

# Disrupted trophic interactions affect recruitment of boreal deciduous and coniferous trees in northern Europe

PER ANGELSTAM,<sup>1,4</sup> MICHAEL MANTON,<sup>1,2</sup> SIMEN PEDERSEN,<sup>1,3</sup> AND MARINE ELBAKIDZE<sup>1</sup>

<sup>1</sup>Faculty of Forest Sciences, School for Forest Management, Forest-Landscape-Society Network, Swedish University of Agricultural Sciences, PO Box 43, SE-739 21, Skinnkatteberg, Sweden

<sup>2</sup>Faculty of Forest Science and Ecology, Institute of Forest Biology and Silviculture, Aleksandras Stulginskis University, Studentų g. 13, LT-53362, Akademija, Kauno r., Lithuania

<sup>3</sup>Department of Forestry and Wildlife Management, Faculty of Applied Ecology and Agricultural Sciences, Inland Norway University of Applied Sciences, Campus Evenstad, N-2480, Koppang, Norway

**Abstract.** Loss of large carnivore populations may lead to increased population densities of large herbivores, and subsequent cascading effects on the composition, structure, and function of ecosystems. Using a macroecological approach based on studies in multiple boreal forest landscapes in the Baltic Sea region and Russia, we tested the hypothesis that disrupted trophic interactions among large carnivores and large herbivores affect the recruitment of both ecologically and economically valuable tree species. We measured damage levels on young trees and large herbivore density in 10 local landscapes representing a gradient from extinct to extant populations of both large carnivores and large herbivores. We also tested the alternative hypothesis that forest management intensity is correlated to reduced recruitment of these tree species. At the macroecological scale there was an inverse relationship between the number of large carnivores and large herbivores. This coincided with a steep gradient in browsing damage on the ecologically important aspen, rowan and sallow as hosts for specialized species, as well as the economically important Scots pine. In one landscape hunting had replaced the presence of carnivores. Mean damage levels of these four tree species were correlated with large herbivore abundance, but not with forest management intensity. We discuss the pros and cons of this macroecological approach, as well as the challenge of governing and managing trophic interactions at multiple scales.

**Key words:** biodiversity conservation; boreal forest; forest landscape management; green infrastructure; landscape restoration; macroecology; trophic interactions.

## INTRODUCTION

Individual species may influence the composition, structure, and function of ecosystems in different ways (Westman 1990). Thus, loss of large top predators may cause cascading effects in forest ecosystems (Ripple and Beschta 2004, Säterberg et al. 2013, Ripple et al. 2014). These trophic interactions may include increased large herbivore densities due to improved survival through reduced predation (Gill 1992*b*), and lead to subsequent effects on the composition of tree species (Gill 1992*a, b*, 2006, Müller et al. 2008), vegetation structure (Gill and Beardall 2001, Gordon and Prins 2008, Putman et al. 2011), and ecosystem processes (Danell et al. 2003, Ritchie et al. 2012). Analogously, meso-predators may become affected by the extirpation of large carnivores, and thus have an effect on prey species (e.g., Elmhagen and Rushton 2007, Elmhagen et al. 2010, Pasanen-Mortensen et al. 2013). The loss of large carnivores and resulting increased densities of large herbivores, as well as associated cascading effects, are good examples of

large-scale challenges for managers of wildlife, conservation areas, recreation, tourism and forestry (e.g., Angelstam 2002, Ripple et al. 2014). Lack of natural control mechanisms that limit herbivore density may thus increase wildlife-forestry-conservation conflicts in managed forest landscapes (Kuijper 2011, Hearn 2015). Large carnivores can be important agents in modifying ungulate-plant interactions. However, despite the abundance of knowledge on carnivore-herbivore-vegetation systems in North America (e.g., Peterson et al. 2003, 2014), there is a lack of knowledge from studies on European systems (Hearn 2015). One reason for this is that the effect of carnivores on ungulate-vegetation interactions and subsequent cascading effects are difficult to document in West and Central European landscapes with small variation in carnivore and large herbivore abundance (Kuijper 2011).

The spatial extent of trophic interactions between large carnivores and herbivores and vegetation, as well as subsequent cascading effects in forest landscapes, limits the application of replicated experiments (Mykrä et al. 2000). An alternative option is natural experiments (*sensu* Diamond 1986) in the form of comparative macroecological studies that trade off the precision of small-scale research with an appropriate spatial scale (Brown 1995,

Manuscript received 23 June 2016; revised 13 October 2016; accepted 25 October 2016. Corresponding Editor: A. David McGuire.

<sup>4</sup>E-mail: per.angelstam@slu.se

Ripple and Beschta 2012). Such studies need to mirror variation in both ecological and social systems (Angelstam et al. 2013). Additionally, vegetation and climate are factors that should be considered when undertaking studies among regions and landscapes (Schönfeld 2009). Consequently, studies that examine the effects of altered trophic interaction at the scale of landscapes across countries within an ecoregion with different large carnivore and herbivore abundances are often not at hand. Studies on relationships among different predator–prey–vegetation systems across a sufficiently long gradient of landscape characteristics may aid actors and stakeholders to better understand the consequences of disrupted trophic interaction, as well as the role of different governance and management regimes. Macroecological studies can therefore contribute to mutual knowledge transfer among actors and stakeholders focusing on different aspects of predator–prey–vegetation interactions. The European continent's boreal forest, i.e., also including countries outside the European Union in Eastern Europe including NW Russia, is an interesting arena for such studies, due to its clear gradients in large herbivore (Melis et al. 2009) and large predator abundance (Kaczensky et al. 2012, Chapron et al. 2014), forestry intensity (Angelstam et al. 2011b), as well as governance systems (Gunst 1989, Huntington 1997, Katchanovski 2006). However, barriers for collaboration among researchers in Europe's West and East are often experienced through different languages, research cultures and opportunities for funding.

A starting point for macroecological studies of trophic interactions and their consequences for ecologically and economically important tree species is the relationship between landscape change leading to regional habitat loss, and the subsequent extirpation of large carnivores. For example, occurrences of lynx (*Lynx lynx*), wolf (*Canis lupus*), and brown bear (*Ursus arctos*) in Europe are clearly linked to macroecological gradients in both economic development (Angelstam et al. 2004) and forest cover (Mikusiński and Angelstam 2004). This stresses the need to use wide gradients in macroecological studies that include both regions with intact large carnivore assemblages, and regions where they are no longer present, or occur in low densities. A good example of this are forest landscapes in northern Europe, from local regions in Fennoscandia (i.e., Norway, Sweden and Finland) where all large carnivore species are extinct or occur at low densities to regions in northwest Russia, where viable populations of all four naturally occurring large carnivores are present (e.g., IUCN 2014). Wolf, brown bear, and lynx commonly prey on browsing large herbivores. By contrast, the wolverine (*Gulo gulo*) is of less importance to boreal forest herbivores, as it does not prey on moose (*Alces alces*) and red deer (*Cervus elaphus*) due to their size, or roe deer (*Capreolus capreolus*) due to its preference for human dominated landscapes.

Conversely, large herbivore densities, especially moose and red deer, have generally increased in Western Europe (Gill 1992b, Danell et al. 2006, Milner et al. 2006,

Apollonio et al. 2010, Hearn 2015). The reasons for these population increases are complex but can be attributed to a combination of changes in land use and management. This includes reduced competition from previously abundant domestic animals grazing in forests (Rackham 2003, Austrheim et al. 2011), moose management practices favoring high reproductive rate (Liberg et al. 2010), increased availability of young forest providing a good food supply (Strandgaard 1982, Cederlund and Bergström 1996), to human-based disturbances in fragmented landscapes (Brazaitis et al. 2014), supplementary winter feeding (Mathisen et al. 2014) and a lack of large carnivores (Solberg et al. 1999, Wabakken et al. 2001, Edenius et al. 2002, Pedersen 2011).

