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

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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 enclosure 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

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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 (Myrsetrud et al., 2010) and using data such as 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; Myrsetrud 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 (Myrsetrud 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 would on abundance would, in addition to moving beyond the scope of this paper, inflict 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 Myrsetrud 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 enclosure 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 comments 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 enclosure-based models (Table 1, Fig. A1), i.e. the temporal change in plant richness in open vs. enclosed 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 enclosure forest plots. Values are mean \pm 1 SE (see methods for statistical procedures). These experimental enclosure-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 enclosure plots....." which hopefully reads better than the previous version.

Line 220 change decline to declines ok

Line 232 -I think you are referring to Fig 3 h ok

Line 259-260 - 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 296 - there is no Figure 5 ? Maybe this is supposed to be figure 3? ok

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

Line 301 underpins should be underpin ok

Line 313-315 - 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 where 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

1 **Old-growth forest floor richness increases with red deer herbivory intensity**

2

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18 **ABSTRACT**

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

42

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

44

45 **1. Introduction**

46 Globally, herbivory by large grazers is one of the most important biotic disturbance types
47 that influence community composition and structure (Diaz et al., 2007) and in many cases it is
48 a disturbance type that is influenced by management decisions. In northern forest systems
49 wild free-ranging ungulates are often a major determinant of plant community structure,
50 composition and dynamics (Pastor et al., 1988, Suzuki et al., 2013) and populations can be
51 partly controlled by hunting based management. The populations of large, wild ungulates

52 such as red deer (*Cervus elaphus*) and moose (*Alces alces*) have expanded and grown rapidly
53 for several decades in Scandinavia, Europe and Northern America, often to concern of
54 conservationists (Côte et al., 2004). The increasing population densities may create a
55 disturbance regime for northern forest ecosystems to which they are not evolutionary adapted
56 (sensu Milchunas et al., 1988). On the other hand, historical population levels are largely
57 unknown, but the increasing cervid densities have mainly been a response to lower livestock
58 numbers in forested areas, increasing forest cover and improved hunting management during
59 the last millennia (e.g. Putman et al., 2011). Whether the present population densities are
60 normal or not there is a current need for operational knowledge on how wild, free-ranging
61 ungulates affect northern forest community composition.

62 Studying ecological interactions along gradients of environmental stress represent a
63 powerful way to develop knowledge under realistic ecological conditions as well as
64 operational guidelines in nature management (e.g. Brooker et al., 2006; Stewart et al. 2006,
65 2009). One approach to this has been by applying the intermediate disturbance hypothesis to a
66 given disturbance-richness relationship (IDH; e.g. Grime 1973; Connell 1978). The
67 hypothesis predicts that the richness of species should be greatest when the intensity,
68 frequency or size of a disturbance is at intermediate level (Svensson et al., 2012; Fox 2013).
69 Too much disturbance means that long-lived species will not survive and too little disturbance
70 results in competitive exclusion of pioneer species (e.g. Shea et al., 2004). The hypothesis has
71 been criticized for low precision in explaining diversity patterns and because of its relative
72 character (Mackey & Currie 2001), i.e. what is intermediate? Nevertheless, the hypothesis can
73 act as a theoretical background to a gradient approach in ecology dealing with herbivory, both
74 as it introduces herbivory as a disturbance as well as predicting that species richness will
75 follow a unimodally peaked relationship with, for example, herbivory intensity. A recent
76 review showed that the intermediate disturbance hypothesis was indeed successful in
77 predicting disturbance-diversity relationships when, according to the original hypothesis,
78 testing is done with richness and not abundance based diversity indices as response variable
79 (Svensson et al., 2012).

