CrossMark

ORIGINAL ARTICLE

Marte Synnøve Lilleeng · Stein Joar Hegland
Knut Rydgren · Stein R. Moe

Red deer mediate spatial and temporal plant heterogeneity in boreal forests

Abstract Selective herbivory can influence both spatial and temporal vegetation heterogeneity. For example, many northern European populations of free-ranging ungulates have reached unprecedented levels, which can influence plant species turnover, long-term maintenance of biodiversity and the subsequent stability of boreal ecosystems. However, the mechanisms by which large herbivores affect spatial and temporal vegetation heterogeneity remain poorly understood. Here, we combined a 10-year exclusion experiment with a herbivore intensity gradient to investigate how red deer (*Cervus elaphus*) acts as a driver of temporal and spatial heterogeneity in the understory of a boreal forest. We measured the two dimensions of heterogeneity as temporal and spatial species turnover. We found that temporal heterogeneity was positively related to herbivory intensity, and we found a similar trend for spatial heterogeneity. Removing red deer (exclosure) from our study system caused a distinct shift in species composition, both spatially (slow response) and temporally (quick response). Vegetation from which red deer had been excluded for 10 years showed the highest spatial heterogeneity, suggesting that the most stable forest understory will occur where there are no large herbivores. However, excluding red deer resulted in lower species diversity and greater dominance by a low number of plant species. If both stable but species rich ecosystems are the management goal, these findings suggest that naturally fluctuating, but moderate red deer densities should be sustained.

Keywords Biodiversity · Cervids · Ecosystem stability · Herbivory intensity · Plant communities

Introduction

Vegetation heterogeneity has two broad functional roles in ecosystem stability: temporal heterogeneity (i.e., temporal species turnover) destabilizes, whereas spatial heterogeneity (i.e., spatial species turnover) stabilizes ecosystems (May 1974). However, factors such as the presence or absence of disturbance can determine the nature of these roles. For example, severe disturbance often leads to high temporal species turnover, dominated by pioneer species, but when long-lived and slower growing species dominate, temporal species turnover is low (Rydgren et al. 2004). Spatial species turnover is the difference in species composition across both local and regional assemblages, with high values reflecting a patchy distribution of plant species at various spatial scales (Koleff et al. 2003). High spatial heterogeneity can make an ecosystem more robust to disturbances. It also facilitates important ecosystem functions such as dispersal and recolonization, and by increasing resources and refugia (Hovick et al. 2015). Therefore, spatial heterogeneity is also important for ecosystem resilience (the ability to reorganize and renew itself following disturbance; Elmqvist et al. 2003).

Large herbivores can act as ecosystem engineers by trampling and feeding selectively (Jones et al. 1994), thereby modifying plant species composition and dynamics. The influence of herbivory on vegetation heterogeneity depends on ecosystem productivity (Proulx and Mazumder 1998), herbivore selectivity (Adler et al. 2001) and intensity (Mackey and Currie 2001), as well as the species of herbivore, as use of habitat and feeding patterns are species specific (Côté et al. 2004; DeGabriel et al. 2011). Some general patterns

M. S. Lilleeng (✉) · S. J. Hegland · K. Rydgren
Faculty of Engineering and Science, Sogn og Fjordane University College, AIN, PO BOX 133, 6851 Sogndal, Norway
E-mail: marte.lilleeng@hisf.no
Tel.: 0047 5767 6000

S. R. Moe · M. S. Lilleeng
Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, PO BOX 5003, 1432 Ås, Norway

are apparent: strongly preferred or herbivory-sensitive plant species become less abundant in the presence of herbivores, whereas herbivory-tolerant and non-preferred species increase (Augustine and McNaughton 1998). Herbivores can also increase vegetation heterogeneity when preferred plant species are unevenly distributed in the landscape (Hester et al. 2000), or if they forage more patchily than the vegetation pattern (Adler et al. 2001), for example, when external factors such as disturbance or stress influence a herbivore's spatial use of habitat.

Few studies simultaneously address the effects of herbivores on spatial and temporal vegetation heterogeneity (Adler et al. 2001), with most focussing on simple measures of diversity such as species richness or alpha diversity (within-plot diversity). However, also other aspects of diversity are important in understanding how herbivory impacts vegetation. For example, landscapes with several sites of low alpha diversity can still be heterogeneous if the variation in diversity between sites is high. Large herbivores can contribute to this spatial heterogeneity by feeding patchily (Adler et al. 2001; Koleff et al. 2003), and herbivory that affects temporal heterogeneity can alter colonization opportunities for new plant species (Bakker et al. 2003). Few studies have examined herbivory-induced changes in the vegetation by conducting long-term monitoring across herbivory-intensity gradients (although see Heckel et al. (2010)), but such studies are crucial for understanding how the intensity of herbivory disturbs ecosystems (Hester et al. 2000; Nuttle et al. 2014).

Densities of red deer (*Cervus elaphus*) have reached unprecedented levels in Northern Europe (Fuller and Gill 2001), causing management concerns for ecosystem stability and biodiversity (Côté et al. 2004). In Fennoscandia, herbivore assemblages have changed from livestock dominance to cervid dominance during the past 60 years, alongside a reduction in total herbivory (Austrheim et al. 2011). However, cervid herbivory has increased most in relatively resource-poor inland forest areas. Differences in both use-of-area and year-round presence compared with past livestock herbivory can be expected (Austrheim et al. 2011). The present intensity of herbivory by red deer may represent a disturbance regime to which the plant species in the Fennoscandian boreal forests are not evolutionarily adapted.