In Fennoscandia, the consequences of disrupted trophic interactions have been debated for a long time (e.g., Angelstam et al. 2000, Sjölander-Lindqvist 2007, Sandström et al. 2009). Recently, after extirpation of populations more than 100 years ago, large carnivore populations have recovered locally in southern-central Norway and Sweden (Wabakken et al. 2001, Liberg et al. 2010). Subsequently, some large herbivore populations are also locally declining (Wabakken et al. 2001, Melis et al. 2009, Gervasi et al. 2012, Sand et al. 2012). There are two debated issues connected to high densities of large herbivores in Fennoscandia.

The first issue concerns biodiversity conservation. Mature individuals of the deciduous tree species aspen (*Populus tremula*), rowan (*Sorbus aucuparia*), and willow (*Salix caprea*) are particularly important as hosts for a range of species of mosses, lichens, insects, and birds. The ecological importance of aspen, rowan, and willow is exemplified by the importance of such tree species for maintenance of viable populations of the umbrella lichen species *Lobaria pulmonaria* and other species requiring bark with high pH (Nilsson et al. 1995), as well as the white-backed woodpecker (*Dendrocopos leucotos*; Roberge et al. 2008b). Such species are not only of conservation concern, but also commonly used as focal species for biodiversity conservation planning and management (Martikainen et al. 1998). There is thus a need for the restoration of this deciduous tree component to maintain viable populations of associated specialized species (e.g., Gren et al. 2014). However, moose has a primary winter food preference order for aspen/sallow/rowan > birches > Scots pine > Norway spruce (Ahlén 1975, Bergström and Hjeljord 1987, Månsson et al. 2007). Therefore, the rate of browsing damage is hampering the maintenance and restoration of sufficient amount of deciduous trees and stands as functional green infrastructures for forest biodiversity (Angelstam et al. 2000, 2011a, Stighäll et al. 2011).

The second issue concerns economic values in forestry. For example, the Swedish state forest company Sveaskog reports that herbivore damage is the largest threat to high quality Scots pine (*Pinus sylvestris*) production and estimated a loss of 850000 m<sup>3</sup> of saw logs per year, or 15% of the total annual wood harvest (Sveaskog 2014). Similarly,

in Norway, the Glommen Forest Owners Association estimated the socioeconomic cost of the destruction of forests by moose to be 1 billion Norwegian Krone per year in Hedmark County alone, or 8% of the county budget (Glommen Skog BA 2010). The damages involve bark stripping, stem breakage, and broken apical shoots on young Scots pine (e.g., Andrén and Angelstam 1993). This damage reduces the volume growth, and causes a reduction in the proportion of Scots pine stems that develop into future high-quality saw logs (Bergqvist et al. 2014).

The aim of this study is to test the hypothesis that disrupted trophic interactions affect the recruitment of mature individuals of deciduous tree species such as aspen, rowan, and sallow, which have a key role for biodiversity conservation, and the economically important Scots pine. We explore the predictions that a reduced number of large carnivore species is correlated with increased herbivore species richness, which leads to reduced recruitment of key deciduous tree species and Scots pine into the population of undamaged mature trees. We also evaluate the alternative hypothesis that forest management intensity is linked to reduced recruitment of these tree species. We thus designed a macroecological study to measure browsing damage levels on key deciduous tree species and Scots pine and local large herbivore abundance in a gradient from extinct to extant populations of large carnivores. Field data was collected in six countries, from dense to sparse populations of large carnivores and herbivores, and high intensive to low intensive forest management across northern Europe from Norway in the west via Sweden, Finland, Latvia, and Belarus to Russia in the east.

#### METHODOLOGY

##### *Identification of boreal landscapes as replicates*

All research questions require identification of the relevant spatial scale to address them. While trees have very small area requirements, the large herbivores that feed on them have very large area requirements, and their predators' area requirements are even larger. To maintain entire ecosystems in forest landscapes with both economically and ecologically valuable trees, and large herbivores and large carnivores, hypothesis testing needs to be addressed at replicated areas of large spatial extents in ecoregions. For example, in Sweden, it is argued that moose management units should exceed 500 km<sup>2</sup> in the south and 1000 km<sup>2</sup> in the north to encompass entire moose populations (Lindqvist et al. 2014). Large carnivore management takes place at an administrative national or regional level, i.e., in areas exceeding one order of magnitude larger size than large herbivores. Because landscapes and regions in any particular country are governed by similar or identical policies and management approaches, predator–prey–vegetation relationships have limited variation within administrative regional units. On the contrary, there are considerable

differences among regions and countries in the boreal biome (Fig. 1) where wildlife management policy and forest industrial regimes differ due to natural, historical, societal, and economical legacies (Lehtinen et al. 2004, Angelstam et al. 2011a, Naumov et al. 2016).

To identify landscapes for field data collection, a desk study was undertaken to create maps showing the spatial distribution of both large carnivores (e.g., brown bear, lynx, and wolf) and large herbivores (e.g., moose, red deer, and roe deer). We created a 50 × 50 km grid over the European continent's boreal biome, and attributed each cell with the occurrence of each species using GIS (ArcMap 10.1, ESRI 2012). For large carnivores, Kaczensky et al. (2012) classified occurrence into three categories using spatial data for the EU. However, as this data set did not cover the entire European continent including the Komi Republic in the northeast, we supplemented the EU data by using presence/absence data from the IUCN Red List of Threatened Species database (IUCN 2014) for wolves (Mech and Boitani 2010), lynx (Breitenmoser et al. 2008) and brown bear (McLellan et al. 2008). There is clear southwest to northeast trend in the current species richness of large carnivores in boreal Europe (Fig. 2). Northwest Russia, most of Finland, and Estonia share a contiguous area with brown bear, wolf, and lynx. Central Sweden and Norway share small isolated populations of the same species. For large herbivores we only used species presence/absence data from the IUCN Red List of Threatened Species database (IUCN 2014), viz. moose (Henttonen et al. 2008), red deer (Lovari et al. 2008a) and roe deer (Lovari et al. 2008b). Based on these datasets we created maps showing the combined presence of these large carnivore and herbivore species, respectively, in each 50 × 50 km grid cell (range 0–3). The number of large herbivore species decreased from southwest to northeast in boreal Europe (Fig. 3). This is thus opposite to the trend for large carnivore species.

Forest management intensity was estimated as the annual forest loss defined as “a stand-replacement disturbance, or a change from a forest to non-forest state” as reported by Hansen et al. (2013). Assuming 100-yr forest rotations, average forest losses >1% should indicate higher than average forest management intensity. Loss of forest due to fire or wind in the selected study areas was negligible during the study period. The results were calculated and presented using the same 50 × 50 km grid as for large carnivores and herbivores, using GIS (ArcMap 10.1, ESRI 2012). To represent these gradients across the boreal biome in Europe, we selected ten case study landscapes. The forest proportions ranged from 27% to 67%, and the human population ranged from 3.0 to 107 people/km<sup>2</sup> (see Table 1).