80 Many other disturbances that influence plant communities, such as storms and fires, are
81 non-selective (Laliberté et al., 2013) and outside the direct influence of humans. On the
82 contrary, herbivory by domestic and wild herbivores are both selective (Augustine &
83 McNaughton 1998) and among those ecological factors that can partly be controlled by
84 managers. Therefore, herbivory disturbance by large herbivores may have complex influence
85 on community composition and can interact with different parts of the species pool in

86 contrasting ways. Which plant traits are advantageous in a given plant community is most
87 often an interplay between tolerance and avoidance (Augustine and McNaughton 1998),
88 which may also change competitive interactions among plants (Hester et al., 2006). Most
89 studies show that both the richness and abundance of woody vegetation may decline when
90 herbivory from ungulates becomes more intense (reviewed by Gill 2006). Also, plants with a
91 short growth form have an advantage in grazed landscapes (Diaz et al., 2007, Evju et al.,
92 2010), and this may be even more prominent in forest ecosystems as large herbivores may
93 selectively utilize taller understory plants, especially during wintertime (Danell et al., 2003).
94 Herbivory may thus increase the total species richness of the lower growing non-woody
95 species if herbivores selectively decrease woody abundance and richness (c.f. Paine 1966).

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

116

117 **2. Material and Methods**

118 *2.1. Study area and study design*

119 The study was carried out in 2001 to 2011 on the 11 km² island Svanøy at the western
120 coast of Norway (61°30N, 5°05E). Svanøy is situated in the boreonemoral zone and old-
121 growth forest vegetation dominated by pine (*Pinus sylvestris*) and an understory dominated by
122 Ericacea dwarf-shrubs covers most of the island. Twelve study sites were located within old-
123 growth pine-bilberry forest, according to a vegetation map (Skogen & Lunde 1997), and
124 spread across the island on elevations from 20 to 140 m during wintertime 2000-2001 (see
125 also Hegland et al., 2005 for more details). The study sites can be viewed as communities and
126 all sites as a meta-community. A macroplot of 9x9 m was located at each site adjacent to a
127 deer enclosure (see also model validation). We randomly placed seven permanent plots of 1 ×
128 1 m on flat ground at least 0.5 m from the closest tree within the macroplot. Tree height and
129 canopy openness showed relatively little variation between sites (pers. obs.). The sites
130 experienced herbivory intensities varying from very low to extremely high (Fig. 1; see also
131 Data collection). Ten of the sites were situated in forest with wild free-ranging red deer and
132 data suggest they cover a natural variation from very low to naturally high herbivory
133 intensities (see 2.2.). Two sites were located within the forest areas of a deer farm
134 representing deer densities at artificially high levels that would represent a population level
135 beyond carrying capacity because these animals receive supplementary feeding. Thus, our
136 data represents a gradient in herbivory intensity.

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

148

149 2.2. Data collection

150 We recorded plant species richness in each of the seven permanent plots per macroplot in
151 2011, except for understory trees (20-300 cm) which were recorded on the 9x9 m macroplot-
152 level. All plant species in the understory layer were sampled: 1) understory trees (ca. 20-300

153 cm); 2) tree juveniles (trees < 20 cm) 3) dwarf-shrubs (here Ericaceae); 4) forbs; 5) graminoids
154 (Poaceae, Juncaceae and Cyperaceae); 6) ferns; 7) mosses and 8) liverworts.

155 We recorded red deer browsing on the dominant winter forage plant bilberry, *Vaccinium*
156 *myrtillus*, and used this as basis for estimating herbivory intensity of red deer. Bilberry is
157 highly abundant in boreal forests, it is intermediately preferred by red deer (Mysterud et al.,
158 2010), but both individual plants and populations survive rather well even at high intensities
159 of browsing and accordingly bilberry is a good indicator plant for herbivory intensity
160 (Hegland et al., 2010; Mysterud et al., 2010). Although the level of bilberry browsing largely
161 estimate autumn-to-spring herbivory, red deer in Norway has been found to use the winter
162 ranges on average eight months of the year (Bischof et al., 2013), and browsing on bilberry
163 correlate strongly with other indices of population densities such as winter-spring pellet
164 counts or autumn harvest data (Mysterud et al., 2010). We therefore believe that level of
165 bilberry browsing is a suitable proxy for the herbivory intensity at individual sites.

