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Associational relationships at multiple spatial scales affect forest damage by moose

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ABSTRACT

Increasing abundance of large herbivores combined with changes in forestry practices has led to increased forest damage in many temperate and boreal forest areas. The role of alternative forage as a driver for browsing pressure on tree species important for forestry has received increased attention. However, actions to reduce damage through altering forage abundance must be carried out at spatial scales that correspond to the behavioural processes that generate the browsing pattern. We used a multi-scaled dataset on browse abundance and utilisation in Southern Norway to assess how pine browsing damage was related to abundance and quality of browse measured at different spatial scales. Pine trees had a lower probability to be browsed at high pine abundance at all spatial scales. However, the abundance and quality of alternative browse was negatively related to pine browsing (i.e. associational resistance) at several spatial scales, with the highest explanatory power at the largest spatial scale. Management actions to reduce pine browsing by moose should focus on facilitating high abundance of both pine and alternative high-quality browse, and should be carried out at sufficiently large spatial scales (moose home range scale or larger).

1. Introduction

Many populations of large herbivores have experienced large increases in abundance during recent decades following reduced abundance of natural predators, changes in harvesting strategies, and increased availability of food due to changes in human land use practices (Apollonio et al., 2010). In many areas this increase represents a re-establishment of previous densities of herbivores after decades of decline, and is in some cases considered positive for biodiversity conservation reasons or for the recreational or economic value associated with the herbivore species (Putman et al., 2011a). High abundances of large herbivores do, however, also come with costs, both from an ecological (Côté et al., 2004) and human perspective (Putman et al., 2011a, 2011b). For instance, some of the most valuable tree species for the forest economy are also important forage for herbivores (e.g. Edenius et al., 2002; Milner et al., 2013; Tremblay et al., 2007), giving rise to increased human-wildlife conflicts (Putman et al., 2011a; Weisberg and Bugmann, 2003).

Perhaps the two most efficient actions to prevent forest damage by browsing herbivores – physical barriers around vulnerable forest stands or trees (e.g. Cutini et al., 2011; Ward et al., 2000) and reducing herbivore abundance by increasing harvesting (e.g. Hothorn and Müller, 2010) – are both costly and may have unwanted ecological and economic side-effects (Kuijper, 2011). Altering the local browsing pressure by changing the amount and/or spatial distribution of forage has therefore received increased interest (Heikkilä and Härkönen, 1996; Mathisen et al., 2014; Putman and Staines, 2004; van Beest et al., 2010). While supplementary feeding can be expensive and logistically challenging, the natural food base can be altered as part of standard silvicultural practices such as pre-commercial cleaning and thinning. Selectively performing these operations can alter both the quantity and quality of alternative browse species with the aim to reduce the browsing pressure on the focal tree species. The association of a browsed species with other preferred or avoided species can either increase (associational susceptibility) or decrease (associational resistance) the detection probability of a focal species (Barbosa et al., 2009). Alternatively, the contrast between a focal species and preferred plants in the surroundings can divert the browsing pressure towards the latter (associational

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resistance by contrast or attractant-decoy hypothesis; Atsatt and O'Dowd, 1976). Depending on whether the focal species receives associational resistance or susceptibility from abundance of other browse species, increasing quantity and/or quality of alternative forage will reduce or increase forest damage. Accordingly, knowledge about the relationships between forest damage and the food base is needed in order to target actions efficiently.

Animals are thought to be distributed in their landscape according to the distribution of resources (e.g. Bjørneraas et al., 2012; Fretwell and Lucas, 1969; Månsson et al., 2012), and one should therefore expect that the browsing pressure per capita food resource should be evenly distributed in space. However, several mechanisms influence animals' behavioural decisions resulting in browsing patterns that do not necessarily reflect the spatial variation in forage abundance. Firstly, the foraging decisions of herbivores are a result of many factors that are not only related to the quality and quantity of forage. Factors such as predation risk and environmental stress can reduce the net gain obtained from a foraging patch (Brown, 1999). Such factors may influence the animals at larger spatial scales compared to the local variation in food abundance (Johnson et al., 2001; Rettie and Messier, 2000), and therefore may generate browsing patterns that are disproportionate to the resource distribution (Cassing et al., 2006; Hamilton et al., 1980; Palmer and Truscott, 2003). Secondly, animals forage in landscapes where their resources are unevenly distributed. Optimal foraging theory predicts that the time spent in a foraging patch, and the proportion of resources in the patch that is utilised, depend on the patch quality and costs such as searching time and locomotion costs occurring when moving between patches (Charnov, 1976). Accordingly, in areas with high movement costs the utilisation rate of resources in a foraging patch is expected to be higher (Charnov, 1976).

