Denne fila er lasta ned frå Høgskulen i Sogn og Fjordane sitt institusjonelle arkiv, Brage, http://brage.bibsys.no/hsf/

Dette er forfatterens aksepterte versjon av artikkelen som originalt er publisert i Forest Ecology and Management (Elsevier):

Title: Old-growth forest floor richness increases with red deer herbivory intensity

Article Type: FLA Full Length Article

Keywords: browsing; cervus; disturbance; diversity; functional group; grazing

Abstract: Herbivory is one of the most important biotic disturbance types globally and is important for community structure and composition through species filtering. In northern forest ecosystems the population densities of wild-ranging ungulates, which are managed through hunting, have reached historically high numbers. Conservation concerns frequently arise, both in media and scientific literature. One key question is whether increased deer densities negatively affect biodiversity and whether management should implement reduction in deer densities. Few studies have addressed wild herbivores-plant richness relationships using a full length gradient of herbivory. Such gradient approach where herbivory is studied from very low to very high intensity, may enable us to develop operational management guidelines for deer densities. We recorded the ungulate herbivory intensities on the island Svanøy in west Norway across ten years and related this to the present plant richness of an old-growth pine-forest system, recording all plant species groups of the forest understory. The herbivory intensity-plant richness relationship followed a unimodally peaked curved, but plant richness was lower only at forest sites with artificially high red deer herbivory. Overall, the herbivory-richness relationships of functional groups fitted expectations in that the richness of low-growing functional groups as forbs, graminoids and mosses all increased within natural levels of herbivory intensities, whereas the richness of the taller growing woody species of the forest understory, dwarf-shrubs and young trees, decreased along the intensity gradient. We validated the gradient approach by experimental exclosure data. Management for relatively high deer densities may benefit the overall understory plant richness of such forest ecosystems at the expense of richness of woody plants. We suggest that the herbivory-induced reduction of the understory woody layer is the key to understand the overall increase in plant species richness.
Dear Editor

We are grateful for the constructive comments to our manuscript. We do believe the comments have improved the manuscript.

We have followed most of the comments and give detailed comments below each suggestion/comment with reference to new line number when required.

In addition we have done a few linguistics and other changes to improve readability that have not been commented in detail below.

On behalf of the authors

Stein J. Hegland
Sogndal, Norway, 13 August, 2013
Highlights

Does increased herbivory by red deer harm boreal forest floor richness?

We examine this by relating a herbivory intensity gradient to plant species richness.

Increasing herbivory intensity enhance richness except at artificially high herbivory levels.

Low-growing species groups benefit at the expense of taller growing woody species.

Boreal forest floor richness may benefit from relatively high red deer herbivory intensity.
Dear Reviewers

We are grateful for the constructive comments to our manuscript. We do believe the comments have improved the manuscript.

We have followed most of the comments and give detailed comments below each suggestion/comment with reference to new line number when required.

In addition we have done a few linguistics and other changes to improve readability that have not been commented in detail below.

On behalf of the authors

Stein J. Hegland
Sogndal, Norway, 13 August, 2013

Reviewers’ comments and our responses:

Reviewer #1: The authors have produced an interesting paper on the species richness of plants in relation to foraging intensity of red deer. The strength of the paper is the long-term nature of the data set and varying intensities of herbivory. I do have several concerns with the paper that are listed below in no particular order of importance.

1. Samples apparently were collected during winter, but foraging on some of the species would have taken place in spring, summer, and autumn. Is the index to intensity developed for red deer during winter valid for other seasons? For instance, Clutton-Brock (1987 Journal of Zoology London) noted that the sexes of red deer spatially separate from one another for much of the year. How might those differences in spatial distribution and density affect the index to intensity of herbivory?

Reply: Samples were collected in mid-summer (ca 10-25 June), but we agree with the reviewer that bilberry browsing mainly occur during autumn, winter and spring and that we therefore have mainly estimated September to May herbivory using the collected data. However, we use bilberry browsing as a proxy for the overall red deer herbivory intensity of sites. Other studies have shown that bilberry is a good indicator for estimating herbivory intensity and herbivore density (Mysterud et al., 2010) and using data such a pellet counts may have other problems related to its use (see statement and reference to Putman 1984 in ms). Also it is important to remember that densities of deer are highest in autumn-to-spring ranges and therefore is the ecosystem impact thought to be the highest. Moreover, the red deer in Norway has shown to be using these ranges the largest proportion of the year, i.e. in average 8 months per year. Thus this is the main deer occupancy area (and the coniferous-bilberry forest is the most important habitat type). Together these factors make us believe that we can use bilberry as indicator for the year-round effect of red deer herbivory intensity in the ecosystem. We have added some explanations in the methods around this (line 158-165): “......but both individual plants and populations survive rather well even at high intensities of browsing and accordingly bilberry is a good indicator plant for herbivory intensity (Hegland et al., 2010; Mysterud et al., 2010). Although the level of bilberry browsing largely estimate autumn-to-spring herbivory, red deer in Norway has been found to use the winter ranges on average eight months of the year (Bischof et al., 2013), and browsing on bilberry correlate strongly with other indices of population densities such as winter-spring pellet counts or autumn harvest data (Mysterud et al., 2010). We therefore believe that level of bilberry browsing is a suitable proxy for the herbivory intensity at individual sites.”

2. The authors cite the work Fox (2013) concerning the potential shortcomings of the IDH, but then forage ahead anyway without addressing potential limitations to the hypothesis. Especially
problematical is that there may be other mechanisms that would produce a humped distribution at intermediated levels of herbivory that were not discussed (a point I will return to later).

Reply: We do see that problem and we have chosen to focus less on testing the IDH, according to comment 5. We believe that we have addressed any shortcomings by our reduced focus on IDH and by focusing more on the gradient approach, which is the overall key point in this study.

3. Many of the underpinning explanations for the IDH involve competitive interactions among plants. The authors, however, only examine species richness of plants. Competition must involve the abundance of competitors, and I was disappointed that plant diversity was not also evaluated.

Reply: We agree that abundance is important. The IDH and disturbance effects/herbivory effects involve competitive interaction indirectly as well as the direct effects of plant traits in plants such as tolerance and avoidance and the preferences of deer in the given habitat. We chose not to focus on all these different possible explanations for understanding the ungulate effects on plant richness in this paper. In addition, we have just recently submitted another paper that focuses more on the spatial and temporal diversity and the heterogeneity of the forest caused by red deer herbivory. Including data on abundance, in addition to moving beyond the scope of this paper, conflict with that manuscript potentially creating problems with double-reporting.

4. Changes in the intensity of herbivory in large mammals involve density-dependent processes. The relationship of the population to carrying capacity (K) over time can have huge effects on levels of herbivory. This was neither mentioned nor was an effort made to investigate where the population was with respect to K.

Reply: This is an important but difficult point to address. In the revised version we state that the densities of red deer in the farm is far beyond carrying capacity (because they need supplementary feeding), line 133-136; “Two sites were located within the forest areas of a deer farm representing deer densities at artificially high levels that would represent a population level beyond carrying capacity because these animals receive supplementary feeding. Thus, our data represents a gradient in herbivory intensity.” For the natural population ecosystem studies as ours (in addition to population studies including data on fertility and body weights) can help to say something about where the population is in relation to K. But we believe it would be wrong of us to speculate too much around where we are in these forests without having detailed data on all these variables which is important for evaluating this in terms of herbivory and ‘overgrazing’ (See excellent discussion in Mysterud A. (2006). The concept of overgrazing and its role in management of large herbivores. Wildlife Biology, 12, 129-141.)