In this paper we investigate how red deer herbivory mediates spatial and temporal vegetation heterogeneity in the understory of a boreal forest ecosystem by combining a 10-year red-deer exclosure experiment with a substantial natural gradient in herbivory intensity. We monitored plant-species richness and abundance at 12 sites, each with one exclosure macroplot paired with one macroplot open to red deer herbivory. The open macroplots covered a range of intensities of herbivory, allowing us to examine the importance of herbivory along gradients of intensity. Removing herbivory can reveal vegetation resilience in relation to long-term disturbance (Elmqvist et al. 2003; Beschta and Ripple 2009). We previously investigated the effect of herbivory intensity on species richness, and found that overall species richness showed a unimodal peaked response to increasing herbivory, in accordance with the intermediate disturbance hypothesis (Hegland et al. 2013). However, the functional groups differed in their responses. The richness of forbs, graminoids and mosses increased, while dwarf-shrubs and young trees decreased with increasing herbivory intensity (Hegland et al. 2013). There was actually twice as many species benefitting from red deer herbivory. However, how this translates into spatial and temporal heterogeneity remains unclear.

We predicted that excluding red deer would lead to higher temporal species turnover shortly after exclusion, but reduced turnover in the long term (Prediction 1a). As intense herbivory can enhance light availability and opportunities for recruitment of new species (Rydgren et al. 2004), we expected a positive relationship between the intensity of herbivory and temporal species turnover (Prediction 1b). We also hypothesized that red deer reduce species turnover spatially, because selective herbivory may depress highly digestible plant species, enhance browse-tolerant and avoided ones (Augustine and McNaughton 1998), and aid seed dispersal through zoochory (Steyaert et al. 2009). Therefore, we predicted that excluding red deer would increase spatial species turnover (Prediction 2a), and expected a negative relationship between the intensity of herbivory and spatial species turnover (Prediction 2b; Rooney 2009).

Methods

Study area

We conducted our study at Svanøy Island (61°30′N, 5°05′E), western Norway. The island is situated in the boreo-nemoral zone and covered mainly by old-growth boreal forest dominated by Scots pine (*Pinus sylvestris*, Skogen and Lunde 1997). Mean annual precipitation and temperature are 2000 mm and 8 °C, respectively (Florø airport, http://www.eklima.met.no). The deer density is approximately 7.5 deer km^{-2}, which is considered high in Norway (Hegland et al. 2013). The island includes a red-deer farm with more than 30 deer km^{-2}, but wild and farmed deer are separated by a game fence. Some domestic sheep (*Ovis aries*) are free-ranging, mainly during summer.

Study design and sampling

In 2001, we established 12 sites in pine-bilberry (*Vaccinium myrtillus*) forest. Each site contained one exclosure macroplot and one open macroplot, both 9 × 9 m with seven permanent 1 × 1 m plots inside (Fig. 1). All plots were in flat areas, randomly placed but rejected and re-placed if adult trees were within 0.5 m. The
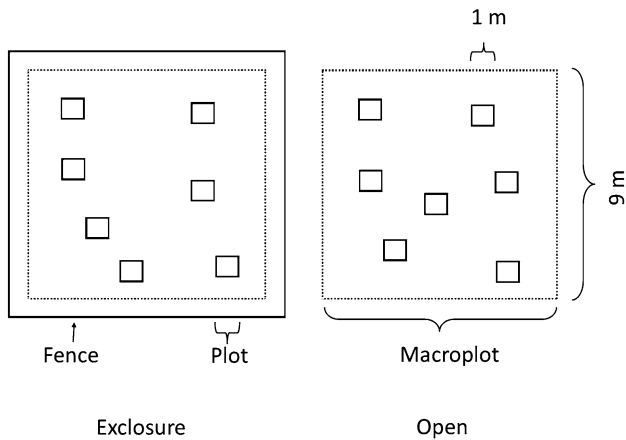
Fig. 1 Our study included 12 sites. The design shows the placement of seven plots in one open and one exclosure macroplot at each site. Due to topography, the distance between exclosure and open macroplots varied between 10 and 50 m

exclosures were surrounded by 3 m tall fences with 10×10 cm wire mesh. To avoid edge effects, we left a 0.5 m zone between the fence and the macroplot. Small herbivores could move freely into the exclosures, although few or none were present. Common boreal herbivores such as the mountain hare (*Lepus timidus*) have not been observed on the island, and we caught no rodents in 350 rodent trap-nights during 2011. Henceforth, 'treatment' refers to exclosures and open plots. Two sites were situated within the red deer farm, and these contained only six and three open plots, respectively, because some plot positions were lost. We surveyed the vegetation in June 2001, 2006 and 2011. Each 1×1 m plot was divided into 100 subplots. We recorded the vascular and bryophyte species in each plot and measured their abundance as frequency in these 100 subplots. In addition, the abundance and richness of young trees (50–400 cm in 2011) was recorded at the macroplot scale.