##### *Field data collection*

*Browsing damage on trees.*—We measured browsing damage that impedes the development of mature tree species of ecological importance (i.e., aspen, rowan, and

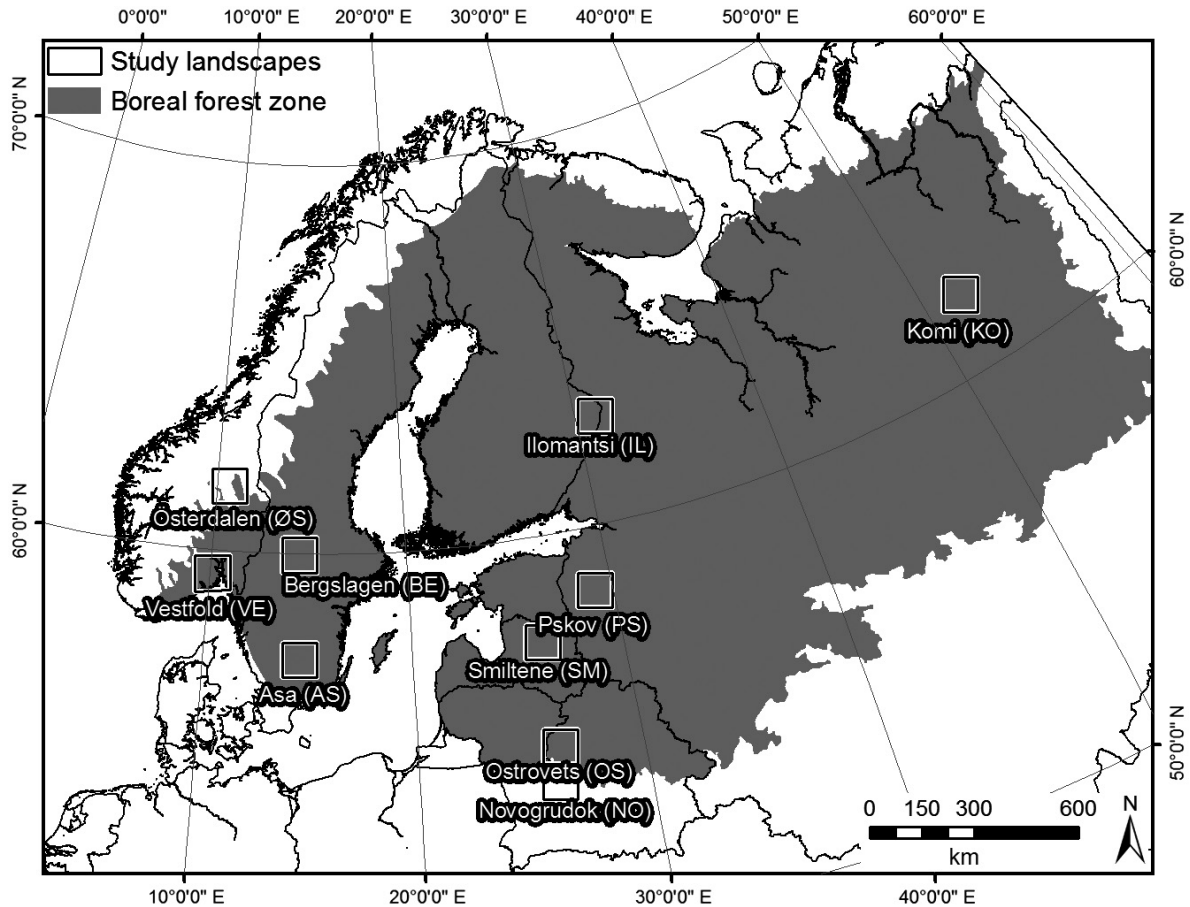


FIG. 1. Location of case study landscapes, visualized as  $100 \times 100 \text{ km}^2$ , in the boreal biome where sampling of browsing pressure, browse food supply, and herbivore densities were made.

sallow) and economic importance (i.e., Scots pine). All *Salix* spp. were assessed irrespective of species as a proxy for willow. We sampled 10 randomly selected young forest stands in each of the 10 focal landscapes. Young forest was defined as tree height of 1.5–4.0 m, which corresponded to 6–27 yr after clear-felling. By selecting young forest stands within the forest mask but outside protected areas, we ensured that sampling targeted stands that were managed for timber and pulpwood production. The requirements for the selected forest stands were  $>3 \text{ ha}$  in size, located  $>100 \text{ m}$  away from any road, and situated  $>500 \text{ m}$  from towns and villages. This was made to ensure consistency in the opportunity for large herbivores to access browse food in the sampled stands.

In the center of each young forest stand, we established a sampling triangle with sides of 100 m, and with six sampling plots of  $100 \text{ m}^2$  ( $r = 5.64 \text{ m}$ ) located at 50 m intervals (Angelstam et al. 2000). In total we surveyed 600 plots in 10 landscapes with 10 young forest stands per landscape and 6 plots per young forest stand. To assess the impact of trophic interactions affecting the success of young deciduous trees and Scots pine in reaching biological and economic maturity, respectively, rather than sampling

last winter's browsing, we sampled the accumulated browsing pressure (Pedersen et al. 2007). For deciduous trees, we counted the number of individual stems or defined clusters of stems in five damage levels: 0 (not browsed), 1 ( $<50\%$  of long shoots browsed), 2 ( $>50\%$  of long shoots browsed), 3 (all long shoots browsed), and 4 (all browsed and dead; Angelstam et al. 2000). For Scots pine, we counted the number of individual stems with (A) bark stripping, (B) stem breakage, and (C) top shoot browsing. All these damage categories are particularly destructive when it comes to development of future high quality saw-logs (Andrén and Angelstam 1993). To analyze the effect of herbivores on deciduous tree recruitment we calculated the mean browsing damage level per plot for the focal deciduous tree species aspen, rowan, willow, and used this as a dependent variable. For Scots pine we also calculated the mean damage level per plot (damage levels 0–4), additionally, we gave the damage categories A, B, and C a damage value of 3 (equal to damage level “all long shoots browsed”).

*Herbivore abundance and food availability.*—Large herbivore abundance was estimated by counting species-

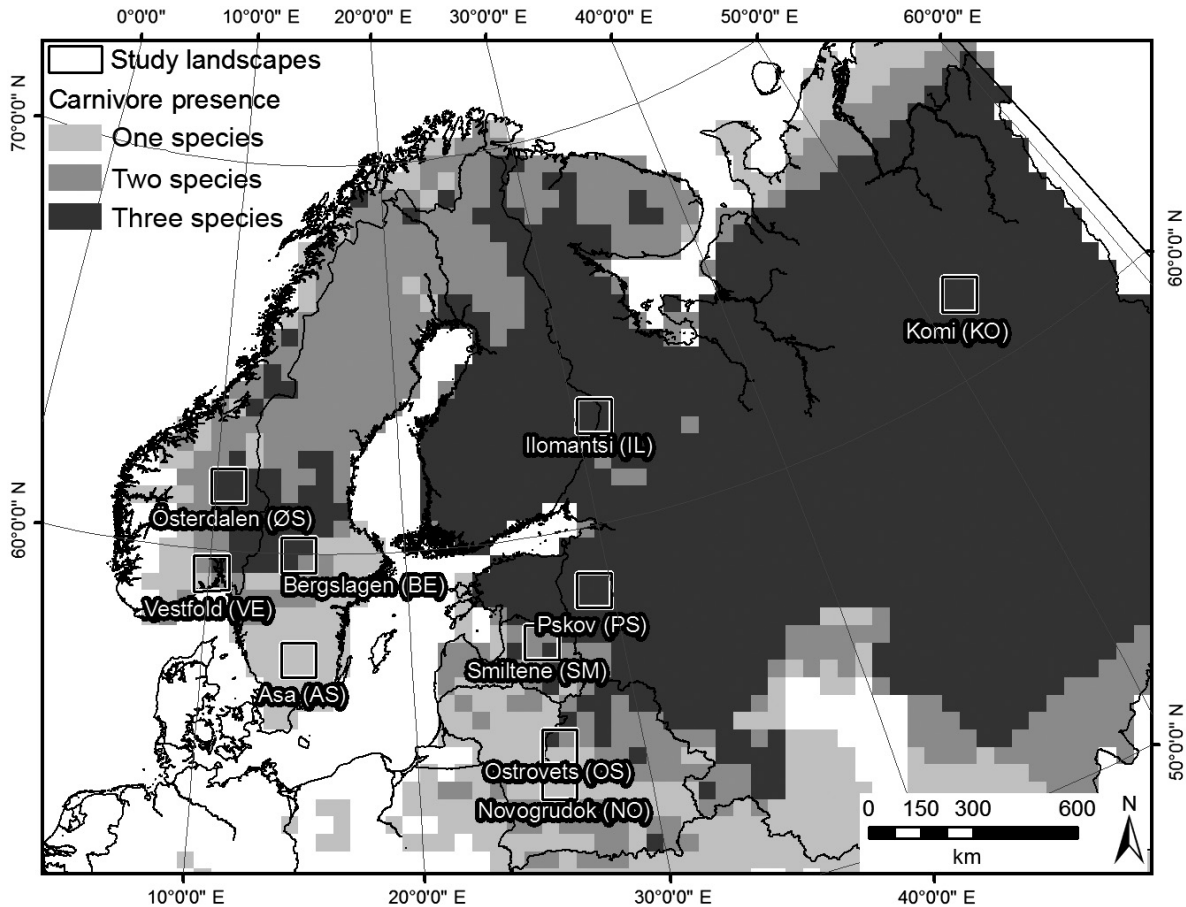


FIG. 2. Map showing the number of carnivore species present within  $50 \times 50$  km grid cells in northern Europe.