166 As changes in plant species assemblages occur at relatively slow pace in these northern
167 forest systems, we need to monitor herbivory intensity on a sufficient time scale. We
168 performed sampling in June of 2001, 2006, and 2011 within the permanent plots to acquire a
169 measure of red deer herbivory intensity that included a timeframe that could result in present-
170 time plant community composition. The browsing level was measured on a scale from 0 to 4;
171 0: no browsing, 1: > 0 to 24.9% of annual shoots clipped, 2: 25 to 49.9% of annual shoots
172 clipped, 3: 50 to 74.9% of annual shoots clipped, and 4: >75% of annual shoots clipped. In
173 2001 five randomly selected bilberry ramets in each of the seven permanent plots per
174 macroplot was measured, but because of time constraints we only sampled three ramets in a
175 random selection of four of the seven permanent plots per macroplot in 2006 and three ramets
176 in each of the seven permanent plots per macroplot in 2011. The varying sampling effort did
177 not influence the variance strongly (SD: 0.16 in 2001, 0.18 in 2006 and 0.25 in 2011). We
178 also obtained biometric measures (see Hegland et al., 2005 for details) of the sample ramets.
179 The herbivory intensity was calculated as the browsing level divided on the plant height. To
180 further confirm that this index reflected red deer herbivory intensity, we correlated the
181 variable with the frequency of faeces groups sampled in 2001, 2006 and 2011 in 100 1-m²
182 square plots randomly distributed within a radius of 100 m around each site. There was a
183 strong association ($r = 0.94$, $N = 12$, $p < 0.001$) between these independent measures.
184 Although these variables were obtained on different scales the correlation strengthens the
185 assumption that the herbivory intensity could be described using the browsing level on
186 bilberry ramets divided by plant height. The measure has the advantage that it was obtained at

187 the same scale as plant species richness and is more robust than the density indicator
188 represented by faeces as it is not confounded by, for example, weather dependent decaying
189 rates (e.g. Putman 1994). Figure 1 shows examples of the visual difference among sites with
190 high, intermediate and low herbivory intensities.

191

192 **2.3. Data analysis and model validation**

193 To investigate the relationships between plant species richness and herbivory intensity we
194 used linear mixed effects models. Plots were nested within sites and accounted for in the
195 random effects using R 2.15.0 (R Development Core Team 2012), library nlme (Pinheiro et al
196 2011) and lme4 (Bates et al 2011). To test whether relationships between herbivory intensity
197 and plant richness showed a unimodal peak or were linear within the studied herbivory
198 gradient we first included a quadratic component of the mean herbivory intensity index (at
199 site level) before we tested a linear relationship and compared models using AIC-values. We
200 used total plant species richness and richness within functional groups (at plot level) as
201 response variables. In the total plant richness model understory trees (< 20 cm) were not
202 included as they were sampled on site level. The understory tree model was hence not nested.
203 As the red deer farm sites represent artificially intensive herbivory we also ran models
204 without these sites when quadratic models were selected to test whether quadratic
205 relationships were merely caused by these extreme disturbance conditions.

206 In studies that utilise natural gradients as ours we must minimise and control for potential
207 confounding effects deriving merely from herbivore preferences rather than herbivory effects
208 of red deer. First, the potential preference effects were minimised through study design; study
209 sites were placed in a geographically restricted area (one island), within one main vegetation
210 type (pine-bilberry forest), and within a limited elevation gradient (20-140m). Investigating
211 relationships across multiple scales can result in erroneous correlations (Crawley 2007), and
212 we believe preference effects could have acted stronger if our study had sampled on coarser
213 scales, i.e. in larger areas, across vegetation types and, for example, between sites at low and
214 high altitude. Second, we validated the herbivory intensity models with analyses from an
215 enclosure based temporal data-set on species richness from the same study area. In every site
216 a 10x10m enclosure was established during winter 2001 together with the herbivory
217 macroplots that are the main study subjects in this study. We established a 9x9 m macroplot
218 and permanent plots corresponding to herbivory areas within the enclosures. We sampled
219 plant species richness accordingly in June 2001, 2006 and 2011. The change in species
220 richness during time between herbivory plots and enclosure plots was addressed by means of

221 linear mixed effects models where the nested design (site, macroplot and plot) was addressed
222 in the random effects. Standard models were performed with the herbivory plots in 2001 as
223 reference. The interaction between time and treatment tell us whether the change under ceased
224 herbivory was different than in the herbivory controls. If the temporal change was consistent
225 with the findings along the spatial gradient of herbivory intensity, we concluded that the
226 spatial model was validated. For example, to validate a statistical positive or a unimodally
227 peaked herbivory - richness relationship, the temporal change should be statistically positive
228 in herbivory plots relative to exclosure plots.