The intensity of red deer herbivory varied among the 12 open macroplots. To quantify this we estimated the intensity of herbivory on randomly selected bilberry ramets at each site (see also; Hegland et al. 2013). Bilberry is widely distributed, abundant, intermediately preferred by red deer, and therefore a good indicator species for monitoring the intensity of red deer herbivory (Mysterud et al. 2010). In June 2001 and 2011, we measured five and three randomly selected ramets, respectively, in all seven plots in each macroplot, and three ramets in four randomly selected plots per macroplot in 2006. We calculated the intensity of herbivory on each ramet as the percentage of annual shoots browsed, in five categories: 0, 1 (1–24 %), 2 (25–49 %), 3 (50–74 %), 4 (75–100 %), (sensu Frelich and Lorimer 1985), divided by ramet height. Hereafter we term this as 'herbivory intensity'. We used the mean herbivory intensity of all ramets per macroplot per year as our measure of intensity when analysing spatial heterogeneity statistically. To analyse temporal heterogeneity

we compare these mean values across the periods 2001–2006 and 2006–2011. Our herbivory-intensity measure was strongly related to an independent fecal count survey (r = 0.94, N = 12, P < 0.001, Hegland et al. 2013).

Heterogeneity measures

To calculate alpha diversity we used the Shannon diversity index (H′) and evenness (exp[H′]/S, where S is the number of species; (Kindt and Coe 2005)) for all species pooled and repeated this for the bottom layer (bryophytes), field layer (all vascular plants, including trees < 50 cm), and the understory tree layer (trees 50–400 cm). For temporal species turnover (Predictions 1a and 1b), we calculated Bray-Curtis dissimilarity (per cent dissimilarity/100, BC; Legendre and Legendre 1998) within each plot for the first five years (2001–2006) and the last five years (2006–2011). For spatial species turnover (Predictions 2a and 2b), we calculated BC between each plot and all other plots within each macroplot and year and used the mean of these six values as the BC value for each plot. Prior to all BC calculations we changed the range of the abundance scale for each species from 100 to 16 with a power function (van der Maarel 1979), and thereby achieved a recommended intermediate weighting of species (Økland 1990; Rydgren 1993).

Statistical analyses

We analysed all responses with linear mixed effects models (packages lme4 (Bates et al. 2014) and lmerTest (Kuznetsova et al. 2015) in R version 3.1.1 (R Core Team 2014). We started with full models, applied backward elimination of fixed effects, and validated the final models as proposed by Crawley (2007, Table S1). Although species turnover is a proportion, we specified all our models for Gaussian distribution, as the residuals showed normal distributions, resulting in more conservative p-values. As the two sites in the red deer farm had much higher red deer densities than the other sites, we ran all models with and without 'farm' as a factor.

Results

Across the three sampling years, we recorded 70 plant species, 52 of which occurred in both treatments. Overall, the mean number of species per plot was 16 (± 0.2 SE). *Vaccinium myrtillus*, *Avenella flexuosa* and *Hylocomium splendens* were common, and occurred in almost all plots all years (Table 1). *Viola riviniana*, *Maianthemum bifolium* and *Veronica serpyllifolia* were among the eight species only occurring in open plots. *Corylus avellana* and *Populus tremula* were among the 10 species unique to the exclosure plots. Occurences of species unique to one treatment were rare, however.

Table 1 Frequency, F (percent of all plots where the species occurred; n = 84 for each treatment), and mean subplot frequency, MSF (arithmetic mean of the subplot frequencies for a species, calculated from the plots where the species occurred), for species occurring in ≥25 % of the plots in one year and treatment

Species	Grazed						Ungrazed					
	2001		2006		2011		2001		2006		2011	
	F	MSF	F	MSF	F	MSF	F	MSF	F	MSF	F	MSF
Calluna vulgaris	33	16	25	25	21	24	42	24	45	55	39	62
Empetrum nigrum	54	38	46	54	43	56	58	34	48	47	48	32
Pinus sylvestris	0	0	6	1	44	3	0	0	5	1	30	2
Sorbus aucuparia	74	6	70	6	64	7	69	4	58	6	64	6
Vaccinium myrtillus	100	74	100	82	99	81	100	68	99	80	99	80
Vaccinium vitis-idaea	98	47	93	35	88	27	96	47	93	43	94	36
Agrostis capillaris	5	32	24	35	25	41	5	29	14	18	11	15
Anemone nemorosa	29	10	31	10	26	8	17	8	12	9	12	12
Avenella flexuosa	100	85	100	95	100	92	100	85	100	96	100	96
Linnaea borealis	77	31	80	33	76	19	74	29	85	28	73	17
Luzula sylvatica	60	35	57	35	61	43	58	40	56	44	58	48
Melampyrum pratense	32	9	33	8	44	6	57	8	62	12	51	7
Oxalis acetosella	56	20	58	28	54	31	51	26	52	23	60	21
Potentilla erecta	58	22	63	25	60	29	57	19	54	22	54	25
Pteridium aquilinum	10	6	19	15	21	14	12	4	26	8	18	14
Trientalis europaea	68	12	75	11	65	10	70	9	63	10	49	7
Dicranum spp.	69	22	68	25	70	26	65	20	64	14	63	19
Hylocomium splendens	100	73	100	79	100	88	100	70	99	63	100	82
Plagiothecium undulatum	21	11	18	9	31	8	25	16	14	7	27	11
Pleurozium schreberi	52	9	38	7	31	3	46	9	27	4	36	5
Polytrichum spp.	33	17	31	23	40	16	30	20	27	19	32	14
Pseudoscleropodium purum	58	19	69	20	71	17	60	18	73	20	81	18
Ptilium crista-castrensis	71	22	68	26	77	26	63	16	58	18	67	26
Rhytidiadelphus loreus	85	29	83	20	83	29	82	27	71	17	76	15
Sphagnum spp.	26	22	32	22	32	28	29	26	29	26	31	27