specific fecal pellet groups in each of the sampling plots in each stand outside the summer vegetation period, i.e., when trees and shrubs form the bulk of the diet. We used counts of accumulated large herbivore (moose, red deer, roe deer) pellets as an index of local habitat use by large herbivores. This has been shown to be a reliable estimate of abundance, especially as the aim is to study spatial changes in habitat use (Månsson et al. 2011). A pellet group was defined as a minimum of 10 pellets in a distinctive pile, with the center of the pile within the sampling plot (Pedersen et al. 2007). As an index of expected impact of large herbivores (Large Herbivore Index) on deciduous trees, we summed the number of pellet piles after correction for body mass by multiplying the number of pellet groups with the body mass (in tons) of the respective large herbivore, assuming a constant defecation rate of the four large herbivores. We assumed a live body mass of 21 kg for roe deer, 154 kg for red deer, and 346 kg for moose (Silva and Downing 1995).

We calculated food availability for large herbivores, by measuring both the amount of shrubs and seedlings within browsing height of moose (<4 m), as well as field layer species preferred by large herbivores (e.g., Angelstam et al. 2000). For shrub and field layer vegetation, we calculated

the volume of browse biomass per 100 m<sup>2</sup> plot (m<sup>3</sup> and dm<sup>3</sup>, respectively) available to large herbivores, by multiplying estimated percent cover with height, corrected for plot size. Field layer browse included bilberry (*Vaccinium myrtillus*) and heather (*Calluna vulgaris*), which are the most common dwarf shrub forage species for moose (Cederlund et al. 1980).

#### Statistical analyses

The variables studied are presented in Table 2. First, we described the 10 landscapes by testing for differences among them regarding (1) moose pellet counts and (2) large herbivore body mass index (large herbivore index). We did this by running linear mixed effects models (LME) and generalized linear mixed effects models (GLMM) with landscape as independent variable and stand as a random term to avoid pseudo-replication. We applied  $\chi^2$  tests for GLMMs and *F* test for LME to test for significance (Zuur et al. 2009). Large herbivore index was log + 1-transformed to achieve a normal distribution.

Second, we described the landscapes further by testing for differences in (1) field layer and (2) tree layer browse. We did this by running LMEs with landscape as

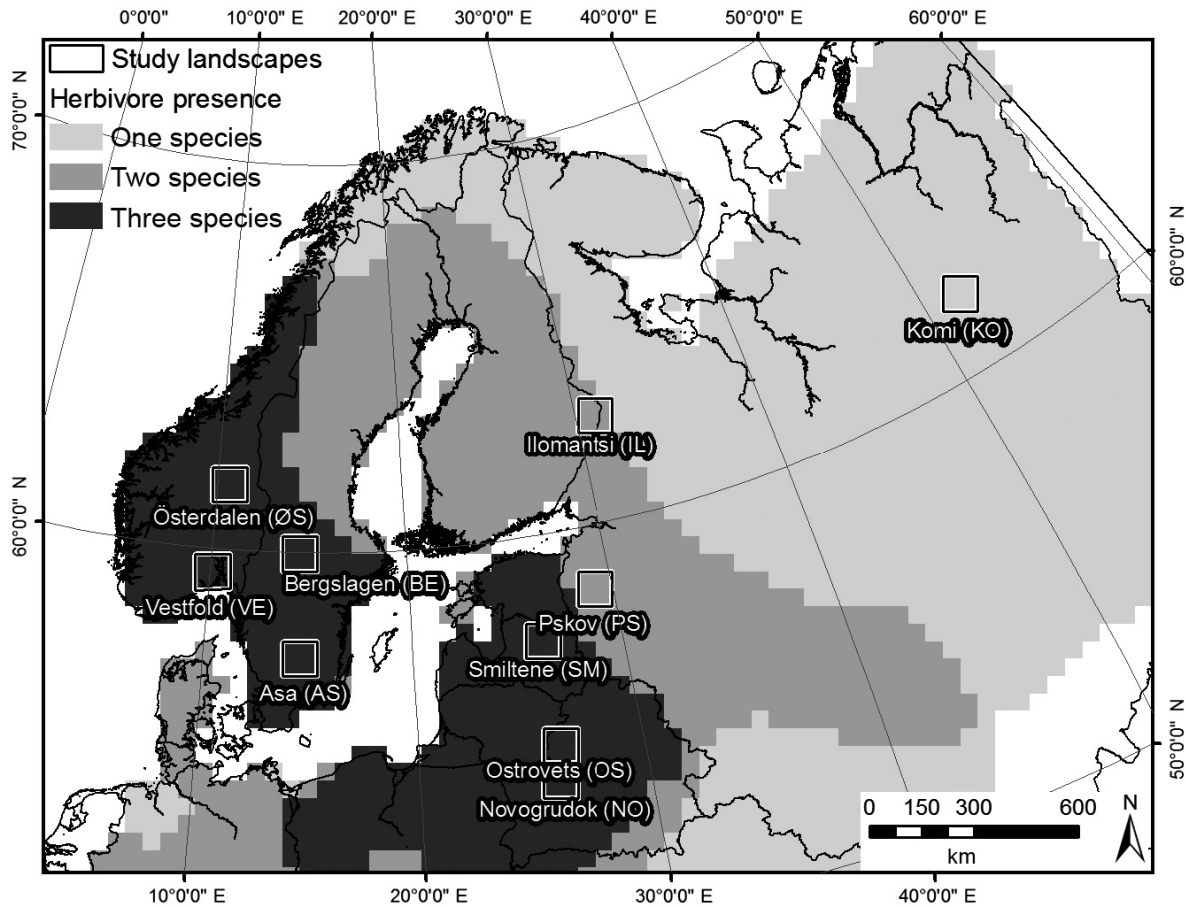


FIG. 3. Map showing the number of large herbivore species present within  $50 \times 50$  km grid cells in northern Europe.

independent variable and stand as a random term to avoid pseudo replication. We applied  $F$  tests to test for significance (Zuur et al. 2009). Tree and field layer were log + 1 transformed to achieve a normal distribution. Next, we tested for differences in tree damage level among

landscapes on the three focal deciduous tree species and Scots pine. We applied  $F$  tests for LME to test for significance (Zuur et al. 2009). Finally, we made a meta-analysis of the entire data set of the 10 landscape replicates. First, we tested the hypotheses that large herbivore abundance

TABLE 1. Description of case study landscapes arranged from west to east in the European boreal biome where field sampling of browsing pressure, browse food supply, and herbivore densities were made.