5. Some of the linear regressions in Figure 3 appear to be leveraged. More importantly, the humped-shaped curves in Figures 2 and 3 presented as evidence for the IDH have no data associated with the hump; there is no way to know what the true shape of the relationship at intermediate intensities might be.

Reply: As reported the figures are not taking into account the hierarchical nature of the study design and hence the statistical testing (lme with random effects), and the lines are therefore not reproducing the statistical relationships to a full extent. Although we already recognized the limitations of the gaps in the gradient we have in the revised version chosen to reduce the focus on testing the IDH explicitly. We now use it more as an overall theoretical background for understanding red deer herbivory effects and to discuss management implications. In the revised version we focus more on the gradient-approach (e.g. lines 62-.96-, 267-, 337) which was already the most important aspect with this study, and we have deleted several parts discussing the intermediate disturbance hypothesis. The main message will be that the two farm sites represent an extreme that is probably never found in nature, whereas the ecologically intermediate levels, at least in Norway, will be somewhere in the middle of the rest of the herbivory intensity
gradient. We also produce statistical tests without the farm sites when quadratic relationships were selected (reply to comment by reviewer 2) and these indeed show that such relationships were driven farm sites and are otherwise linear. Hopefully, the reviewer can concur with this overall change of approach.

6. The authors cite some of Sam McNaughton’s work, but never mention herbivore optimization and a potential cause of increases in plant productivity and diversity at intermediate levels of herbivory, which also can occur in forested habitats (Stewart et al. 2006 Wildlife Monographs, Stewart et al. 2009 Oecologia).

Reply: The McNaughton reference from 1979 should not have been included. We understand herbivore optimization as a concept focusing mainly on how herbivores may increase plant productivity. Plant productivity has the potential to affect richness patterns, but as this is not included in this study we prefer not to speculate around this. On the other hand we believe the the Stewart et al.-references are vital for our work and we included reference to them because they involve a gradient approach that is very useful when investigating ungulate effects on ecosystems.

In conclusion, I do not believe that authors have obtained a critical test of IDH.

Reply: See comments above

Reviewer #2: This manuscript describes an unusual study which utilized a gradient in herbivory intensity in an old growth Norwegian forest to test the Intermediate disturbance hypothesis. The authors recognize the limitations of their gradient - the intermediate part of their disturbance gradient is not really well-represented -and interpret the results with caution. They support their gradient study with work from an exclosure study, which lends support to their conclusion. Properly caveated, which the authors have done for the most part, this manuscript represents work that should be published. Particular strengths are the repeated sampling over 10 years, and the use of experimental work to bolster the conclusions. There is a nice, clear statement of the hypotheses at the end of the Introduction.

The manuscript is a little difficult to follow, and needs some work to help the reader understand what the authors are thinking.

Reply: We have performed the changes below mostly as suggested and in addition reviewed the paper for linguistics and inconsistencies in terminology to improve the readability of the paper.

The authors use the term "semi-experimental" to describe their gradient, and also spatial models resulting from that work. I really don’t like that term, and think it should be dropped. Its not accurate (its either an experiment or not), nor grammatically appropriate.

Reply: We have re-phrased and simply call it a gradient leaving the semi-experimental term.

The authors also refer to their full-length gradient approach. Technically they do have a full-length gradient because it includes very low levels and very high levels (deer farm) of herbivory. I'm hoping they can consider in the ms, the impact of the large gap in the middle of the herbivory range. Their models are clearly skewed by the deer farm - which is not necessarily a bad thing, but the statistical implications for testing the IDH hypothesis and for their interpretations of results should be described for the reader.

We agree and we now present statistical testing for the significant quadratic relationships without farm sites in the results, which makes discussion and conclusion more straightforward. Concurring with suggestions from Reviewer 1 we also use less space on the IDH and more space on the gradient approach itself (e.g. lines 89- ,163- , 532-544, 609-612; and deleted several parts discussing the intermediate disturbance hypothesis).
The terms herbivory intensity and deer grazing intensity and deer densities are occasionally used interchangeably, and the authors should perhaps define them as being identical terms, if indeed they are (I'm not entirely convinced this is the case) or be consistent about using the appropriate terms. We use bilberry browsing levels as a proxy for herbivory intensity. We have tried to be consistent in using the term 'herbivory intensity' throughout the manuscript and rephrased according to this. The authors could utilize papers on other systems (for example white-tailed deer in Pennsylvania, USA or elk in the western US (Starkey Experimental Range) to strengthen the discussion and particularly identify some possible mechanism - is it competition for light, or other mechanisms?

Reply: The work from the Starkey experimental range was partly known to us through the works of Stewart et al 2006 which is important to our study because it is one of the ungulate studies that have utilised the gradient approach in a good way, and we now refer to this study in the revised version. We had different sections on mechanisms in the discussion. One dealing with safe-sites and one with the competition for light among understory trees/shrubs and the lower growing functional groups. We have rephrased these sections slightly and introduced the word ‘mechanism’ to pinpoint the importance of these factors stronger and also a concluding line within this section (see 320-336).

Specific comments (our response is ‘ok’ when changes performed as suggested and otherwise marked with ‘reply’

Abstract: change "conservational" to "conservation" ok
Change "artificial high red deer herbivory" to "artificially high red deer herbivory" ok
(and see earlier comment about terminology to describe herbivory levels

Line 49 suggestion ".free-ranging ungulates are often.." ok

Line 50 sugges ". and can be partly controlled by hunting based management." ok

Line 56-60 I'm not sure I follow this, and I think some more details could help. I think the authors are saying that the current population densities are returning to levels that may be previously existed. When were wild ungulates nearly extinct, and when were higher levels "normal" or perhaps "historical levels" is better terminology?
Reply: Rephrased to “On the other hand, historical population levels are largely unknown, but the increasing cervid densities have mainly been a response to lower livestock numbers in forested areas, increasing forest cover and improved hunting management during the last millennia (e.g. Putman et al., 2011).”

Line 65 -67 (and elsewhere) suggest replacing "highest" with "greatest" when discussing numerical levels; "too high disturbance" with "too much disturbance", and "too low disturbance" with "too little disturbance"
Reply: Changed in these specific cases, but not all other: e.g. “varying from very low to extremely high intensity” as we feel that ‘high’ in these cases are more correct.

Line 70 - is there a better word than "invalidities" ? I've not seen it before.
Reply: due to reviewer 1’s coments on the test of IDH we changed the whole section

Line 71 suggest "Nevertheless the hypothesis survives.." ok

Line 78 suggest "many other disturbances that influence ." ok

Line 84 "which plant traits are advantageous." ok
Line 92 "selectively decreases woody abundance and thereby benefits richness." ok

Line 95 "Although IDH is one .." ok

Line 112 - is there a better way to describe the relationship than "peaked" maybe curvilinear?
Reply: We believe that peaked (often used in relation to the IDH) is more intuitive than curvilinear that is a bit technical. We now use unimodal together with ‘peaked’, e.g. “.....show an unimodal peak.....”, “.....unimodally peaked browsing-richness relationship...” when ‘peaked’ were standing alone in the text.