Ten years of excluding red deer significantly decreased alpha diversity (Shannon index 2011 ± SE: open plots, 2.21 ± 0.02; exclosure plots, 2.14 ± 0.03, T = −2.046, df = 332, P = 0.042, Table S2). However, herbivory intensity and alpha diversity were uncorrelated (P = 0.918, Table S2). Evenness did not differ between open and exclosure plots (evenness 2011 ± SE: open plots, 0.57 ± 0.01; exclosure plots, 0.57 ± 0.01, P = 0.568), but there was a negative effect of herbivory intensity on evenness within the open plots (β = −0.132 ± 0.043, T = −3.052, df = 25.7, P = 0.005, Table S2). Excluding red deer did not affect the alpha diversity within the bottom, field or understory tree layer (all, P > 0.05, Table S3), but herbivory intensity reduced the field layer alpha diversity (β = −0.747 ± 0.239, T = −3.121, P = 0.002, Table S3). Evenness was negatively related to herbivory intensity in the field (β = −0.201 ± 0.060, T = −3.331, P = 0.002) and understory tree layers (β = −0.464 ± 0.1655, T = −2.807, P = 0.010, Table S3).

Effect of red deer herbivory on temporal heterogeneity

Temporal species turnover (Bray-Curtis dissimilarity, BC, within plot, between years) was significantly higher in exclosure plots than in open ones for the first five-year period (P = 0.005). In the last five-year period, however, temporal species turnover in the exclosures was reduced (P = 0.023), reaching the same level as in the open plots (Fig. 2; Table 2). Temporal species turnover increased significantly with increasing intensity of herbivory (P < 0.001, Fig. 3; Table 2), but became non-significant, although still positive, when the plots in the red deer farm were omitted (P = 0.136, Table S4, Fig. S1).

Effect of red deer herbivory on spatial heterogeneity

Spatial species turnover (BC between plots in same macroplot) was higher in exclosures than in open plots 10 years after the experiment started (P < 0.001), whereas five years of exclusion was not enough to reveal the effect of red deer (P = 0.270). On the open plots, BC remained stable throughout (Fig. 4; Table 2). Similar results were obtained when plots in the red deer farm were omitted (Table S4). Spatial species turnover tended to be positively correlated with the intensity of herbivory overall (P = 0.089, Table 2), but the effect disappeared when the plots in the red deer farm were omitted from the model (P = 0.488, Table S4).

Discussion

The two dimensions of vegetation heterogeneity have contrasting characteristics. Temporal heterogeneity can
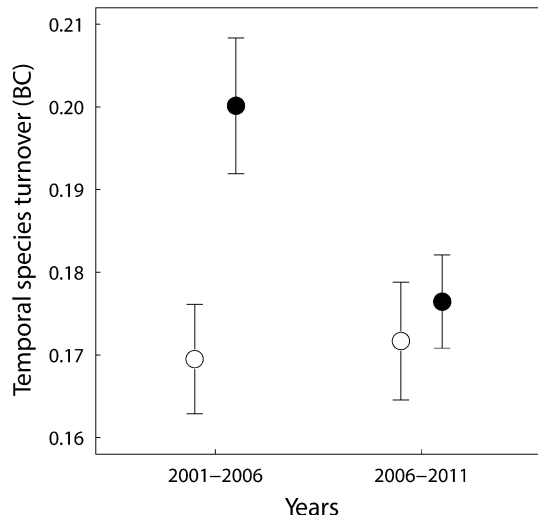
Fig. 2 Mean (±SE) five-year temporal species turnover, measured by the Bray-Curtis dissimilarity index within plot: exclosure (*black circles*) and open (*white circles*) plots during 10 years of experiment

destabilize the ecosystem, whereas spatial heterogeneity can stabilize the ecosystem (May 1974). A temporally heterogeneous forest will favour early succession species and will be more susceptible to invading species, stochastic events such as small-scale fires or wind throws, and state shifts. A spatially heterogeneous forest, on the other hand, will have higher resilience, and will thus be more robust to stochastic events.

In this study, we investigated the role of the red deer in forming the heterogeneity of the boreal forest understory vegetation over 10 years, and found two key effects. Firstly, excluding red deer caused a distinct shift in species composition, reflected in both spatial and

temporal species turnover (Predictions 1a and 2a). Secondly, we found that the intensity of herbivory had a strong positive impact on temporal species turnover (Prediction 1b), and a weak positive impact on spatial species turnover (Prediction 2b).