Country	Case study landscape	Location (latitude and longitude of mid-point)	Forest cover in $100 \times 100$ km area (%) <sup>†</sup>	Altitude (m) <sup>‡</sup>	Human population density (n/km <sup>2</sup> ) <sup>§</sup>
Norway	Vestfold (VE)	59°22' N, 10°07' E	46	0–1074	106.8 <sup>¶</sup>
Norway	Østerdalen (ØS)	61°39' N, 10°39' E	27	160–2020	3.2
Sweden	Bergslagen (BE)	59°57' N, 14°30' E	65	200–400	12.6
Sweden	Asa (AS)	57°15' N, 14°36' E	61	133–368	27.4
Latvia	Smiltene (SM)	57°17' N, 26°14' E	51	42–276	13.5
Belarus	Ostrovets (OS)	54°33' N, 26°04' E	37	117–318	36.5
Belarus	Novogrudok (NO)	53°40' N, 26°18' E	31	116–311	29.6
Russian Federation	Pskov (PS)	58°22' N, 29°09' E	65	30–190	8.1
Finland	Ilomantsi (IL)	62°42' N, 31°06' E	55	68–324	3.0
Russian Federation	Komi (KO)	61°53' N, 52°09' E	67	72–263	11.9

<sup>†</sup> Hansen et al. (2013).

<sup>‡</sup> Jarvis et al. (2008).

<sup>§</sup> Center for International Earth Science Information Network (CIESIN), Columbia University; International Food Policy Research Institute (IFPRI), The World Bank; and Centro Internacional de Agricultura Tropical (CIAT 2011, Balk et al. 2006).

<sup>¶</sup> High human population density, due to the inclusion of Oslo city in this grid cell.

TABLE 2. Properties of the 10 sampled case study landscapes.

Area	LH index	Moose (%)	Red deer (%)	Roe deer (%)	Moose pellets	Field layer	Tree layer	Carn sp	Herb sp	Formanint
Vestfold (VE)	0.07 (0.07)	100	0	0	0.20 (0.19)	9.4 (5.0)	13.93 (3.42)	1.6	3.0	0.27
Østerdalen (ØS)	0.56 (0.18)	100	0	0	1.62 (0.53)	60.5 (15.0)	0.81 (0.18)	3.0	3.0	0.22
Bergslagen (BE)	0.42 (0.12)	99.2	0	0.01	1.20 (0.35)	68.1 (23.7)	0.81 (0.18)	2.9	3.0	0.74
Asa (AS)	0.16 (0.11)	81.6	0	18.3	0.45 (0.33)	12.8 (8.8)	4.00 (1.12)	1.0	3.0	0.89
Smiltene (SM)	0.05 (0.04)	72.1	9.2	18.8	0.12 (0.10)	22.7 (8.5)	4.42 (1.54)	2.6	3.0	0.60
Ostrovets (OS)	0.21 (0.15)	96.7	0	3.3	0.60 (0.44)	0.7 (0.6)	1.90 (0.45)	1.6	3.0	0.23
Novogrudok (NO)	0.13 (0.10)	88.1	9.3	2.5	0.35 (0.30)	30.3 (14.5)	5.71 (1.57)	1.1	3.0	0.18
Pskov (PS)	0	-	-	-	0	191.8 (110.3)	19.17 (6.23)	3.0	2.2	0.25
Ilomanisi (IL)	0.01 (0.01)	100	0	0	0.02 (0.03)	84.5 (20.6)	6.68 (1.74)	3.0	1.9	0.44
Komi (KO)	0.02 (0.02)	100	0	0	0.05 (0.06)	2.9 (3.0)	16.65 (4.7)	3.0	1.0	0.28

Notes: Values include large herbivore index (LH index) and the percentage contribution of the surveyed cervid species to this index (moose, red deer, and roe deer), mean ( $\pm 95\%$  CI) number of pellet piles of moose (moose pellets), field layer food (field layer;  $\text{dm}^3/100 \text{ m}^2$ ), tree layer food (tree layer;  $\text{m}^3/100 \text{ m}^2$ ), the average number of carnivore (Carn sp) and herbivore (Herb sp) species in the local landscape based on data from Figs. 2 and 3, and forest management intensity (Formanint) from Fig. 4 (mean forest harvest/yr).

and forest management intensity, respectively, is related to mean damage levels among the landscape replicates, by running a linear regression with mean damage level of the four tree species as response variable, and large herbivore index and forest management intensity as explanatory variables, respectively. Second, we did a multivariate analysis using PCA to describe the 10 landscapes further.

RESULTS

Herbivore abundance

The herbivore index decreased from west to east ( $F_{9,90} = 9.06, P < 0.001$ , Table 2). Moose was the dominant contributor to this index, and the number of moose pellet piles was heterogeneous among the 10 landscapes sampled ( $\chi^2 = 74.06, \text{df} = 9, P < 0.001$ ), with an overall decrease from west to east, except for Vestfold in Norway (Table 2).

Forest management intensity

The analysis of the mean annual rate of forest loss as a proxy of forest management intensity shows large variation among the case study landscapes (Fig. 4). This ranged from homogenously higher values ( $>0.3\%$  per year) in Sweden, Finland, and Latvia than in Norway, Belarus, and northwest Russia (Table 2).

Field and tree layer browse

For field layer browse, we found a significant difference among the landscapes ( $F_{9,90} = 2.23, P = 0.027$ , Table 2), but with no consistent west-east pattern. Also for tree layer browse, we found a significant difference among the landscapes ( $F_{9,90} = 11.29, P < 0.001$ , Table 2), and here (with the exception of Vestfold in Norway) there was an increase in tree layer browse from west to east.

Browsing damage

We observed a significant decrease in mean browsing damage from west to east across the boreal biome for aspen ( $F_{9,58} = 10.01, P < 0.001$ ), rowan ( $F_{9,67} = 12.06, P < 0.001$ ), and willow ( $F_{9,71} = 13.87, P < 0.001$ ; Fig. 5). The same significant pattern was observed for Scots pine ( $F_{9,78} = 17.47, P < 0.001$ ; Fig. 6).

Meta-analyses of landscapes

Positive correlations ( $P < 0.05$ ) were observed for LH index vs. Tree damage and Herb sp vs. Tree damage, and negative correlations for young tree browse (Tree layer) vs. LH index, Tree layer vs. Tree damage, and Herb sp vs. Tree layer, and Herb sp vs. Carn sp (Table 3, see Table 2 for abbreviations). The mean damage level on the four tree species at the landscape level increased as the large herbivore index increased ( $t = 3.99, \text{df} = 7, P = 0.005, r^2 = 0.59$ ).