Line 135-136 suggest ".1995 until today has experienced the highest post-glacial densities." ok

Line 142 replace "impossible" with "difficult to accurately establish" ok

Lines 164-168 -- why are the number of ramets and plots different over time?
Reply: Due to time-consuming sampling performed in 2001 we made some choices to reduce sampling effort. Explain why this does ( or doesn't) matter. We believe that this does not matter as the variance was not much larger and not the largest when less sampling performed (2006). We included a short statement about this: “The varying sampling effort did not influence the variance strongly (SD: 0.16 in 2001, 0.18 in 2006 and 0.25 in 2011)” (line 282-285). Also, as we used the average of those three sampling events in this paper that also help reducing the potential bias as long as sampling effort is similar across sites at the same sampling event.

Line 191 " were not included" ok

Line 192 suggest changing "without nesting" to "not nested" ok

Line 195 ".preference effects were minimized." This is a good explanation of your reasoning. This is helpful to the reader.
Reply: Good point. We also use this explanation in other parts of the text, e.g. the discussion, see line 267-268

Line 196 "geographically restricted area" ok

Lines 206-215 - when explained here I understand (I think) your methodology for validating the spatial model. But I didn't understand this when I look at Fig A1, and your figure heading or in section 3.2. A bit more detail is needed Section 3.2, and in the legend for Figure A.1 and perhaps you can use some of this language to make it clear. This is an interesting way to do this, and you might want to spend more time on it.
Reply: Good point. We included some of the explanation from the method at the start of 3.2. e.g. line 251- “In general our herbivory intensity-plant richness models were validated by the temporal exclosure-based models (Table 1, Fig. A1), i.e. the temporal change in plant richness in open vs. exclosed forest plots was largely consistent with the findings along the spatial gradient of herbivory intensity”. and then we refer to the appendix which is rephrased to (line 524-534): “Plant richness, in total and for functional groups of the forest understory at Svanøy, western Norway, during 2001, 2006 and 2011 in herbivore and exclosure forest plots. Values are mean ± 1 SE (see methods for statistical procedures). These experimental exclosure-based models were used to validate the herbivory intensity-plant richness models. Example of model validation: to validate a statistical positive or a unimodally peaked herbivory-richness relationship, the temporal change should be statistically positive in herbivore plots relative to exclosure plots......” which hopefully reads better than the previous version.

Line 220 change decline to declines ok
I think you are referring to Fig 3 h ok

Looking at the photo from the deer Farm in Fig 1, I think the deer have killed significant parts of adult plants in that photo. Is that representative of the rest of the area inside the deer farm? I think this statement is maybe just a little under-estimating?

Reply: We meant that the disturbance from ungulates in general, but we see your point and rephrased (line 547-552): “The unimodally peaked signal in the herbivory-richness relationships was, however, not very strong and dependent on artificial high disturbance levels in our study. In general, the disturbance from free-ranging large herbivores is seldom severe enough to kill significant parts of adult plants. When disturbance becomes substantial, such as in the deer farm in our study, colonising plants are predated at early stage before they are able to tolerate biomass loss. .”

Line 287 suggestion "meta-studies and literature review" ok

Line 297 "deer herbivory has contracting." we use ‘opposite’ instead

Line 301 underpins should be underpin ok

While I agree that the IDH could be used to develop operational guidelines, I’m not sure you had sufficient points to do so, and you haven’t really defined these guidelines.

Reply: We now focus more on the gradient approach and less on the IDH (according to your comment and also Reviewer 1). We agree that we were a bit vague on the operational part. We have included a separate section in the discussion were we discuss the level of herbivory intensity in this study compared to other studies and try to make some general operationalized statements based on this (line 337-356).

Lines 317-321 - what about a time frame for your conclusions - based on 10 years of data, which is excellent, but can you say that moderate to high densities lead to higher understory species richness over decades? A time frame would be helpful.

Reply: We agree that we cannot predict for the future, and need longer time series. We slightly rephrase our statement not to push things too far (line 363-369): “Considering the extreme high herbivory intensity in the deer farm sites, the main message from our study is that within the densities and timeframes studied here moderate to relatively high red deer densities lead to greater understory species richness than low deer densities. Based on this particular study, and comparing herbivory intensity and harvest data with literature and statistics from other areas, we may conclude that the red deer densities currently found in Norway rarely reach levels that reduce plant species richness.”

Line 322 should be Richness ok

Figure legends (particularly #3) - need more detail to help sort this out. Figure 3 graphs f and h are not identified. Ok

Figure legend Figure A.1 - I'm not sure why this is in an Appendix, but I guess I'm okay with it. Need to define "ceased plots" earlier in the legend. This figure is not clear to me.

Reply: This is an appendix because we used it for model validation but did not focus on the temporal changes, that was beyond the scope of this paper and we treat that in another paper which have recently been submitted. As we have addressed in an earlier comment we have rephrased the text in the appendix according to reviewers comment. We now use herbivore vs exclosure plots in text and all figures have been reformatted (see line 524-536).
Line 481 suggest "continuous herbivory plots" has been rewritten according to comment mentioned above

Line 485 herbivory ok
Old-growth forest floor richness increases with red deer herbivory intensity

Stein J. Hegland,
Corresponding author: email stein.joar.hegland@hisf.no; telephone +47 41501553
1. Norwegian Red deer Centre, N-6914 Svanøybukt, Norway
2. Faculty of Science, University College of Sogn and Fjordane, P.O. Box 133, N-5861 Sogndal, Norway

Marte S. Lilleeng
1. Faculty of Science, University College of Sogn and Fjordane, P.O. Box 133, N-5861 Sogndal, Norway
2. Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, N-1432 Ås, Norway

Stein R. Moe
1. Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, N-1432 Ås, Norway
ABSTRACT

Herbivory is one of the most important biotic disturbance types globally and is important for community structure and composition through species filtering. In northern forest ecosystems, the population densities of wild-ranging ungulates, which are managed through hunting, have reached historically high numbers. Conservation concerns frequently arise, both in media and scientific literature. One key question is whether increased deer densities negatively affect biodiversity and whether management should implement reduction in deer densities. Few studies have addressed wild herbivores-plant richness relationships using a full length gradient of herbivory. Such gradient approach where herbivory is studied from very low to very high intensity, may enable us to develop operational management guidelines for deer densities. We recorded the ungulate herbivory intensities on the island Svanøy in west Norway across ten years and related this to the present plant richness of an old-growth pine-forest system, recording all plant species groups of the forest understory. The herbivory intensity-plant richness relationship followed a unimodally peaked curve, but plant richness was lower only at forest sites with artificially high red deer herbivory. Overall, the herbivory-richness relationships of functional groups fitted expectations in that the richness of low-growing functional groups as forbs, graminoids and mosses all increased within natural levels of herbivory intensities, whereas the richness of the taller growing woody species of the forest understory, dwarf-shrubs and young trees, decreased along the intensity gradient. We validated the gradient approach by experimental exclosure data. Management for relatively high deer densities may benefit the overall understory plant richness of such forest ecosystems at the expense of richness of woody plants. We suggest that the herbivory-induced reduction of the understory woody layer is the key to understand the overall increase in plant species richness.