Higher temporal species turnover in sites with high intensities of herbivory (Prediction 1b) implies that the species composition in such sites was less stable than in sites with lower herbivory intensity. High levels of herbivory benefit pioneer and unpalatable species, and inhibit the growth and reproduction of slow growing species such as trees or shrubs (Hegland and Rydgren 2016), and this pattern is reflected in the reduction in evenness among the plant species (Table S2). By contrast, unpalatable species declined under high densities of white-tailed deer (*Odocoileus virginianus*) in Pennsylvania, USA, perhaps because trampling by the deer caused soil compression, limiting the growth potential of all plants (Heckel et al. 2010). In an old-growth, temperate forest in Poland, Kuijper et al. (2010) found that herbivory limited trees from growing larger than 50 cm. Likewise, we have previously shown that in our study area young deciduous trees germinated better in sites experiencing high levels of herbivory, but when seedlings became taller than the field layer vegetation, tree species richness decreased (Hegland et al. 2013). Red deer also strongly limit the abundance (number of individuals) in this size class (Hegland and Rydgren 2016). Thus, increased herbivory intensity reduces the number of trees reaching reproductive age, and therefore is a crucial factor in forest regeneration (Tremblay et al. 2006).

Temporal species turnover increased significantly in the exclosures during the first 5 years of the study. This implies that removing red deer herbivory from the system created a distinct and rapid shift in the species

Table 2 Effect of (a) exclosure treatment, and (b) herbivory intensity on temporal and spatial species turnover (BC); parameter estimates for the most parsimonous model of the effects of year, treatment or herbivory intensity, and interactions

| (a) Exclosure vs open plots						(b) Herbivory intensity					
Fixed effects	Estimate	SE	df	t	P	Fixed effects	Estimate	SE	df	t	P
Temporal species turnover											
(1a)						(1b)					
Intercept	0.173	0.011	17.5	15.652	< 0.001	Intercept	0.136	0.008	8.2	17.690	< 0.001
Exclosure (vs open)	0.027	0.009	25.1	3.069	**0.005**	Herbivory intensity	0.287	0.044	13.0	6.507	**< 0.001**
Year 2006–2011 (vs 2001–2006)	0.002	0.008	161.0	0.271	0.787						
Exclosure × year 2006–2011	−0.026	0.011	161.0	−2.298	**0.023**						
Spatial species turnover											
(2a)						(2b)					
Intercept	0.281	0.019	18.3	15.157	< 0.001	Intercept	0.276	0.017	12.3	16.374	< 0.001
Exclosure (vs open)	−0.007	0.019	11.6	−0.369	0.719	Herbivory intensity	0.055	0.032	168.3	1.712	0.089
Year 2006	0.007	0.005	314.2	1.591	0.113						
Year 2011	0.001	0.005	314.2	0.162	0.872						
Exclosure × year 2006	0.007	0.006	312.0	1.106	0.270						
Exclosure × year 2011	0.021	0.006	312.0	3.268	**0.001**						

The models are linear mixed models fit with REML Satterthwaite approximations to calculate degrees of freedom, with spatial random factor plot in macroplot by site for model 1a and 2a, and plot by site for model 1b, and plot by site plus temporal random factor year for 2b. Reference factors are Open 2001–2006 and Open 2001 for 1a and 2a, respectively, and represented by the intercept. A significant interaction term means that the turnover is different in exclosure than in open plots the last five years (1a) and after 10 years (2a)
Bold values indicate significant *p*-values (*p* ≤ 0.05)
SE standard error, *df* degrees of freedom
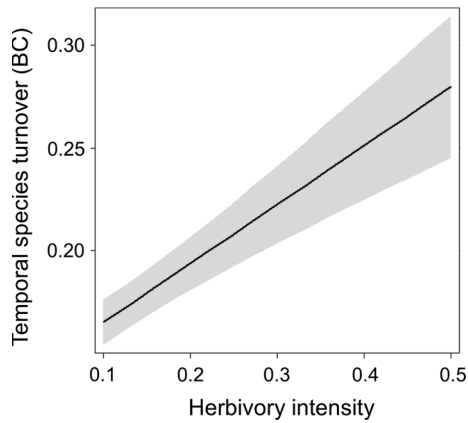
Fig. 3 Fitted relationship (*black line*, $P < 0.001$) and 95 % CI ($\beta \pm 1.96 * SE$, *grey shade*) between temporal species turnover, measured with Bray-Curtis dissimilarity index within plot between years, in relation to the gradient of herbivory intensity
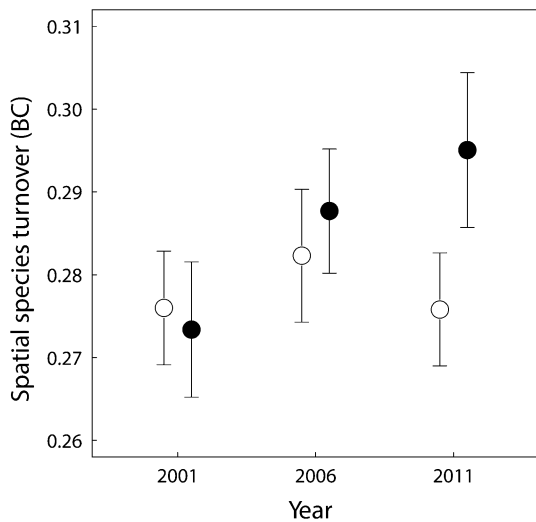
Fig. 4 Mean ($\pm SE$) spatial species turnover, measured with Bray-Curtis dissimilarity index between plots within the same macroplots: exclosure (*black circles*) and open (*white circles*) plots during the 10-year experiment

composition. Changes in vegetation inside exclosures after removing a cause of disturbance can reveal the plants' recovery abilities (Beschta and Ripple 2009). The marked increase in temporal species turnover demonstrated in our exclusion plots is an important finding because it shows the high capacity of boreal forest plant species to recover, even after experiencing high levels of herbivory. Nevertheless, the effect of herbivory will likely persist for some decades after the reduction or removal of red deer (Nuttle et al. 2014), probably depending on the original density of herbivores (Schütz et al. 2003).