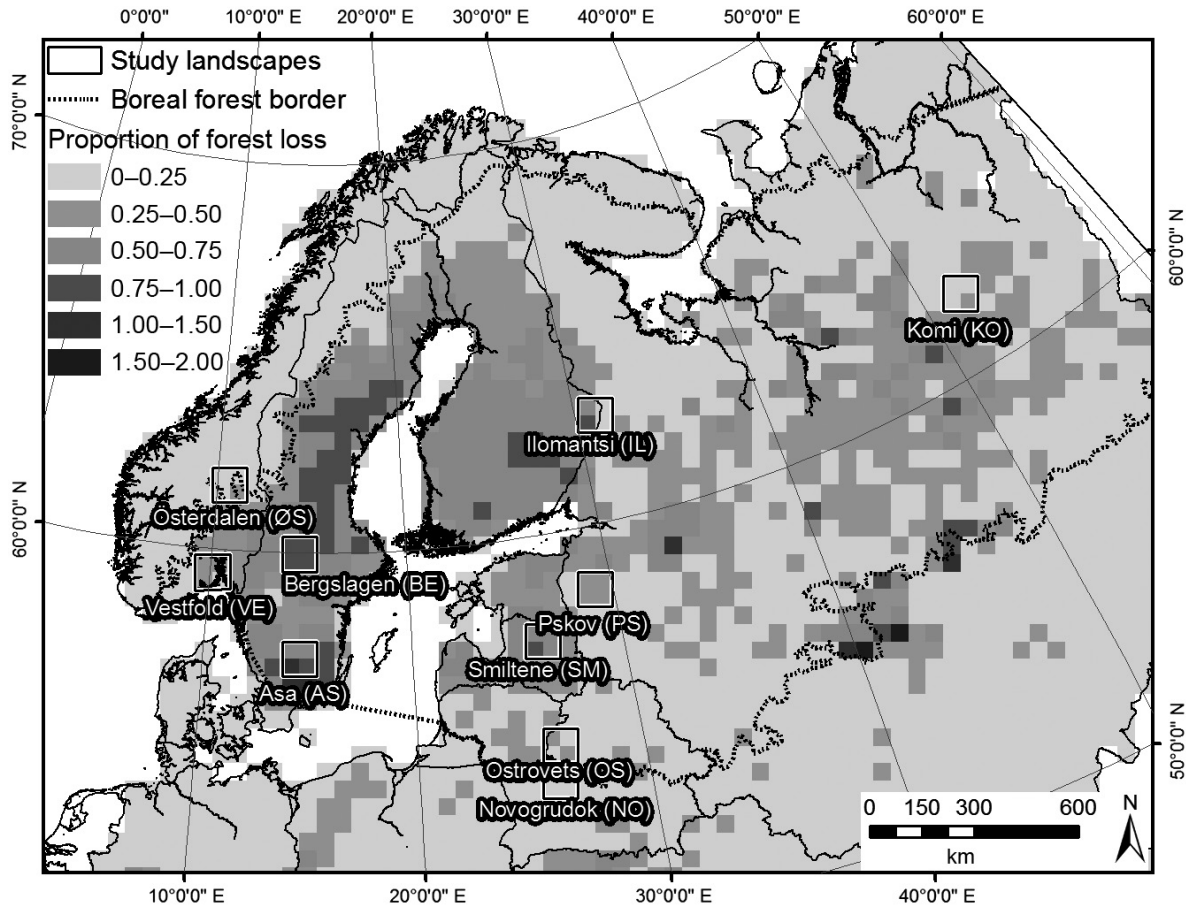


FIG. 4. Variation in forest management intensity in northern Europe. Map showing annual forest loss (Hansen et al. 2013), of which 7% is linked to forest fire and windfall and the rest to clear-felling.

However, there was no relationship between the mean damage level and forest management intensity ( $t = 1.73$ ,  $df = 7$ ,  $P = 0.127$ ,  $r^2 = 0.06$ ; see Fig. 7). The PCA axis 1 and 2 explained 74% of the variation in the data set. The number of herbivore species, large herbivore index, damage of the four focal tree species, and forest management intensity

index were all related to negative values of PC1. On the other hand, the number of large carnivore species, field, and tree layer food were related to positive values of PC1 (Fig. 8, Table 4). Note, however, field layer food was not correlated to any other variable (Table 3). Field layer food and number of large carnivore species were related to the

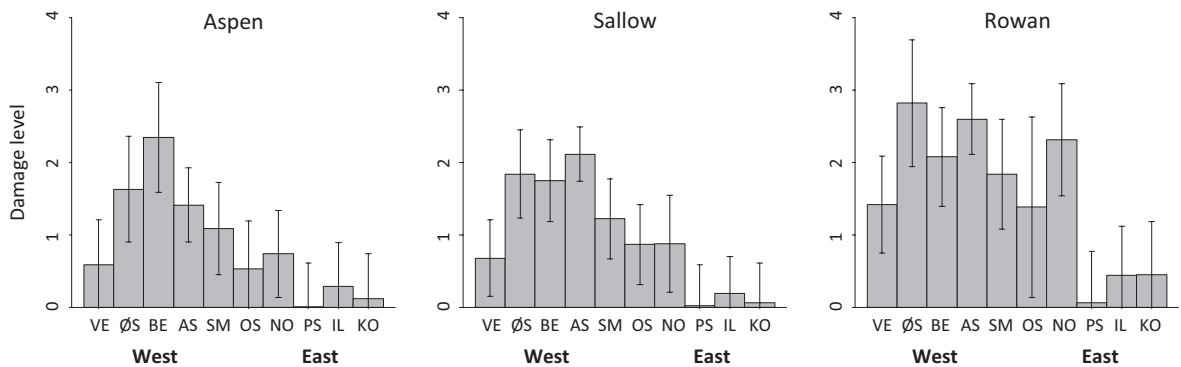


FIG. 5. Estimates of mean damage level for aspen, rowan, and sallow on a scale from 0 (unbrowsed) to 3 (all shoots browsed/bark stripping/stem breakage/top shoot browsing), and 4 (dead by browsing) per stand ( $\pm 95\%$  CI) in the 10 boreal case study landscapes (for abbreviations, see Table 1).



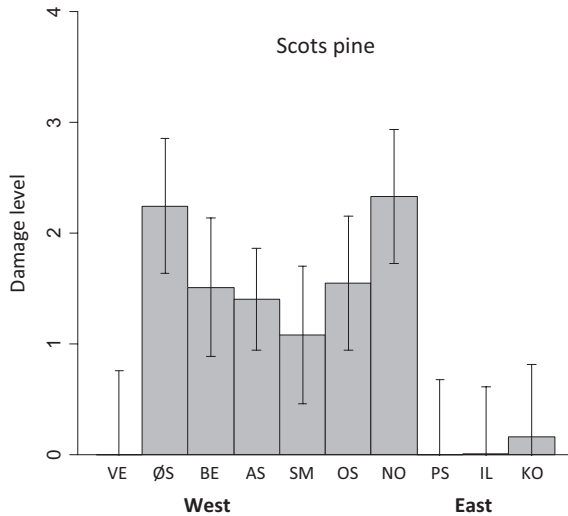


FIG. 6. Estimates of mean damage level for Scots pine on a scale from 0 (unbrowsed) to 3 (all shoots browsed/bark stripping/stem breakage/top shoot browsing), and 4 (dead by browsing) per stand ( $\pm 95\%$  CI) in the 10 boreal case study landscapes (for abbreviations, see Table 1).

negative values of PC2. Thus PC1 can be viewed as herbivore abundance (LH Index) and young tree damage vs. young tree layer browse gradient, while PC2 can be viewed as a carnivore gradient. The 10 landscapes were grouped depending on similarity with regard to the variables in the PCA, with Novogrudok, Ostrovets, Vestfold (and possibly Asa) being one group, Østerdalen and Bergslagen another group, and Komi, Ilomantsi, and Pskov being a third group with the lowest browsing damages. Smiltene displayed intermediate values of most variables, and thus did not belong to any particular group.

DISCUSSION

Clear macroecological patterns

Dose–response relationships require sufficient variation in the independent variable. Because wildlife and forest management approaches are context dependent, relationships may not be found within a homogenous unit such as a country, but may be clear when comparing different

countries (e.g., Roberge et al. 2008a). Thus, while Bergqvist et al. (2014) did not find any relationship between browsing damages of aspen and relative moose density in Sweden, Angelstam et al. (2000) found a strong relationship when including study areas in Sweden, Finland and Russia. The selection principle for choosing the 10 landscapes in 6 countries where field data in this study were collected was based on Peterson et al.'s (2003) observation that, across large geographic regions, ungulates commonly achieve high density only when predation is relatively low (fewer than two species of predators). This was confirmed by the negative correlation between the mean number of large carnivores and herbivores across the 10 landscapes in northern Europe. This is consistent with the macroecological spatial pattern of a contiguous area with three species of large carnivores in the northeast part of the European continent (Fig. 2) and contiguous distribution of three species of large herbivores in the southwest (Fig. 3). The field data showed that moose contributed by far the most to the Large Herbivore Index.

The patterns of moose densities in the contiguous vs. fragmented areas of large carnivores are clearly different. Thus, in the east moose densities were lower than in the west. In European Russia with three large carnivore species moose densities range from less than 0.01 to 0.3 moose/km<sup>2</sup> (Petrosyan et al. 2012). In contrast, where large carnivores have reduced densities or have been extirpated moose densities are higher. Finland is the only country that has official density goals, set by the Ministry of Agriculture and Forestry. Since 1995, the goal has been to have 0.2–0.5 moose/km<sup>2</sup> in most of the country, except for the northernmost areas where the goal has been lower, 0.05–0.3 moose/km<sup>2</sup>. In contrast moose density in Norway and Sweden are higher than in Finland. For Norway Ueno et al. (2014) reported 0.4 to 2.8 moose/km<sup>2</sup>. Lavstund et al. (2003) reviewed moose densities in the Fennoscandia, and reported mean densities of ca. 1 moose/km<sup>2</sup> in Norway and Sweden.