Key-words: browsing, cervus; disturbance; diversity; functional group; grazing;

1. Introduction

Globally, herbivory by large grazers is one of the most important biotic disturbance types that influence community composition and structure (Diaz et al., 2007) and in many cases it is a disturbance type that is influenced by management decisions. In northern forest systems, wild free-ranging ungulates are often a major determinant of plant community structure, composition and dynamics (Pastor et al., 1988, Suzuki et al., 2013) and populations can be partly controlled by hunting based management. The populations of large, wild ungulates
such as red deer (*Cervus elaphus*) and moose (*Alces alces*) have expanded and grown rapidly for several decades in Scandinavia, Europe and Northern America, often to concern of conservationists (Côté et al., 2004). The increasing population densities may create a disturbance regime for northern forest ecosystems to which they are not evolutionary adapted (sensu Milchunas et al., 1988). On the other hand, historical population levels are largely unknown, but the increasing cervid densities have mainly been a response to lower livestock numbers in forested areas, increasing forest cover and improved hunting management during the last millennia (e.g. Putman et al., 2011). Whether the present population densities are normal or not there is a current need for operational knowledge on how wild, free-ranging ungulates affect northern forest community composition.

Studying ecological interactions along gradients of environmental stress represent a powerful way to develop knowledge under realistic ecological conditions as well as operational guidelines in nature management (e.g. Brooker et al., 2006; Stewart et al. 2006, 2009). One approach to this has been by applying the intermediate disturbance hypothesis to a given disturbance-richness relationship (IDH; e.g. Grime 1973; Connell 1978). The hypothesis predicts that the richness of species should be greatest when the intensity, frequency or size of a disturbance is at intermediate level (Svensson et al., 2012; Fox 2013). Too much disturbance means that long-lived species will not survive and too little disturbance results in competitive exclusion of pioneer species (e.g. Shea et al., 2004). The hypothesis has been criticized for low precision in explaining diversity patterns and because of its relative character (Mackey & Currie 2001), i.e. what is intermediate? Nevertheless, the hypothesis can act as a theoretical background to a gradient approach in ecology dealing with herbivory, both as it introduces herbivory as a disturbance as well as predicting that species richness will follow a unimodally peaked relationship with, for example, herbivory intensity. A recent review showed that the intermediate disturbance hypothesis was indeed successful in predicting disturbance-diversity relationships when, according to the original hypothesis, testing is done with richness and not abundance based diversity indices as response variable (Svensson et al., 2012).

Many other disturbances that influence plant communities, such as storms and fires, are non-selective (Laliberté et al., 2013) and outside the direct influence of humans. On the contrary, herbivory by domestic and wild herbivores are both selective (Augustine & McNaughton 1998) and among those ecological factors that can partly be controlled by managers. Therefore, herbivory disturbance by large herbivores may have complex influence on community composition and can interact with different parts of the species pool in
contrast ways. Which plant traits are advantageous in a given plant community is most often an interplay between tolerance and avoidance (Augustine and McNaughton 1998), which may also change competitive interactions among plants (Hester et al., 2006). Most studies show that both the richness and abundance of woody vegetation may decline when herbivory from ungulates becomes more intense (reviewed by Gill 2006). Also, plants with a short growth form have an advantage in grazed landscapes (Diaz et al., 2007, Evju et al., 2010), and this may be even more prominent in forest ecosystems as large herbivores may selectively utilize taller understory plants, especially during wintertime (Danell et al., 2003).

Herbivory may thus increase the total species richness of the lower growing non-woody species if herbivores selectively decrease woody abundance and richness (c.f. Paine 1966).

Surprisingly few studies have addressed the effect of herbivory on plant diversity by large free-ranging herbivores in natural systems within long gradients of herbivory disturbance (but see Stewart et al., 2006, 2009). For example, in reviews of the intermediate disturbance hypothesis (Mackey and Currie 2001, Shea et al., 2004, Svensson et al., 2012) the few studies on large animal herbivory deals with livestock in grasslands. Experimental simulation of full length gradients of herbivory intensity may be challenging, because it is difficult to obtain reliable data on intensity gradients of wild animal herbivory. In this study we used ten years of monitored herbivory intensity by the most numerous wild ungulate, red deer, in the most common forest type in Norway, as model system to examine present spatial patterns in plant species richness. We validated the herbivory gradient approach using experimental exclusion data. The effect on community composition is likely to be an effect of herbivory intensity which may filter species according to their adaptations to herbivory and competition (Augustine & McNaughton 1998; Suzuki et al., 2013). Specifically, we asked whether variation in red deer herbivory intensity could explain the variation in plant species richness, both in total and for functional groups of this forest ecosystem (e.g. trees, dwarf-shrubs, various field plant groups and bryophytes). The results have the potential to guide ecosystem management of such large free-ranging grazers. We expected that 1) overall species richness will show a unimodally peaked-relationship with disturbance intensity, and 2) richness within low-growing functional groups will have a positive response to herbivory in contrast to the richness within the taller-growing woody groups.

2. Material and Methods

2.1. Study area and study design
The study was carried out in 2001 to 2011 on the 11 km² island Svanøy at the western coast of Norway (61°30N, 5°05E). Svanøy is situated in the boreonemoral zone and old-growth forest vegetation dominated by pine (Pinus sylvestris) and an understory dominated by Ericacea dwarf-shrubs covers most of the island. Twelve study sites were located within old-growth pine-bilberry forest, according to a vegetation map (Skogen & Lunde 1997), and spread across the island on elevations from 20 to 140 m during wintertime 2000-2001 (see also Hegland et al., 2005 for more details). The study sites can be viewed as communities and all sites as a meta-community. A macroplot of 9x9 m was located at each site adjacent to a deer exclosure (see also model validation). We randomly placed seven permanent plots of 1 × 1 m on flat ground at least 0.5 m from the closest tree within the macroplot. Tree height and canopy openness showed relatively little variation between sites (pers. obs.). The sites experienced herbivory intensities varying from very low to extremely high (Fig. 1; see also Data collection). Ten of the sites were situated in forest with wild free-ranging red deer and data suggest they cover a natural variation from very low to naturally high herbivory intensities (see 2.2.). Two sites were located within the forest areas of a deer farm representing deer densities at artificially high levels that would represent a population level beyond carrying capacity because these animals receive supplementary feeding. Thus, our data represents a gradient in herbivory intensity.

Red deer, Cervus elaphus, is a forest-dwelling mixed-feeder ungulate species. It has been speculated that the period from ca. 1995 until today has experienced the greatest post-glacial densities of red deer in Norway. In this period 20 000 to 40 000 deer has been harvested nationally per year (e.g. Statistics Norway 2009) corresponding to > 1 deer harvested per km² forest area in the study county Sogn og Fjordane (Solberg et al., 2010). The dense population of red deer at Svanøy is likely to be representative for most areas in western Norway (Hegland et al., 2010). Assuming that about 20 % of the population is culled each year implies that deer numbers are on average 5-6 animals per km² productive forest area in the county. Absolute densities of forest-dwelling cervids are difficult to accurately establish and population estimates used for management of wild-ranging forest ungulates in Norway are generally index-based (e.g., Mysterud et al., 2007).

