Baeten, L., Midolo, G., Blondeel, H., Depauw, L., Landuyt, D., Maes, S. L., De Lombaerde, E., Carón, M. M., Vellend, M., Brunet, J., Chudomelová, M., Decocq, G., Diekmann, M., Dirnböck, T., Dörfler, I., Durak, T., De Frenne, P., … Verheyen, K. (2018). Global environmental change effects on plant community composition trajectories depend upon management legacies. *Global Change Biology*, *24*(4), 1722–1740. https://doi.org/10.1111/gcb.14030

Post, E., & Pedersen, C. (2008). Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(34), 12353–12358. https://doi.org/10.1073/pnas.0802421105

Prach, K. (1985). Succession of vegetation in abandoned fields in Finland. *Annales Botanici Fennici*, *22*(4), 307–314. http://www.jstor.org/stable/23725551

R Core Team. (2019). *R: A Language and Environment for Statistical Computing* (Version 3.6.2) [Computer software]. R Foundation for Statistical Computing. https://www.R-project.org/

Rouvinen, S., & Kuuluvainen, T. (2005). Tree diameter distributions in natural and managed old Pinus sylvestris-dominated forests. *Forest Ecology and Management*, *208*(1), 45–61. https://doi.org/10.1016/j.foreco.2004.11.021

Sundqvist, M. K., Moen, J., Björk, R. G., Vowles, T., Kytöviita, M., Parsons, M. A., & Olofsson, J. (2019). Experimental evidence of the long‐term effects of reindeer on Arctic vegetation greenness and species richness at a larger landscape scale. *The Journal of Ecology*, *107*(6), 2724–2736. https://doi.org/10.1111/1365-2745.13201

Supp, S. R., & Ernest, S. K. M. (2014). Species-level and community-level responses to disturbance: a cross-community analysis. *Ecology*, *95*(7), 1717–1723. https://doi.org/10.1890/13-2250.1

Tonteri, T., Salemaa, M., Rautio, P., Hallikainen, V., Korpela, L., & Merilä, P. (2016). Forest management regulates temporal change in the cover of boreal plant species. *Forest Ecology and Management*, *381*, 115–124. https://doi.org/10.1016/j.foreco.2016.09.015

Väre, H., Ohtonen, R., & Oksanen, J. (1995). Effects of reindeer grazing on understorey vegetation in dry Pinus sylvestris forests. *Journal of Vegetation Science: Official Organ of the International Association for Vegetation Science*, *6*(4), 523–530. https://doi.org/10.2307/3236351

Vellend, M., Baeten, L., Myers-Smith, I. H., Elmendorf, S. C., Beauséjour, R., Brown, C. D., De Frenne, P.,

Verheyen, K., & Wipf, S. (2013). Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(48), 19456–19459. https://doi.org/10.1073/pnas.1312779110

Verheyen, K., Bažány, M., Chećko, E., Chudomelová, M., Closset-Kopp, D., Czortek, P., Decocq, G., Frenne, P. D., Keersmaeker, L. D., García, C. E., Fabšičová, M., Grytnes, J.-A., Hederová, L., Hédl, R., Heinken, T., Schei, F. H., Horváth, S., Jaroszewicz, B., Jermakowicz, E., … Baeten, L. (2018). Observer and relocation errors matter in resurveys of historical vegetation plots. *Journal of Vegetation Science: Official Organ of the International Association for Vegetation Science*, *29*(5), 812–823. https://doi.org/10.1111/jvs.12673

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos* , *116*(5), 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Wieczynski, D. J., Boyle, B., Buzzard, V., Duran, S. M., Henderson, A. N., Hulshof, C. M., Kerkhoff, A. J., McCarthy, M. C., Michaletz, S. T., Swenson, N. G., Asner, G. P., Bentley, L. P., Enquist, B. J., & Savage, V. M. (2019). Climate shapes and shifts functional biodiversity in forests worldwide. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(2), 587–592. https://doi.org/10.1073/pnas.1813723116

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., … Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, *428*, 821. https://doi.org/10.1038/nature02403