Temporal species turnover did not differ significantly between exclosures and open plots (Prediction 1a) during the last 5 years of the study, which suggests rapid stabilization of species composition in our study system. When we omitted data from the red deer farm (those sites with extremely high red deer densities) from our analyses, however, temporal species turnover remained higher in the exclosure plots than in the open plots 10 years after excluding red deer (Table S4). This indicates that rapid changes in temporal species turnover can be expected after dramatic changes in an ecosystem (e.g., removing large herbivores). The continued difference in temporal species turnover between the exclosures and open plots outside the farm shows that red deer can increase temporal species turnover, also at low to medium densities, but that the effect is stronger at high densities.

Spatial species turnover did not decrease as red deer density increased (Prediction 2b); instead it increased weakly. However, in line with Prediction 2a, we found that excluding red deer from forest patches stimulated spatial species turnover. This suggests that red deer herbivory can have a homogenizing effect on the forest understory although in our study, this effect took 10 years to become apparent. The potential for herbivores to alter vegetation heterogeneity depends on the intrinsic spatial pattern of the vegetation and its interaction with that of herbivory (Adler et al. 2001). Our study examined the effects of herbivory in a boreal forest, with relatively homogenous vegetation. Although red deer use a range of different habitat types, productive boreal forest is the habitat where Scandinavian red deer spend most of their time during daylight, as it is more important for foraging than earlier believed (Godvik et al. 2009). Red deer feeding in the forest understory is not spatially homogeneous, based purely on the availability of forage plants, but depends also on factors such as the distance to human infrastructure or predators, and the availability of resting spots and high quality forage (e.g. pastures and meadows, Adrados et al. 2008; Godvik et al. 2009).

Exclusion of red deer resulted in 7 % reduction of the plant species diversity [transforming Shannon index to effective numbers, $\exp(H')$, Jost (2006)]. If all species were evenly common (which they are not), this diversity would translate to a species loss of 1.2 species. Such loss may not seem substantial, but if there are no other functionally similar species, it may affect long-term ecosystem functioning (e.g. Mori et al. 2013; Sitters et al. 2016).

Our study was conducted over a relatively small area, within an island of 11 km^2. By locating our sites along a gradient of herbivory intensity within this island, and focusing on the fine-grained plant-species responses within these sites and all within the pine-bilberry forest ecotype, we eliminated as many sources of variation as possible. We are thus able to isolate the effect of herbivory intensity on plant species heterogeneity. A study across a larger spatial extent and with several vegetation types, could potentially reveal greater effects of excluding red deer, but may not detect the fine scaled effect of herbivory intensity seen here.

Selectivity and aggregation are two important processes governing the effects of herbivory on vegetation

heterogeneity and diversity (Augustine and McNaughton 1998). Patch-grazing herbivores are more likely to increase spatial heterogeneity than species that feed homogenously or highly selectively (Adler et al. 2001). Studies on other large herbivores have shown that herbivory can either reduce (white-tailed deer, Rooney 2009) or increase (sheep, (DeGabriel et al. 2011); black-tailed deer, *Odocoileus hemionus*,(Gaston et al. 2006)) spatial heterogeneity. For example, in a study on the previously ungulate-free islands in British Columbia, Canada, Gaston et al. (2006) found that uninvaded islands were more similar in plant species composition than islands with introduced black-tailed deer. Islands without deer were smaller than those with deer, and therefore theoretically should be more homogeneous (MacArthur and Wilson 1963), suggesting that deer drove biotic differentiation rather than homogenization. Red deer, being intermediate feeders, may have less of an effect on spatial heterogeneity. They feed on a broader range of species than black-tailed deer (Hofmann 1989) and aggregate in smaller groups (Adler et al. 2001). Our results indicate that red deer herbivory spatially homogenize even relatively uniform vegetation, whereas the opposite would be expected (Adler et al. 2001).

Preferred species in heavily browsed areas may depend on ephemeral recruitment opportunities; that is, periods when herbivore populations are low (Fornara and du Toit 2007). Fluctuations in the density of large herbivore populations, spatially and in time, is therefore likely to be important for plant recruitment (Kuijper et al. 2010). Such ephemeral windows are not always sufficient for vegetation regeneration, especially if the ecosystem is not adapted to herbivory by the particular species. For example, in New Zealand, introduced red deer populations were reduced by about 92 % and were kept at low densities for four decades (Tanentzap et al. 2009). Despite this, tree recruitment remained low; showing that recovery in heavily herbivore-disturbed systems, particularly those that have evolved in absence of large herbivores, can take decades (Tanentzap et al. 2009). To permit natural regeneration, managers in areas with high red-deer densities need to provide for periodic ephemeral windows for recruitment, either in time or spatially, in their management plans (Sage et al. 2003).