229

230 **3. Results**

231 *3.1. Herbivory intensity-plant richness relationships*

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

239 When we analysed the functional groups separately only the richness of forbs and ferns
240 resulted in significant peaked quadratic models (Fig. 3. d, f; Table 1). This was merely
241 because of the decline under experimentally very high herbivory intensities, which is
242 underlined by the positive linear relationships found between herbivory intensity and forb
243 richness (Coef=21.9; SE=8.4, DF= 60, 8; P=0.03) and fern richness (Coef=22.3; SE=8.5, DF=
244 60, 8; P=0.008) when excluding farm sites. Richness of trees and dwarf-shrubs showed
245 negative linear responses along the full herbivory intensity gradient (Fig 3 a, c; Table 1),
246 whereas richness of tree-juveniles, graminoids and mosses showed positive linear responses
247 (Fig. 3 b, e, g; Table 1) to the herbivory intensity. Liverworts showed no significant richness
248 response to red deer herbivory intensity (Fig. 3 h; Table 1).

249

250 *3.2. Model validation*

251 In general our herbivory intensity-plant richness models were validated by the temporal
252 exclosure-based models (Table 1, Fig. A1), i.e. the temporal change in plant richness in
253 herbivore vs. exclosure plots was largely consistent with the findings along the spatial
254 gradient of herbivory intensity. For example, in the temporal models the overall richness

255 declined slightly when red deer herbivory ceased whereas it increased slightly under
256 continuous herbivory. Most other models (i.e. for different functional groups) were also
257 validated, either by showing a temporal similar response under ceased herbivory or under
258 continuously red deer herbivory (Table 1, Fig. A1 for details). The only functional groups
259 where the findings of spatial gradient models and temporal exclosure models did not directly
260 link to each other was for richness of tree juveniles (spatial: positive linear relationship;
261 temporal: no significant changes) and liverworts (spatial: no significant relationship;
262 temporal: positive effects of ceased herbivory). Both of these functional groups showed only a
263 statistical weak or no relationship, respectively, between herbivory intensity and functional
264 species richness.

265

266 **4. Discussion**

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

280 The unimodally peaked signal in the herbivory-richness relationships was, however, not
281 very strong and dependent on artificial high disturbance levels in our study. In general, the
282 disturbance from free-ranging large herbivores is seldom severe enough to kill significant
283 parts of adult plants. When disturbance becomes substantial, such as in the deer farm in our
284 study, colonising plants are predated at early stage before they are able to tolerate biomass
285 loss. Thus space and safe sites required for plant colonisation (e.g. Hegland et al., 2001) are
286 not present simultaneously in these forest communities. One may speculate that the lack of
287 these requirements is one reason why so few studies have published verifications of the
288 intermediate disturbance hypothesis in forests with disturbance from free-ranging ungulates

289 (e.g. Mackey & Currie 2001; Svensson et al., 2012). Also, in forest communities with greater
290 diversity of tree species than our study system the plant diversity response may be more
291 pronounced because large herbivore disturbance has the clearest impact on this structural
292 layer (Connell 1978, Molino & Sabatier 2001). For example, the maximum number of tree
293 species at any site at any time in the study sites during 2001-2011 was only seven. In our
294 study system we have sampled all understory plant species, but most ungulate-plant
295 interaction studies do not include the bryophytes (i.e. mosses and liverworts) in the species
296 recordings but as a cover estimate (e.g. Singer and Schoenecker 2003, Tanentzap et al., 2009).
297 A simple exercise of investigating artefacts of sampling effort or researcher choices is to
298 examine how removing bryophytes from the dataset affects the overall herbivory-richness
299 relationship. Mixed effect modelling then resulted in a negative linear disturbance-richness
300 relationship (Coef= -11.3; SE=4.5; DF= 72,10; P=0.032). Thus, if the ecologically important
301 group of bryophytes had not been recorded in this study, the ecological, and hence
302 management interpretation of our analysis could have been the opposite in that red deer
303 herbivory reduce plant richness in the forest understory.