2.2. Data collection

We recorded plant species richness in each of the seven permanent plots per macroplot in 2011, except for understory trees (20-300 cm) which were recorded on the 9x9 m macroplot-level. All plant species in the understory layer were sampled: 1) understory trees (ca. 20-300
cm); 2) tree juveniles (trees < 20 cm) 3) dwarf-shrubs (here Ericacea); 4) forbs; 5) graminoids (Poaceae, Juncaceae and Cyperaceae); 6) ferns; 7) mosses and 8) liverworts.

We recorded red deer browsing on the dominant winter forage plant bilberry, Vaccinium myrtillus, and used this as basis for estimating herbivory intensity of red deer. Bilberry is highly abundant in boreal forests, it is intermediately preferred by red deer (Mysterud et al., 2010), but both individual plants and populations survive rather well even at high intensities of browsing and accordingly bilberry is a good indicator plant for herbivory intensity (Hegland et al., 2010; Mysterud et al., 2010). Although the level of bilberry browsing largely estimate autumn-to-spring herbivory, red deer in Norway has been found to use the winter ranges on average eight months of the year (Bischof et al., 2013), and browsing on bilberry correlate strongly with other indices of population densities such as winter-spring pellet counts or autumn harvest data (Mysterud et al., 2010). We therefore believe that level of bilberry browsing is a suitable proxy for the herbivory intensity at individual sites.

As changes in plant species assemblages occur at relatively slow pace in these northern forest systems, we need to monitor herbivory intensity on a sufficient time scale. We performed sampling in June of 2001, 2006, and 2011 within the permanent plots to acquire a measure of red deer herbivory intensity that included a timeframe that could result in present-time plant community composition. The browsing level was measured on a scale from 0 to 4; 0: no browsing, 1: > 0 to 24.9% of annual shoots clipped, 2: 25 to 49.9% of annual shoots clipped, 3: 50 to 74.9% of annual shoots clipped, and 4: >75% of annual shoots clipped. In 2001 five randomly selected bilberry ramets in each of the seven permanent plots per macroplot was measured, but because of time constraints we only sampled three ramets in a random selection of four of the seven permanent plots per macroplot in 2006 and three ramets in each of the seven permanent plots per macroplot in 2011. The varying sampling effort did not influence the variance strongly (SD: 0.16 in 2001, 0.18 in 2006 and 0.25 in 2011). We also obtained biometric measures (see Hegland et al., 2005 for details) of the sample ramets. The herbivory intensity was calculated as the browsing level divided on the plant height. To further confirm that this index reflected red deer herbivory intensity, we correlated the variable with the frequency of faeces groups sampled in 2001, 2006 and 2011 in 100 1-m² square plots randomly distributed within a radius of 100 m around each site. There was a strong association (r = 0.94, N = 12, p < 0.001) between these independent measures.

Although these variables were obtained on different scales the correlation strengthens the assumption that the herbivory intensity could be described using the browsing level on bilberry ramets divided by plant height. The measure has the advantage that it was obtained at
the same scale as plant species richness and is more robust than the density indicator represented by faeces as it is not confounded by, for example, weather dependent decaying rates (e.g. Putman 1994). Figure 1 shows examples of the visual difference among sites with high, intermediate and low herbivory intensities.

2.3. Data analysis and model validation

To investigate the relationships between plant species richness and herbivory intensity we used linear mixed effects models. Plots were nested within sites and accounted for in the random effects using R 2.15.0 (R Development Core Team 2012), library nlme (Pinheiro et al 2011) and lme4 (Bates et al 2011). To test whether relationships between herbivory intensity and plant richness showed a unimodal peak or were linear within the studied herbivory gradient we first included a quadratic component of the mean herbivory intensity index (at site level) before we tested a linear relationship and compared models using AIC-values. We used total plant species richness and richness within functional groups (at plot level) as response variables. In the total plant richness model understory trees (< 20 cm) were not included as they were sampled on site level. The understory tree model was hence not nested. As the red deer farm sites represent artificially intensive herbivory we also ran models without these sites when quadratic models were selected to test whether quadratic relationships were merely caused by these extreme disturbance conditions.

In studies that utilise natural gradients as ours we must minimise and control for potential confounding effects deriving merely from herbivore preferences rather than herbivory effects of red deer. First, the potential preference effects were minimised through study design; study sites were placed in a geographically restricted area (one island), within one main vegetation type (pine-bilberry forest), and within a limited elevation gradient (20-140m). Investigating relationships across multiple scales can result in erroneous correlations (Crawley 2007), and we believe preference effects could have acted stronger if our study had sampled on coarser scales, i.e. in larger areas, across vegetation types and, for example, between sites at low and high altitude. Second, we validated the herbivory intensity models with analyses from an exclosure based temporal data-set on species richness from the same study area. In every site a 10x10m exclosure was established during winter 2001 together with the herbivory macroplots that are the main study subjects in this study. We established a 9x9 m macroplot and permanent plots corresponding to herbivory areas within the exclosures. We sampled plant species richness accordingly in June 2001, 2006 and 2011. The change in species richness during time between herbivory plots and exclosure plots was addressed by means of
linear mixed effects models where the nested design (site, macroplot and plot) was addressed in the random effects. Standard models were performed with the herbivory plots in 2001 as reference. The interaction between time and treatment tell us whether the change under ceased herbivory was different than in the herbivory controls. If the temporal change was consistent with the findings along the spatial gradient of herbivory intensity, we concluded that the spatial model was validated. For example, to validate a statistical positive or a unimodally peaked herbivory - richness relationship, the temporal change should be statistically positive in herbivory plots relative to exclosure plots.

3. Results

3.1. Herbivory intensity-plant richness relationships

The total species richness increased significantly with increasing herbivory intensity within natural levels until it declines slightly under the artificially high densities of red deer (Fig. 2 and Table 1). If we visually inspect figure 2 we can see that the decline in richness under high red deer herbivory intensities are quite small compared to the increase under natural levels of herbivory. Models without farm data showed positive linear relationship between herbivory intensity and plant species richness (Coef=50.5; SE=14.2, DF= 60, 8; P=0.007).

When we analysed the functional groups separately only the richness of forbs and ferns resulted in significant peaked quadratic models (Fig. 3. d, f; Table 1). This was merely because of the decline under experimentally very high herbivory intensities, which is underlined by the positive linear relationships found between herbivory intensity and forb richness (Coef=21.9; SE=8.4, DF= 60, 8; P=0.03) and fern richness (Coef=22.3; SE=8.5, DF= 60, 8; P=0.008) when excluding farm sites. Richness of trees and dwarf-shrubs showed negative linear responses along the full herbivory intensity gradient (Fig 3 a, c; Table 1), whereas richness of tree-juveniles, graminoids and mosses showed positive linear responses (Fig. 3 b, e, g; Table 1) to the herbivory intensity. Liverworts showed no significant richness response to red deer herbivory intensity (Fig. 3 h; Table 1).