Conclusions

Understanding both the spatial and the temporal components of vegetation heterogeneity is crucial to advancing our knowledge of ecosystem functioning and the associated role of large herbivores (Soininen 2010). Our results show that a combined focus on the effects of exclusion and the intensity of herbivory provides new insights into the ecological role of red deer in boreal forests. Interestingly, temporal heterogeneity of the forest understory increased with increasing red deer herbivory intensity, as well as when red deer were excluded. Increased temporal heterogeneity after excluding red deer either suggests that low densities of deer stabilize the species turnover, or that the recovery after long-term herbivory takes more than a decade. Further monitoring of the vegetation will illuminate this uncertainty. However, the spatial heterogeneity was indeed highest where red deer were excluded. Thus, our results suggest that removing red deer would effectively result in the most stable ecosystem over a prolonged period of time. However, the lowest species diversity of plants appeared where red deer were excluded. If both stable but also species rich ecosystems are the management goal, managers should sustain naturally fluctuating, but moderate red deer densities.

References

Adler PB, Raff DA, Lauenroth WK (2001) The effect of grazing on the spatial heterogeneity of vegetation. Oecologia 128:465–479

Adrados C, Baltzinger C, Janeau G, Pepin D (2008) Red deer *Cervus elaphus* resting place characteristics obtained from differential GPS data in a forest habitat. Eur J Wildl Res 54:487–494. doi:10.1007/s10344-008-0174-y

Augustine DJ, McNaughton SJ (1998) Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. J Wildl Manage 62:1165–1183. doi:10.2307/3801981

Austrheim G, Solberg EJ, Mysterud A (2011) Spatio-temporal variation in large herbivore pressure in Norway during 1949–1999: has decreased grazing by livestock been countered by increased browsing by cervids? Wildl Biol 17:286–298. doi:10.2981/10-038

Bakker C, Blair JM, Knapp AK (2003) Does resource availability, resource heterogeneity or species turnover mediate changes in plant species richness in grazed grasslands? Oecologia 137:385–391. doi:10.1007/s00442-003-1360-y

Bates D, Maechler M, Bolker B, Walker S (2014) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7. https://CRAN.R-project.org/package=lme4, pp

Beschta RL, Ripple WJ (2009) Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biol Cons 142:2401–2414. doi:10.1016/j.biocon.2009.06.015

Côté SD, Rooney TP, Tremblay J-P, Dussault C, Waller DM (2004) Ecological impacts of deer overabundance. Annu Rev Ecol Evol Syst 35:113–147. doi:10.1146/annurev.ecolsys.35.021103.105725

Crawley MJ (2007) The R book. Wiley, Chichester

DeGabriel JL, Albon SD, Fielding DA, Riach DJ, Westaway S, Irvine RJ (2011) The presence of sheep leads to increases in plant diversity and reductions in the impact of deer on heather. J Appl Ecol 48:1269–1277. doi:10.1111/j.1365-2664.2011.02032.x

Elmqvist T, Folke C, Nystrom M, Peterson G, Bengtsson J, Walker B, Norberg J (2003) Response diversity, ecosystem change, and resilience. Front Ecol Envir 1:488–494. doi:10.2307/3868116

Fornara DA, du Toit JT (2007) Browsing lawns? Responses of Acacia nigrescens to ungulate browsing in an African savanna. Ecology 88:200–209. doi:10.1890/0012-9658(2007)88[200:blroan]2.0.co;2

Frelich LE, Lorimer CG (1985) Current and predicted long-term effects of deer browsing in hemlock forests in Michigan, USA. Biol Cons 34:99–120. doi:10.1016/0006-3207(85)90103-x

Fuller RJ, Gill RMA (2001) Ecological impacts of increasing numbers of deer in British woodland. Forestry 74:193–199. doi:10.1093/forestry/74.3.193

Gaston AJ, Stockton SA, Smith JL (2006) Species-area relationships and the impact of deer-browse in the complex phytogeography of the Haida Gwaii archipelago (Queen Charlotte Islands), British Columbia. Ecoscience 13:511–522. doi:10.2980/1195-6860(2006)13[511:sratio]2.0.co;2

Godvik IMR, Loe LE, Vik JO, Veiberg V, Langvatn R, Mysterud A (2009) Temporal scales, trade-offs, and functional responses in red deer habitat selection. Ecology 90:699–710. doi:10.1890/08-0576.1

Heckel CD, Bourg NA, McShea WJ, Kalisz S (2010) Nonconsumptive effects of a generalist ungulate herbivore drive decline of unpalatable forest herbs. Ecology 91:319–326. doi:10.1890/09-0628.1

Hegland SJ, Rydgren K (2016) Eaten but not always beaten: winners and losers along a red deer herbivory gradient in boreal forest. J Veg Sci 27:111–122. doi:10.1111/jvs.12339

Hegland SJ, Lilleeng MS, Moe SR (2013) Old-growth forest floor richness increases with red deer herbivory intensity. For Ecol Manag 310:267–274. doi:10.1016/j.foreco.2013.08.031

Hester AJ, Edenius L, Buttenschon RM, Kuiters AT (2000) Interactions between forests and herbivores: the role of controlled grazing experiments. Forestry 73:381–391. doi:10.1093/forestry/73.4.381

Hofmann RR (1989) Evolutionanry steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive-system. Oecologia 78:443–457. doi:10.1007/bf00378733