304 There were distinct differences in functional group responses. Five of eight functional
305 groups showed linear relationships between species richness and herbivory intensity (three
306 positive and two negative) and one functional group showed no relationship. Only two
307 functional groups showed a quadratic relationship when analysed separately, but these
308 unimodal relationships were caused strictly by the artificially high herbivory intensities at
309 farm sites and showed positive linear relationships when analysed within the natural gradient
310 only (see 3.1.). Overall, the herbivory-richness responses of the different species groups fitted
311 our expectations based on findings from meta-studies and literature reviews (Hester et al.,
312 2006, Diaz et al., 2007, Skarpe & Hester 2008). Low-growing groups such as forbs, grasses
313 and mosses increased in richness in contrast to woody dwarf shrubs and trees. This is in line
314 with Evju et al., (2010) who showed that low stature species profited from ungulate grazing in
315 a mountain area in Scandinavia. In other studies of red deer impact on plant diversity
316 (Woodward et al., 1994, Schreiner et al., 1996), specific responses of plant groups or growth
317 forms have tended to vary and be less predictable and few have studied functional group
318 responses along gradients of disturbance. The detailed sampling of all understory plant
319 species over a considerable time period (sensu Mackey & Currie 2001) may also be a key to
320 why our results fitted expectations better than many other similar studies. The difference in
321 response to herbivory intensity found between understory and juvenile trees (Fig. 3a and b;
322 i.e. complete opposite relationships) may indicate that deer herbivory have opposite effects on

323 recruitment and survival of trees. These results also point towards the driving mechanism
324 behind the red deer herbivory effects on plant richness. Periodic heavy grazing and browsing
325 may increase the recruitment of trees through increased germination caused by reduced
326 competition for light and space between the herbaceous layer and trees (e.g. Riginos 2009).
327 Studies from Białowieża forest in Poland underpin that fluctuations in ungulate density may
328 drive tree recruitment patterns (Kuijper et al., 2010) and it is also known from agricultural
329 systems that rotational stock management, varying the intensity of large herbivore
330 disturbance, may increase overall biodiversity (Sjödin et al., 2008, Farruggia et al., 2012).
331 When dominant plants are preferred by ungulates, plant diversity is expected to increase,
332 whereas diversity may decrease if herbivory-tolerant or resistant species become dominant as
333 a result of herbivory (Côte et al., 2004, Hester et al., 2006). The key mechanism to the overall
334 increase in plant species richness along the red deer herbivory intensity gradient in our study
335 is thus likely the reduction of dominant woody vegetation that increases resource and
336 substrate availability at the benefit of a richer low-growing species assemblage.

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

357

358 *4.1. Conclusions and implications for management*

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

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

378

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384

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507

508 *Figure legends:*

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

513

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

518

519 **Fig. 3.** The relationship between red deer herbivory intensity index and the species richness of
520 the functional groups (a-h) of the forest understory at Svanøy, western Norway. Lines are

521 shown for significant relationships of the selected models (linear vs. quadratic), but do not
522 take the random effects from the mixed effects modelling into account.

523

524 **Appendix**

525 **Figure A. 1**

526 Plant richness, in total and for functional groups of the forest understory at Svanøy, western
527 Norway, during 2001, 2006 and 2011 in herbivore and exclosure forest plots. Values are
528 mean \pm 1 SE (see methods for statistical procedures). These experimental exclosure-based
529 models were used to validate the herbivory intensity-plant richness models. Example of model
530 validation: to validate a statistical positive or a unimodally peaked herbivory -richness
531 relationship, the temporal change should be statistically positive in herbivore plots relative to
532 exclosure plots. In this sense all gradient models were supported by experimental models
533 except for tree-juveniles and liverworts, which showed weak or no statistical significance in
534 gradient models, respectively. See methods for statistical procedures, Table 1 for all statistical
535 testing including model validation, and Figure 2 and 3 for the herbivory intensity-plant
536 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)