3.2. Model validation

In general our herbivory intensity-plant richness models were validated by the temporal exclosure-based models (Table 1, Fig. A1), i.e. the temporal change in plant richness in herbivore vs. exclosure plots was largely consistent with the findings along the spatial gradient of herbivory intensity. For example, in the temporal models the overall richness
declined slightly when red deer herbivory ceased whereas it increased slightly under continuous herbivory. Most other models (i.e. for different functional groups) were also validated, either by showing a temporal similar response under ceased herbivory or under continuously red deer herbivory (Table 1, Fig. A1 for details). The only functional groups where the findings of spatial gradient models and temporal exclosure models did not directly link to each other was for richness of tree juveniles (spatial: positive linear relationship; temporal: no significant changes) and liverworts (spatial: no significant relationship; temporal: positive effects of ceased herbivory). Both of these functional groups showed only a statistical weak or no relationship, respectively, between herbivory intensity and functional species richness.

4. Discussion

The herbivory intensity-plant richness relationship followed a unimodally peaked curved, but plant richness was lower only at forest sites with artificially high red deer populations (i.e. the local deer farm). As such, the result presented here shows mainly a positive overall effect of red deer herbivory on the understory species richness of the old-growth pine-bilberry forest. The combined design attributes (i.e. restricted geographic and ecological range of the study and the relative long term monitoring) along with the model validation (i.e. using temporal models to confirm the spatial models) strengthen our conclusions and minimize the potential confounding effects of herbivore preference. We believe the strength of our study is that we have used a full-length gradient of herbivory, spanning from very low to very high herbivory intensity, to explain the effects of large animal herbivory on species richness in terrestrial non-cultivated ecosystem. Such gradient approaches has earlier been used to show that community biomass production may peak along herbivory intensity gradients (Stewart et al., 2006), which again may influence the plant diversity patterns (Stewart et al., 2009).

The unimodally peaked signal in the herbivory-richness relationships was, however, not very strong and dependent on artificial high disturbance levels in our study. In general, the disturbance from free-ranging large herbivores is seldom severe enough to kill significant parts of adult plants. When disturbance becomes substantial, such as in the deer farm in our study, colonising plants are predated at early stage before they are able to tolerate biomass loss. Thus space and safe sites required for plant colonisation (e.g. Hegland et al., 2001) are not present simultaneously in these forest communities. One may speculate that the lack of these requirements is one reason why so few studies have published verifications of the intermediate disturbance hypothesis in forests with disturbance from free-ranging ungulates.
(e.g. Mackey & Currie 2001; Svensson et al., 2012). Also, in forest communities with greater diversity of tree species than our study system the plant diversity response may be more pronounced because large herbivore disturbance has the clearest impact on this structural layer (Connell 1978, Molino & Sabatier 2001). For example, the maximum number of tree species at any site at any time in the study sites during 2001-2011 was only seven. In our study system we have sampled all understory plant species, but most ungulate-plant interaction studies do not include the bryophytes (i.e. mosses and liverworts) in the species recordings but as a cover estimate (e.g. Singer and Schoenecker 2003, Tanentzap et al., 2009).

A simple exercise of investigating artefacts of sampling effort or researcher choices is to examine how removing bryophytes from the dataset affects the overall herbivory-richness relationship. Mixed effect modelling then resulted in a negative linear disturbance-richness relationship (Coef= -11.3; SE=4.5; DF= 72,10; P=0.032). Thus, if the ecological important group of bryophytes had not been recorded in this study, the ecological, and hence management interpretation of our analysis could have been the opposite in that red deer herbivory reduce plant richness in the forest understory.

There were distinct differences in functional group responses. Five of eight functional groups showed linear relationships between species richness and herbivory intensity (three positive and two negative) and one functional group showed no relationship. Only two functional groups showed a quadratic relationship when analysed separately, but these unimodal relationships were caused strictly by the artificially high herbivory intensities at farm sites and showed positive linear relationships when analysed within the natural gradient only (see 3.1.). Overall, the herbivory-richness responses of the different species groups fitted our expectations based on findings from meta-studies and literature reviews (Hester et al., 2006, Diaz et al., 2007, Skarpe & Hester 2008). Low-growing groups such as forbs, grasses and mosses increased in richness in contrast to woody dwarf shrubs and trees. This is in line with Evju et al., (2010) who showed that low stature species profited from ungulate grazing in a mountain area in Scandinavia. In other studies of red deer impact on plant diversity (Woodward et al., 1994, Schreiner et al., 1996), specific responses of plant groups or growth forms have tended to vary and be less predictable and few have studied functional group responses along gradients of disturbance. The detailed sampling of all understory plant species over a considerable time period (sensu Mackey & Currie 2001) may also be a key to why our results fitted expectations better than many other similar studies. The difference in response to herbivory intensity found between understory and juvenile trees (Fig. 3a and b; i.e. complete opposite relationships) may indicate that deer herbivory have opposite effects on
recruitment and survival of trees. These results also point towards the driving mechanism behind the red deer herbivory effects on plant richness. Periodic heavy grazing and browsing may increase the recruitment of trees through increased germination caused by reduced competition for light and space between the herbaceous layer and trees (e.g. Riginos 2009). Studies from Białowieża forest in Poland underpin that fluctuations in ungulate density may drive tree recruitment patterns (Kuijper et al., 2010) and it is also known from agricultural systems that rotational stock management, varying the intensity of large herbivore disturbance, may increase overall biodiversity (Sjödin et al., 2008, Farruggia et al., 2012).

When dominant plants are preferred by ungulates, plant diversity is expected to increase, whereas diversity may decrease if herbivory-tolerant or resistant species become dominant as a result of herbivory (Côté et al., 2004, Hester et al., 2006). The key mechanism to the overall increase in plant species richness along the red deer herbivory intensity gradient in our study is thus likely the reduction of dominant woody vegetation that increases resource and substrate availability at the benefit of a richer low-growing species assemblage.

A starting point to operationalize the knowledge from gradient approaches such as ours into management guidelines is to examine when key variables start to decline. As the studied gradient has a gap between the highest natural and artificial levels of herbivory intensity we cannot be conclusive in this study. However, the highest herbivory intensity found in unfenced forest concurs with 56% of the current shoots of bilberry browsed and a bilberry plant height of 11.7 cm in 2011 (vs. 9% and 14 cm, respectively, in the site with the lowest herbivory intensity). At this level of red deer herbivory, species richness in our study system was not reduced and we may therefore speculate that the herbivory intensity must be greater to cause richness reduction in these northern forest ecosystems. Holechek et al. (1999) found that heavy livestock grazing was equivalent to 57% biomass removal. Although these measures are not directly comparable, i.e. biomass vs. frequency of shoots browsed in our study, the comparison may point towards a resilient study system that can tolerate quite high herbivory intensities. According to the analysis of Mysterud et al. (2010) a browsing frequency on bilberry of ca. 50% is equal to densities in areas were 2 to 3 red deer/km² are harvested, whereas the average harvest at the whole island in our study was ca. 1.8 deer/km² (J.T.Solheim, pers comm.). In conclusion, the herbivory intensities that occur in areas were about 50% of bilberry shoots are browsed or 2-3 red deer/km² are harvested appear largely to be positive for understory plant species richness. Red deer densities are rarely at such high levels in Norway when assessed at the same spatial scale as our study island (i.e., 10 km²; Statistics Norway 2013).
4.1. Conclusions and implications for management

The relative long-term (10-years) nature of the study presented here suggests that the increasing densities of free-ranging red deer in northern forest ecosystems may not necessarily adversely affect the plant richness aspect of biodiversity. The old-growth forest understory species richness at Svanøy, western Norway, increased along with greater deer densities except at artificial high levels. Considering the extreme high herbivory intensity in the deer farm sites, the main message from our study is that within the densities and timeframes studied here moderate to relatively high red deer densities lead to greater understory species richness than low deer densities. Based on this particular study, and comparing herbivory intensity and harvest data with literature and statistics from other areas, we may conclude that the red deer densities currently found in Norway rarely reach levels that reduce plant species richness.