We argue that the gradients in large carnivore and herbivore distribution are a result of the landscape history of the European continent (e.g., Angelstam et al. 2004, Hearn 2015). The often homogenous policy and management regimes of natural resources within individual countries in boreal Europe have led to small differences in human influence on biophysical characteristics, trophic

TABLE 3. Correlation matrix for key variables in this study.

Variables	Formanint	LH index	Tree damage	Field layer	Tree layer	Carn sp.	Herb sp.
Formanint	1	0.09	0.40	-0.13	-0.38	-0.10	0.23
LH index		1	0.80*	-0.08	-0.69*	0.11	0.50
Tree damage			1	-0.34	-0.83*	-0.33	0.74*
Field layer				1	0.36	0.53	-0.17
Tree layer					1	0.20	-0.64*
Carn sp.						1	-0.53*
Herb sp.							1

Notes: Data from table 2, except tree damage, which was estimated as the mean of tree damage levels for the data presented in Figs. 5 and 6.

\* $P < 0.05$ .

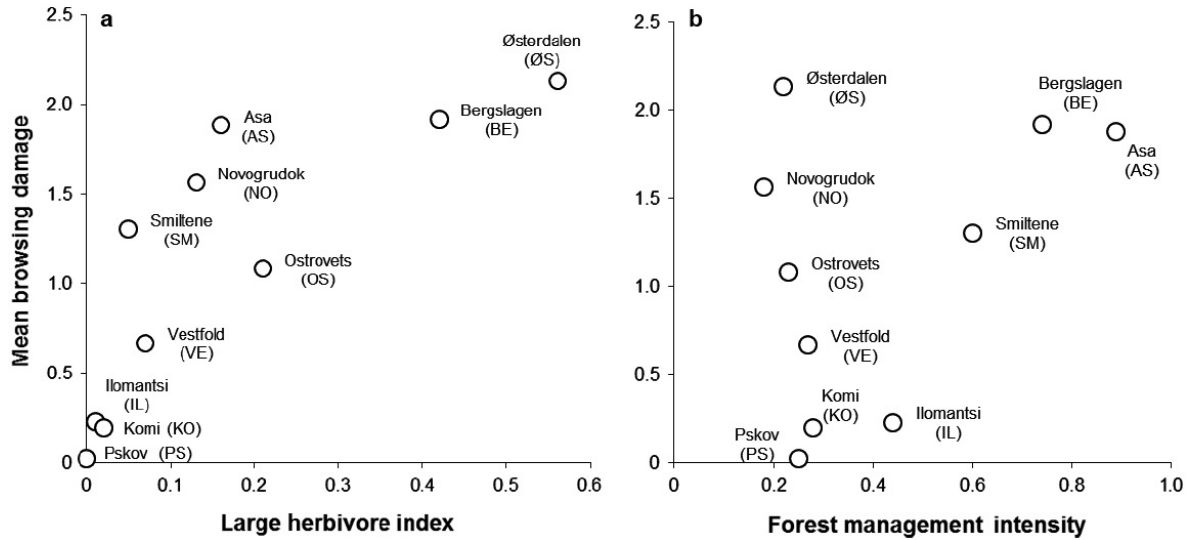


FIG. 7. Relationship between (a) the large herbivore index and (b) forest management intensity and average damage levels of aspen, rowan, willow, and Scots pine among the 10 case study landscapes in northern Europe's boreal biome.

interactions and tree damage levels within countries. However, the variation among different countries can be vastly different based on their past and present land uses (Danilov 1987, Nygrén 1987). Forests and woodland once dominated Europe (Mayer 1984, Rackham 2003). Most of the continent has been severely altered throughout history (Hannah et al. 1995). The rate of change increased with the advent of the industrial revolution (Thomas 1956,

Good 1994, Sylla and Toniolo 1991). The development of transport infrastructures and the associated intensification of human land use resulted in an increase in hunting and decimation of large vertebrate populations (Breitenmoser 1998, Mikusiński and Angelstam 2004). Consequently, the parts of Europe that were situated far from the transport infrastructures, such as railroads and rivers draining into the North and Baltic Seas, remained less economically developed than the rest of Europe (Chirot 1989). This means that landscapes were affected differently regarding the loss of species with large area requirements, depending on their location in relation to the center and periphery of human economic activity (Trauger et al. 2003).

The field data about browsing damage on ecologically and economically important tree species demonstrated a gradient that paralleled both carnivore–herbivore distribution and the Large Herbivore Index. As predicted, a decreasing large herbivore density index was linked to lower levels of tree damage, and more available tree layer browse. However, one case study landscape indicated there may also be variation within countries based on specific management actions. This relates to the western-most study landscape, Vestfold in Norway, which deviated from the general negative relationship between Large Herbivore Index and browsing damage. A plausible reason for this is that moose management in Vestfold region in Norway undertook dramatic management actions to reduce the moose population (Solberg et al. 2006) due to a long history of high browsing pressure by moose on trees. Thus, Vestfold is more similar to the landscapes found further east such as Ostrovets or Novogrudok in Belarus, as also shown in the PCA (Fig. 8). This argument is supported by the clear overall positive relationships observed between mean browsing damage levels on the four tree species on the one hand, and the large herbivore index on the other.

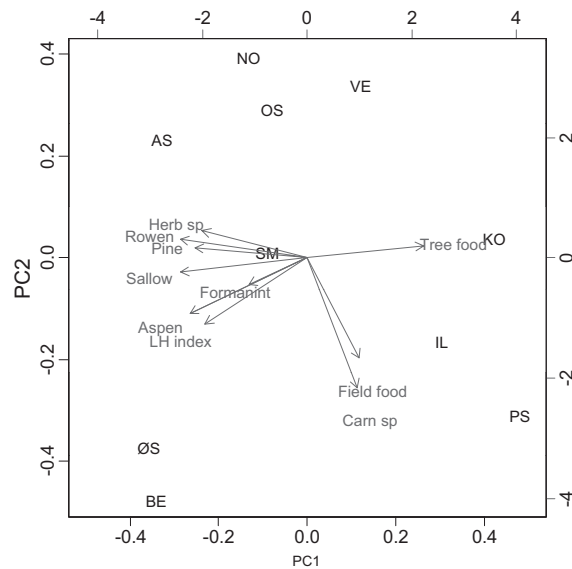


FIG. 8. PCA of the 10 boreal case study landscapes (for abbreviations, see Table 1), and the means for each landscape of the respective main variables of this study: forest management intensity (Formanint), number of herbivore species (Herb sp), number of carnivore species (Carn sp), Large herbivore index (LH index), field layer food (Field food), tree layer food (Tree food), as well as mean damage for the focal tree species aspen, rowan, willow, and Scots pine.

TABLE 4. Loadings for principal component factor 1 and factor 2 of the key variables in this study.

Variables	Factor 1	Factor 2
Forestry	-0.43	-0.02
LHI	-0.72	-0.56
Tree damage	-0.96	-0.15
Field layer	0.45	-0.64
Tree layer	0.89	0.18
Carn sp.	0.45	-0.81
Herb sp.	-0.82	0.07

Note: Data from table 2, except tree damage, which was estimated as the mean of tree damage levels for the data presented in Figs. 5 and 6.

The alternative hypothesis that tree damage levels are related to the local forest management intensity was not supported. Both Sweden and Finland have the same forest industrial regimes based on maximum sustained yield forestry by using an even-aged forest management system (e.g., Elbakidze et al. 2013), but in spite of this they have clear differences in browsing damages of both ecologically and economically important tree species.