Richness variable	Gradient in herbivory intensity					Experimental validation model: herbivore exclosure				
	Predictor	Coef	SE	DF	P	Variable	Coef	SE	DF	P
Total richness	Intercept	9.71	1.75	72	<0.001	Intercept (Herbivore 01)	15.61	0.67	332	<0.001
	Herbivory intensity	86.99	24.46	9	0.006	Herbivore 06 vs 01	0.27	0.27	332	0.318
	Herbivory intensity ²	-171.36	57.39	9	0.015	Herbivore 11 vs 01	0.88	0.27	332	0.001
						Main effect 01	0.23	0.4	155	0.569
						Exclosure 06 vs 01	-1.02	0.39	332	0.008
						Exclosure 11 vs 01	-1.19	0.39	332	0.002
Trees (20-300 cm)	Intercept	3.3698	0.45		<0.001	Intercept (Herbivore 01)	1.58	0.36	55	<0.001
	Herbivory intensity	-9.479	2.63		0.005	Herbivore 06 vs 01	0.50	0.47	55	0.287
						Herbivore 11 vs 01	0.50	0.48	55	0.287
						Main effect 01	0.58	0.49	55	0.215
						Exclosure 06 vs 01	1.17	0.66	55	0.081
						Exclosure 11 vs 01	1.42	0.66	55	0.036
Tree juveniles (poisson)	Intercept	-0.02	0.17		0.923	Intercept (Herbivore 01)	0.06	0.13		0.622
	Herbivory intensity	1.78	0.86		0.038	Herbivore 06 vs 01	-0.06	0.15		0.709
						Herbivore 11 vs 01	0.16	0.14		0.259
						Main effect 01	-0.08	0.15		0.599
						Exclosure 06 vs 01	-0.06	0.22		0.797
						Exclosure 11 vs 01	0.02	0.2		0.914
Dwarf-shrubs (poisson)	Intercept	1.16	0.12		<0.001	Intercept (Herbivore 01) ^a	2.94	0.25	332	<0.001
	Herbivory intensity	-1.69	0.79		0.033	Herbivore 06 vs 01	-0.19	0.07	332	0.007
						Herbivore 11 vs 01	-0.35	0.08	332	<0.001
						Main effect 01	0.24	0.1	155	0.027
						Exclosure 06 vs 01	0.04	0.1	332	0.721
						Exclosure 11 vs 01	0.14	0.1	332	0.154
Forbs	Intercept	0.80	1.31	72	0.544	Intercept (Herbivore 01)	3.70	0.38	332	<0.001
	Herbivory intensity	44.60	18.09	9	0.036	Herbivore 06 vs 01	0.17	0.12	332	0.185
	Herbivory intensity ²	-105.17	42.16	9	0.034	Herbivore 11 vs 01	0.06	0.13	332	0.636
						Main effect 01	0.05	0.18	155	0.796
						Exclosure 06 vs 01	-0.21	0.18	332	0.228
						Exclosure 11 vs 01	-0.51	0.18	332	0.004
Graminoids (poisson)	Intercept	0.53	0.12	4.40	<0.001	Intercept (Herbivore 01)	0.70	0.11		<0.001
	Herbivory intensity	2.09	0.59	3.51	<0.001	Herbivore 06 vs 01	0.12	0.10		0.234
						Herbivore 11 vs 01	0.11	0.10		0.299
						Main effect 01	0.10	0.10		0.348
						Exclosure 06 vs 01	-0.18	0.15		0.227
						Exclosure 11 vs 01	-0.30	0.15		0.048
Ferns (binomial)	Intercept	-3.32	1.06		0.002	Intercept (Herbivore 01)	-4.35	0.94		<0.001
	Herbivory intensity	39.83	13.97		0.004	Herbivore 06 vs 01	1.34	0.57		0.02
	Herbivory intensity ²	-98.93	32.78		0.003	Herbivore 11 vs 01	1.91	0.58		<0.001
						Main effect 01	0.30	0.87		0.735
						Exclosure 06 vs 01	0.41	0.85		0.629
						Exclosure 11 vs 01	-1.72	0.84		0.04
Mosses	Intercept	4.25	0.58	72	<0.001	Intercept (Herbivore 01)	5.46	0.44	332	<0.001
	Herbivory intensity	11.92	3.36	10	0.005	Herbivore 06 vs 01	-0.02	0.17	332	0.89
						Herbivore 11 vs 01	0.42	0.17	332	0.016
						Main effect 01	-0.15	0.23	155	0.5
						Exclosure 06 vs 01	-0.54	0.24	332	0.028
						Exclosure 11 vs 01	-0.24	0.24	332	0.327
Liverworts (binomial)	Intercept	-1.15	2.03		0.570	Intercept (Herbivore 01)	-6.40	1.25		<0.001
	Herbivory intensity	-11.69	16.10		0.468	Herbivore 06 vs 01	0.30	0.73		0.685
						Herbivore 11 vs 01	2.75	0.75		<0.001
						Main effect 01	-3.60	1.70		0.035
						Exclosure 06 vs 01	3.54	1.74		0.042
						Exclosure 11 vs 01	3.62	1.77		0.041