Richness of several individual functional groups showed a positive response to increased herbivory intensities. If management goals imply targeting specific groups of species this study suggest that intense herbivory is favourable mainly for richness of forbs, grasses and mosses whereas low herbivory intensities are required, spatially or temporally, for preserving the richness of woody species. An important lesson from the functional group approach is that the herbivory-richness relationship may strongly be influenced by which functional groups are sampled. Our results therefore call for additional long-term studies including other sessile groups such as fungi and adult trees, as well as multitrophic aspects.

Acknowledgements


References


Figure legends:

**Fig. 1.** Photographs showing from left to right: an intensive herbivory farm-forest site with the exclosed macroplot as background, a typical forest site with moderate herbivory intensity including a permanent 1x1 m plot for species recordings, and a low-intensity herbivory forest site.

**Fig. 2.** The relationship between red deer herbivory intensity index and total species richness of the forest understory at Svanøy, western Norway. Line is shown for significant relationships of the selected model (quadratic), but do not take the random effects from the mixed effects modelling into account.

**Fig. 3.** The relationship between red deer herbivory intensity index and the species richness of the functional groups (a-h) of the forest understory at Svanøy, western Norway. Lines are
shown for significant relationships of the selected models (linear vs. quadratic), but do not take the random effects from the mixed effects modelling into account.

Appendix

Figure A. 1

Plant richness, in total and for functional groups of the forest understory at Svanøy, western Norway, during 2001, 2006 and 2011 in herbivore and exclosure forest plots. Values are mean ± 1 SE (see methods for statistical procedures). These experimental exclosure-based models were used to validate the herbivory intensity-plant richness models. Example of model validation: to validate a statistical positive or a unimodally peaked herbivory -richness relationship, the temporal change should be statistically positive in herbivore plots relative to exclosure plots. In this sense all gradient models were supported by experimental models except for tree-juveniles and liverworts, which showed weak or no statistical significance in gradient models, respectively. See methods for statistical procedures, Table 1 for all statistical testing including model validation, and Figure 2 and 3 for the herbivory intensity-plant richness relationships.
Table 1. Linear mixed effects models that explained plant species richness as a function of red deer herbivory intensity and herbivore exclosures (experimental validation models)