The foraging niche of large herbivores can be separated into three components: quality, quantity and availability of forage (Skogland, 1984; Sæther and Andersen, 1990). The importance of these components for patch utilisation can vary depending on forage characteristics in the surroundings as well as on other environmental conditions in interaction with the decision-making process of the animal (Andersen and Sæther, 1992; Bergman et al., 2005; Sæther and Andersen, 1990). Accordingly, we may expect associational relationships between the surrounding forage and the detection probability and browsing pressure of a focal species (Atsatt and O'Dowd, 1976; Barbosa et al., 2009). A meta-analysis by Barbosa et al. (2009) suggests that associational resistance is more likely than susceptibility in mammalian herbivores. However, other relationships are also reported, from no significant associational relationships (e.g. Danell et al., 1991a; Edenius, 1991; Jalkanen, 2001), to evidence for associational susceptibility (e.g. Milligan and Koricheva, 2013; Vehvilainen and Koricheva, 2006), indicating that the role of associational relationships is not straightforward for mammalian herbivores. Still, the utilisation of the focal species as food is likely to be affected both by the quantity and quality of alternative forage, but the strength of the association will be shaped by the spatial distribution of the higher and lower quality forage resources (Bergvall et al., 2008).

The factors related to management actions and animal foraging decisions described above all require that the characteristics of food sources are interpreted at the appropriate spatial scales. Forestry operations are done at scales dictated by management strategies for forest stands, land properties or other management units. Accordingly, actions should best be done at an appropriate spatial scale that incorporates the ecological mechanisms affecting the distribution of animals and their browsing pressure. However, little is known about the spatial scales of herbivore foraging damages according to ecological mechanisms affecting the distribution of animals and their browsing pressure, and whether or not the forest management scales currently applied are appropriate for addressing such damage. This calls for a multi-scale evaluation of forest herbivore damage in order to target actions to efficiently reduce silviculture-herbivore conflicts (Tanentzap et al., 2011; Weisberg and Bugmann, 2003).

We used a large dataset on winter browse availability and utilisation by moose (*Alces alces*) in Southern Norway to assess how browse abundance and composition at several spatial scales affected browsing damage on Scots pine (*Pinus sylvestris*). The Norwegian moose population has increased considerably since the 1960's (Lavsund et al., 2003; Solberg et al., 2006), and in many areas current moose densities are probably higher than ever before (Rosvold et al., 2012). The high moose abundance represents a considerable income for land-owners through hunting permits and hunting-related services (Storaas et al., 2001, but see also Wam and Hofstad, 2007). During the same period, forestry practice changed from selective felling of trees to clear cutting (Lavsund et al., 2003). This opened large areas which provided concentrated abundances of high-quality forage for moose, and this has been proposed as an important reason for the increase in moose density (Lavsund et al., 2003; Milner et al., 2013). However, regeneration of pine-dominated forest stands is compromised in many areas due to intense browsing by moose during winter (Edenius et al., 2002). Pine is an important part of moose winter diet if the availability of alternative browse is scarce (Hörnberg, 2001; Wam and Hjeljord, 2010), but its quality as moose forage is considered to be of moderate value compared to several deciduous species (Histøl and Hjeljord, 1993; Hjeljord et al., 1982, 1994).

We focused on the following questions: (1) Is the degree of pine browsing affected by quality or quantity of alternative browse in the browsing patch, forest stand, home range or municipality scale? (2) Is the degree of pine browsing in a patch best explained by absolute value of browse (i.e. the abundance of browse of different type), or is it modified by the relative abundance of browse in the surroundings (i.e. the difference in abundance between a browsing patch and the abundance in surrounding areas)? (3) Does the spatial scale of forest management and actions capture the spatial scales at which variation in quality or quantity of alternative browse explains pine browsing frequency?

2. Materials and methods

2.1. Study area

Our study area was made up of 12 sub-areas of approximately 10,000 ha each, distributed throughout southern Norway (Fig. 1). With the exception of the two southernmost sub-areas, the sub-areas are situated within the boreal forest zone (Moen, 1999), dominated by Scots pine and Norway spruce (*Picea abies*) mixed with deciduous trees like birches (*Betula* spp.), rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) and goat willow (*Salix caprea*). The two southernmost sub-areas constitute an ecotone between the boreal and temperate forest (i.e. boreo-nemoral zone, Moen, 1999), with oak (*Quercus* spp.) being an additional common tree species. Because of the wide geographical distribution of this study, the areas covered large gradients in plant growth conditions: the start of growing season varied from 20 April to 10 May, while the proportion of the range area comprising intermediate to high forest productivity (Site Index $\geqslant$ G14 on the H40 scale) varied from 27% to 96% (Wam et al., 2010). The H40 Site Index indicates the height of the dominant tree species when the age of the tree (measured at 130 cm height) is 40 years (Tveite, 1977).

The timber logging activity was fairly similar between sub-areas: recently cleared forest (stands with dominating tree height < 4 m) covered 5–13% of the range area. The forest had been