



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 10 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.

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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 (Côte et al., 2004). The increas-

ing population densities may create a disturbance regime for northern forest ecosystems to which they are not evolutionary adapted (sensu Milchunas and Lauenroth, 1993). 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

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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 criticised for low precision in explaining diversity patterns and because of its relative character (Mackey and 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 and 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 contrasting 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., 2006), and this may be even more prominent in forest ecosystems as large herbivores may selectively utilise 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 10 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 enclosure 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 and 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. Materials 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°30'N, 5°05'E). 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 and 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 9 × 9 m was located at each site adjacent to a deer enclosure (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, *C. 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 20,000–40,000 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., 2012). 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 9 × 9 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

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