<table>
<thead>
<tr>
<th>Richness variable</th>
<th>Predictor</th>
<th>Coef</th>
<th>SE</th>
<th>DF</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total richness</td>
<td>Intercept</td>
<td>9.71</td>
<td>1.75</td>
<td>72</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Herbivory intensity</td>
<td>86.99</td>
<td>24.46</td>
<td>9</td>
<td>0.006</td>
</tr>
<tr>
<td></td>
<td>Herbivory intensity²</td>
<td>-171.36</td>
<td>57.39</td>
<td>9</td>
<td>0.015</td>
</tr>
<tr>
<td>Trees (20-300 cm)</td>
<td>Intercept</td>
<td>3.3698</td>
<td>0.45</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Herbivory intensity</td>
<td>-9.479</td>
<td>2.63</td>
<td>0.005</td>
<td></td>
</tr>
<tr>
<td>Tree juveniles</td>
<td>Intercept</td>
<td>-0.02</td>
<td>0.17</td>
<td>0.923</td>
<td></td>
</tr>
<tr>
<td>(poisson)</td>
<td>Herbivory intensity</td>
<td>1.78</td>
<td>0.86</td>
<td>0.038</td>
<td></td>
</tr>
<tr>
<td>Dwarf-shrubs</td>
<td>Intercept</td>
<td>1.16</td>
<td>0.12</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>(poisson)</td>
<td>Herbivory intensity</td>
<td>-1.69</td>
<td>0.79</td>
<td>0.033</td>
<td></td>
</tr>
<tr>
<td>Forbs</td>
<td>Intercept</td>
<td>0.80</td>
<td>1.31</td>
<td>72</td>
<td>0.544</td>
</tr>
<tr>
<td></td>
<td>Herbivory intensity</td>
<td>44.60</td>
<td>18.09</td>
<td>9</td>
<td>0.036</td>
</tr>
<tr>
<td></td>
<td>Herbivory intensity²</td>
<td>-105.17</td>
<td>42.16</td>
<td>9</td>
<td>0.034</td>
</tr>
<tr>
<td>Graminoids</td>
<td>Intercept</td>
<td>0.53</td>
<td>0.12</td>
<td>4.40</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>(poisson)</td>
<td>Herbivory intensity</td>
<td>2.09</td>
<td>0.59</td>
<td>3.51</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Ferns</td>
<td>Intercept</td>
<td>-3.32</td>
<td>1.06</td>
<td>0.002</td>
<td></td>
</tr>
<tr>
<td>(binomial)</td>
<td>Herbivory intensity</td>
<td>39.83</td>
<td>13.97</td>
<td>0.004</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Herbivory intensity²</td>
<td>-98.93</td>
<td>32.78</td>
<td>0.003</td>
<td></td>
</tr>
<tr>
<td>Mosses</td>
<td>Intercept</td>
<td>4.25</td>
<td>0.58</td>
<td>72</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Herbivory intensity</td>
<td>11.92</td>
<td>3.36</td>
<td>10</td>
<td>0.005</td>
</tr>
<tr>
<td>Liverworts</td>
<td>Intercept</td>
<td>-1.15</td>
<td>2.03</td>
<td>0.570</td>
<td></td>
</tr>
<tr>
<td>(binomial)</td>
<td>Herbivory intensity</td>
<td>-11.69</td>
<td>16.10</td>
<td>0.468</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Experimental validation model: herbivore exclosure</th>
<th>Predictor</th>
<th>Coef</th>
<th>SE</th>
<th>DF</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total richness</td>
<td>Intercept</td>
<td>15.61</td>
<td>0.67</td>
<td>332</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Herbivore 06 vs 01</td>
<td>Herbivore 06 vs 01</td>
<td>0.27</td>
<td>0.27</td>
<td>332</td>
<td>0.318</td>
</tr>
<tr>
<td>Herbivore 11 vs 01</td>
<td>Herbivore 11 vs 01</td>
<td>0.88</td>
<td>0.27</td>
<td>332</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Main effect 01</td>
<td>Main effect 01</td>
<td>0.16</td>
<td>0.48</td>
<td>332</td>
<td>0.287</td>
</tr>
<tr>
<td>Exclosure 06 vs 01</td>
<td>Exclosure 06 vs 01</td>
<td>-1.02</td>
<td>0.39</td>
<td>332</td>
<td>0.008</td>
</tr>
<tr>
<td>Exclosure 11 vs 01</td>
<td>Exclosure 11 vs 01</td>
<td>-1.19</td>
<td>0.39</td>
<td>332</td>
<td>0.002</td>
</tr>
<tr>
<td>Trees (20-300 cm)</td>
<td>Intercept</td>
<td>2.94</td>
<td>0.25</td>
<td>332</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Herbivore 06 vs 01</td>
<td>Herbivore 06 vs 01</td>
<td>-0.19</td>
<td>0.07</td>
<td>332</td>
<td>0.007</td>
</tr>
<tr>
<td>Herbivore 11 vs 01</td>
<td>Herbivore 11 vs 01</td>
<td>-0.35</td>
<td>0.08</td>
<td>332</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Main effect 01</td>
<td>Main effect 01</td>
<td>0.24</td>
<td>0.15</td>
<td>155</td>
<td>0.027</td>
</tr>
<tr>
<td>Exclosure 06 vs 01</td>
<td>Exclosure 06 vs 01</td>
<td>-0.06</td>
<td>0.22</td>
<td>797</td>
<td>0.797</td>
</tr>
<tr>
<td>Exclosure 11 vs 01</td>
<td>Exclosure 11 vs 01</td>
<td>0.02</td>
<td>0.2</td>
<td>914</td>
<td></td>
</tr>
<tr>
<td>Tree juveniles</td>
<td>Intercept</td>
<td>3.70</td>
<td>0.38</td>
<td>332</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>(poisson)</td>
<td>Herbivore 06 vs 01</td>
<td>0.12</td>
<td>0.10</td>
<td>332</td>
<td>0.234</td>
</tr>
<tr>
<td>Herbivore 11 vs 01</td>
<td>Herbivore 11 vs 01</td>
<td>0.11</td>
<td>0.10</td>
<td>332</td>
<td>0.299</td>
</tr>
<tr>
<td>Main effect 01</td>
<td>Main effect 01</td>
<td>0.10</td>
<td>0.10</td>
<td>332</td>
<td>0.348</td>
</tr>
<tr>
<td>Exclosure 06 vs 01</td>
<td>Exclosure 06 vs 01</td>
<td>-0.18</td>
<td>0.15</td>
<td>332</td>
<td>0.227</td>
</tr>
<tr>
<td>Exclosure 11 vs 01</td>
<td>Exclosure 11 vs 01</td>
<td>-0.30</td>
<td>0.15</td>
<td>332</td>
<td>0.048</td>
</tr>
<tr>
<td>Dwarf-shrubs</td>
<td>Intercept</td>
<td>3.50</td>
<td>0.11</td>
<td>0.001</td>
<td></td>
</tr>
<tr>
<td>(poisson)</td>
<td>Herbivore 06 vs 01</td>
<td>0.70</td>
<td>0.11</td>
<td>332</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Herbivore 11 vs 01</td>
<td>Herbivore 11 vs 01</td>
<td>0.12</td>
<td>0.10</td>
<td>332</td>
<td>0.234</td>
</tr>
<tr>
<td>Main effect 01</td>
<td>Main effect 01</td>
<td>0.11</td>
<td>0.10</td>
<td>332</td>
<td>0.299</td>
</tr>
<tr>
<td>Exclosure 06 vs 01</td>
<td>Exclosure 06 vs 01</td>
<td>-0.18</td>
<td>0.15</td>
<td>332</td>
<td>0.227</td>
</tr>
<tr>
<td>Exclosure 11 vs 01</td>
<td>Exclosure 11 vs 01</td>
<td>-0.30</td>
<td>0.15</td>
<td>332</td>
<td>0.048</td>
</tr>
<tr>
<td>Graminoids</td>
<td>Intercept</td>
<td>1.34</td>
<td>0.57</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td>(poisson)</td>
<td>Herbivore 06 vs 01</td>
<td>1.91</td>
<td>0.58</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Herbivore 11 vs 01</td>
<td>Herbivore 11 vs 01</td>
<td>3.00</td>
<td>0.87</td>
<td>0.735</td>
<td></td>
</tr>
<tr>
<td>Main effect 01</td>
<td>Main effect 01</td>
<td>0.41</td>
<td>0.85</td>
<td>0.629</td>
<td></td>
</tr>
<tr>
<td>Exclosure 06 vs 01</td>
<td>Exclosure 06 vs 01</td>
<td>-1.72</td>
<td>0.84</td>
<td>0.04</td>
<td></td>
</tr>
<tr>
<td>Exclosure 11 vs 01</td>
<td>Exclosure 11 vs 01</td>
<td>-2.24</td>
<td>0.24</td>
<td>332</td>
<td>0.327</td>
</tr>
<tr>
<td>Mosses</td>
<td>Intercept</td>
<td>5.46</td>
<td>0.44</td>
<td>332</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Herbivory 06 vs 01</td>
<td>Herbivore 06 vs 01</td>
<td>-0.02</td>
<td>0.17</td>
<td>332</td>
<td>0.89</td>
</tr>
<tr>
<td>Herbivore 11 vs 01</td>
<td>Herbivore 11 vs 01</td>
<td>0.42</td>
<td>0.17</td>
<td>332</td>
<td>0.016</td>
</tr>
<tr>
<td>Main effect 01</td>
<td>Main effect 01</td>
<td>-0.15</td>
<td>0.23</td>
<td>155</td>
<td>0.5</td>
</tr>
<tr>
<td>Exclosure 06 vs 01</td>
<td>Exclosure 06 vs 01</td>
<td>-0.54</td>
<td>0.24</td>
<td>332</td>
<td>0.028</td>
</tr>
<tr>
<td>Exclosure 11 vs 01</td>
<td>Exclosure 11 vs 01</td>
<td>-0.24</td>
<td>0.24</td>
<td>332</td>
<td>0.327</td>
</tr>
<tr>
<td>Liverworts</td>
<td>Intercept</td>
<td>-6.40</td>
<td>1.25</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>(binomial)</td>
<td>Herbivore 06 vs 01</td>
<td>0.30</td>
<td>0.73</td>
<td>0.685</td>
<td></td>
</tr>
<tr>
<td>Herbivore 11 vs 01</td>
<td>Herbivore 11 vs 01</td>
<td>2.75</td>
<td>0.75</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Main effect 01</td>
<td>Main effect 01</td>
<td>-3.60</td>
<td>1.70</td>
<td>0.035</td>
<td></td>
</tr>
<tr>
<td>Exclosure 06 vs 01</td>
<td>Exclosure 06 vs 01</td>
<td>3.54</td>
<td>1.74</td>
<td>0.042</td>
<td></td>
</tr>
<tr>
<td>Exclosure 11 vs 01</td>
<td>Exclosure 11 vs 01</td>
<td>3.62</td>
<td>1.77</td>
<td>0.041</td>
<td></td>
</tr>
</tbody>
</table>

a) Distribution of selected models was consistent between gradient and exclosure models for functional groups except for dwarf-shrubs where exclosure model could be analysed with a normal distribution model.

Example of model validation: if values in exclosure models are increasing for herbivore vs. exclosure plots this is consistent with findings of both positive linear models and quadratic peaked spatial models. All gradient models were validated by exclosure models except for tree juveniles and liverworts (see appendix for details on model validation).