Hovick TJ, Elmore RD, Fuhlendorf SD, Engle DM, Hamilton RG (2015) Spatial heterogeneity increases diversity and stability in grassland bird communities. Ecol Appl 25:662–672. doi:10.1890/14-1067.1.sm

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386. doi:10.2307/3545850

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

Kindt R, Coe R (2005) Tree diversity analysis: a manual and software for common statistical methods for ecological and biodiversity studies. World Agroforestry Centre (ICRAF), Nairobi, Kenya

Koleff P, Gaston KJ, Lennon JJ (2003) Measuring beta diversity for presence-absence data. J Anim Ecol 72:367–382. doi:10.1046/j.1365-2656.2003.00710.x

Kuijper DPJ, Jędrzejewska B, Brzeziecki B, Churski M, Jędrzejewski W, Żybura H (2010) Fluctuating ungulate density shapes tree recruitment in natural stands of the Białowieża Primeval Forest, Poland. J Veg Sci 21:1082–1098. doi:10.1111/j.1654-1103.2010.01217.x

Kuznetsova A, Brockhoff PB, Christensen RHB (2015) lmerTest: Tests in Linear Mixed Effects Models. R package version 2.0, p 25

Legendre P, Legendre L (1998) Numerical ecology. Elsevier, Amsterdam

MacArthur RH, Wilson EO (1963) An equilibrium theory of insular zoogeography. Evolution 17:373–387. doi:10.2307/2407089

Mackey RL, Currie DJ (2001) The diversity-disturbance relationship: is it generally strong and peaked? Ecology 82:3479–3492. doi:10.1890/0012-9658(2001)082[3479:tddrii]2.0.co;2

May R (1974) Ecosystem patterns in randomly fluctuating environments. In: Rosen R, Snell F (eds) Progress in theoretical biology. Academic Press, New York, pp 1–50

Mori AS, Furukawa T, Sasaki T (2013) Response diversity determines the resilience of ecosystems to environmental change. Biol Rev 88:349–364. doi:10.1111/brv.12004

Mysterud A, Askilsrud H, Loe LE, Veiberg V (2010) Spatial patterns of accumulated browsing and its relevance for management of red deer Cervus elaphus. Wildl Biol 16:162–172. doi:10.2981/09-043

Nuttle T, Ristau TE, Royo AA (2014) Long-term biological legacies of herbivore density in a landscape-scale experiment: forest understoreys reflect past deer density treatments for at least 20 years. J Ecol 102:221–228. doi:10.1111/1365-2745.12175

Økland R (1990) Vegetation ecology: theory, methods and applications with reference to Fennoscandia. Sommerfeltia Suppl 1:1–233

Proulx M, Mazumder A (1998) Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. Ecology 79:2581–2592. doi:10.1890/0012-9658(1998)079[2581:rogiop]2.0.co;2

R Core Team (2014) R: A language and environment for statistical computing. The R Foundation for Statistical Computing, Vienna, Austria

Rooney TP (2009) High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. Plant Ecol 202:103–111. doi:10.1007/s11258-008-9489-8

Rydgren K (1993) Herb-rich spruce forests in W Nordland, N Norway: an ecological and methodological study. Nordic J Bot 13:667–690. doi:10.1111/j.1756-1051.1993.tb00112.x

Rydgren K, Økland RH, Hestmark G (2004) Disturbance severity and community resilience in a boreal forest. Ecology 85:1906–1915. doi:10.1890/03-0276

Sage JRW, Porter WF, Underwood HB (2003) Windows of opportunity: white-tailed deer and the dynamics of northern hardwood forests of the northeastern US. J Nat Conserv 10:213–220

Schütz M, Risch AC, Leuzinger E, Krusi BO, Achermann G (2003) Impact of herbivory by red deer (Cervus elaphus L.) on patterns and processes in subalpine grasslands in the Swiss National Park. For Ecol Manage 181:177–188. doi:10.1016/s0378-1127(03)00131-2

Sitters H, Di Stefano J, Christie F, Swan M, York A (2016) Bird functional diversity decreases with time since disturbance: does patchy prescribed fire enhance ecosystem function? Ecol Appl 26:115–127. doi:10.1890/14-1562

Skogen A, Lunde BN (1997) Flora og vegetasjon på Svanøy i Sunnfjord, med vegetasjonskart. Botanical Institute, University of Bergen, Norway

Soininen J (2010) Species turnover along abiotic and biotic gradients: patterns in space equal patterns in time? Bioscience 60:433–439. doi:10.1525/bio.2010.60.6.7

Steyaert S, Bokdam J, Braakhekke W, Findo S (2009) Endozoochorical plant seed dispersal by red deer (Cervus elaphus) in the Polana Biosphere Reserve, Slovakia. Ekológia 28:191–205

Tanentzap AJ, Burrows LE, Lee WG, Nugent G, Maxwell JM, Coomes DA (2009) Landscape-level vegetation recovery from herbivory: progress after four decades of invasive red deer control. J Appl Ecol 46:1064–1072. doi:10.1111/j.1365-2664.2009.01683.x

Tremblay JP, Huot J, Potvin F (2006) Divergent nonlinear responses of the boreal forest field layer along an experimental gradient of deer densities. Oecologia 150:78–88. doi:10.1007/s00442-006-0504-2

van der Maarel E (1979) Transformation of cover-abundance values in phytosociology and its effects on community similarity. Vegetatio 39:97–114. doi:10.1007/BF00052021