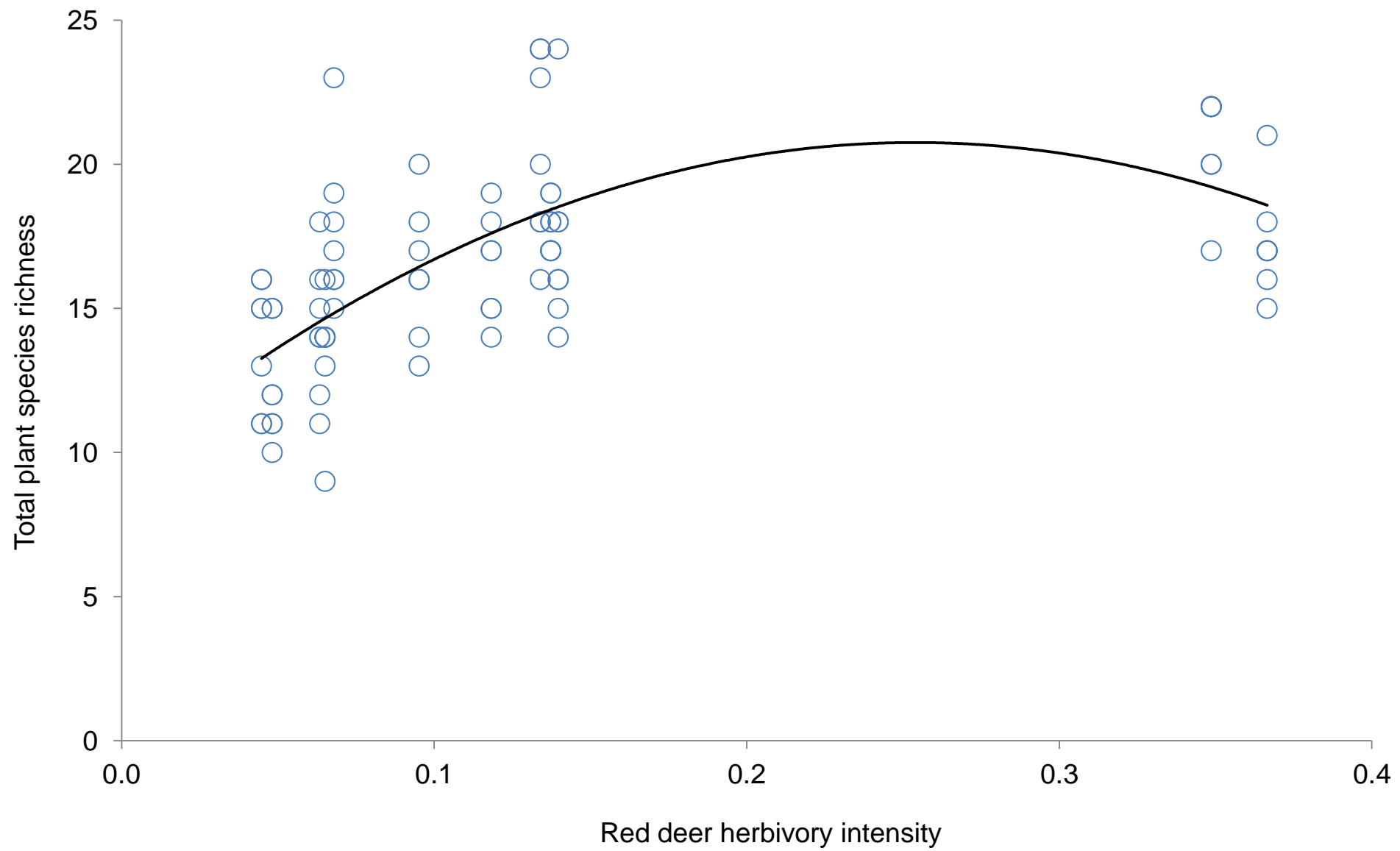
a) Distribution of selected models was consistent between gradient and exclosure models for functional groups except for dwarf-shrubs where exclosure model could be analysed with a normal distribution model.

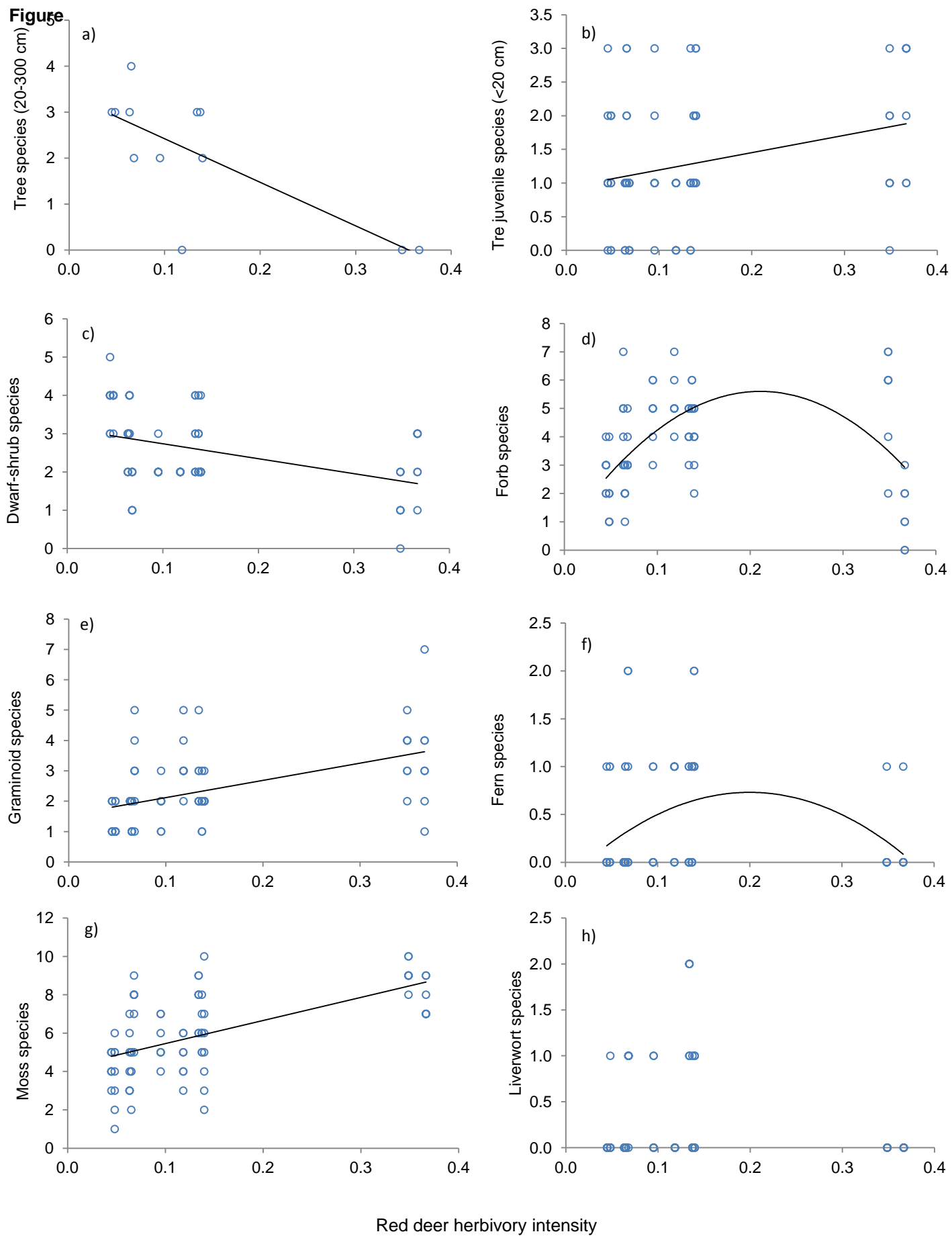
Example of model validation: if values in exclosure models are increasing for herbivore vs. exclosure plots this is consistent with findings of both positive linear models and quadratic peaked spatial models. All gradient models were validated by exclosure models except for tree juveniles and liverworts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

Figure



Figure





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