A long history of high browsing pressure makes it difficult to comprehend the magnitude of change in the abundance of mature individuals of preferred browse species (e.g., Ripple and Beschta 2007). Additionally, as illustrated by the two Norwegian landscapes in this study there may be variation among regions within countries based on specific management actions. The macroecological approach in this study clearly illustrates the need to secure sufficient variation in independent variables (i.e., large herbivore abundance at the landscape level) to detect their effects on vegetation (i.e., browsing damages on ecologically and economically important tree species). This confirms the importance of studying the consequences of altered trophic interactions in multiple landscapes rather than in a single landscape or region alone.

On average, moose accounted for 93% of the large herbivore density index. Also other studies have reported clear relationships between moose density and damage levels on young trees. In Russia, a density of 0.3–0.5 moose/km<sup>2</sup> was associated with retarded growth of preferred forage species such as aspen, whereas normal stand development occurred at 0.2–0.3 moose/km<sup>2</sup> (Abaturov and Smirnov 1992). Similarly, Bergeron et al. (2011) found a direct correlation between browse damage and moose density in northern New Hampshire in the USA. A long-term study of dramatic local increase in moose density, ~0.5 to 9.8 moose/km<sup>2</sup>, in the Prioksko-Terrasny Reserve in Russia led to severe alteration of tree species composition (Zablotskaya and Zablotskaya 2002).

#### *Managing trophic interactions and cascading effects through learning*

The ecosystem service concept captures the diversity of human benefits from landscapes' ecosystems (Millennium Ecosystem Assessment 2005, Norgaard 2010). The role

of basic regulating and traditional provisioning ecosystem services are thus complemented by supporting and cultural services (Kumar 2010). Historically, non-wood products, including grazing land for livestock and game meat, were the main goods used from a boreal forest landscape. With industrialization this changed to expanding animal husbandry, agriculture, as well as intensive harvesting and production of wood. Today, nature-based recreation and tourism is emerging, and becoming economically and culturally interesting and important for rural development (e.g., Oliver and Jenkins 2003, Gössling and Hultman 2006). This development towards a very diverse portfolio of ecosystems services as a base for local and regional development may result in different views among stakeholders (Lidskog et al. 2013, Mattisson et al. 2014), and even conflicts among competing actors. Good examples are maintaining green infrastructures for biodiversity vs. sustained yield forestry (Angelstam et al. 2011a), satisfying social forest values vs. wood production (Andersson et al. 2013, Giergiczny et al. 2015), and large carnivore conservation vs. rural development (Ericsson and Heberlein 2003, Gangaas et al. 2013).

It is vital and challenging to understand and manage trophic interaction between predators, prey and the associated cascading effects in forest landscapes (Graham et al. 2005). Disruption of trophic interactions at various spatial scales may pose multiple threats to ecosystem services benefiting human well-being, as well as green infrastructure as habitats for species (Treves and Karanth 2003, Treves et al. 2006). Policy and management decisions impact trophic interactions, which can often cause a mixture of human–human, human–wildlife, and wildlife–wildlife induced conflicts (Graham et al. 2005). Ongoing policy and management debates in Fennoscandia on large carnivores provide a good example. The distribution and abundance of large carnivores have been severely reduced during past centuries (Curry-Lindahl 1972, Spong and Hellborg 2002, Flagstad et al. 2003). The past history of forest management with a strong focus on conifers was clearly negative on the amount of ecologically important old deciduous trees (Halme et al. 2013, Lindbladh et al. 2014). Similarly, in Germany conflicts arose by the return of large carnivores because of perceived negative effects of predation on animal husbandry and hunting (Reinhardt et al. 2013). Additionally, serious conflict has arisen between foresters and hunters concerning large herbivore browsing damage (Kuijper 2011), where both increased hunting and viable large carnivore populations can reduce browsing damage (Hothorn and Müller 2010). This has led to EU-level conservation policy that requires member states to support the development of viable populations of large carnivores. In contrast, many hunters' desire to reduce large carnivore numbers for the safety of their hunting dogs, and to increase the numbers of large herbivores as a resource for game meat and recreation value (Angelstam 2002). Similarly, farmers are concerned with increased

economic loss through predation of livestock. Attitudes towards large carnivores differ between urban and rural inhabitants (Sjölander-Lindqvist 2007), as well as among rural inhabitants (Gangaas et al. 2013). In contrast, the forest industry is highlighting their economic loss caused by high numbers of large herbivores and their effects on recruitment of economically important tree species (Glommen Skog BA 2010, Sveaskog 2014). Management of large carnivores, large herbivores and cascading effects in forest landscapes thus need to be integrated (Schwartz et al. 2003).

The key herbivore species in all the 10 landscapes was moose. In Fennoscandia the populations of moose have increased considerably over recent decades (e.g., Edenius et al. 2002). These large and productive populations have led to major socio-economic challenges. At the landscape level, the most prominent effects of moose seem to be suppression of preferred browse species (Edenius et al. 2002). This includes the distribution of costs and benefits associated with the species' effects on young Scots pine stands and preferred deciduous tree species, as well as moose hunting, which includes both provisioning ecosystem services (meat) as well as cultural ecosystem services (recreation and maintenance of social capital in rural areas). Large moose densities also leads to socio-economic costs associated with traffic accidents (Seiler 2003).

This study was designed based on the observed negative relationship between the number of large carnivore and large herbivore species among regions in northern Europe (Figs. 2, 3). This suggests that predators control prey, and this study shows that there is a relationship between large herbivore abundance and the level of browsing damage on trees. Can hunters replace large carnivores as predators in the ecosystem? The situation in the Vestfold landscape in Norway suggests that this is the case. Collaborative management of moose and forests requires comprehensive monitoring programs for plants and animals across spatial scales, as well as extensive ecological knowledge of the relationships between moose and their food plants and subsequent cascading effects (Edenius et al. 2002). However, Sandström et al. (2013) showed that there are major challenges remaining to be tackled in the Swedish social system on establishing inclusive partnerships between forest owners and hunters for managing moose in landscapes with fragmented property rights and structure. In addition, Skaarnæs-Moldestad (2012) showed that youth are less committed to the management of moose than their parents and grandparents. This implies a potential problem for their acceptance into the community of hunters and may present further challenges to sustaining the number of hunters. Because stakeholder groups have different objectives, this is likely to lead to difficulties in reaching a collective agreement and actions. Additionally, Bjärstig et al. (2014) showed that lack of funding and unclear roles and responsibilities appear to be the most serious barriers for introducing ecosystem management for moose-forest

interactions. We suggest that macroecological studies comparing countries and regions with different traditions and governance systems can support the development of more holistic views by learning about the management of complex trophic interactions across wider gradients of key variables than can be found within any individual country.

In conclusion, the scale of labor, effort, and commitment associated with intensive large-scale case studies, and limited experience in managing trophic interactions calls for both integrated interdisciplinary work including both researchers and stakeholder, and for a network of case studies that match the spatial extent of trophic interactions (Angelstam et al. 1997). To arrive at robust conclusions about suitable approaches for management of trophic interactions one has to consider landscapes with different predator-prey ratios, landscape uses, and past histories, as well as with different governance arrangements and their legitimacy (Angelstam et al. 2013, Peterson et al. 2014). To support knowledge production about the integrated management of large carnivores, large herbivores, and cascading effects on forest ecosystems and their ecosystem services, we encourage researchers to carry out macroecological comparative studies that include variation in both landscape history, and different governance and management regimes. This provides opportunity for initiating a process of collaborative learning among actors and stakeholders with different portfolios of landscape benefits (e.g., Granados-Cabezas 1995, Faludi 2000, Albrechts 2004).

#### ACKNOWLEDGMENTS

We thank Vladimir Naumov, Gintare Narauskaite, Maxim Trishkin, Eirik Gran Seim, Vårin Vedaa Pedersen, Michail Maksimenkov, Vasili Shakun, and Sergey Uglianets for their dedicated field assistance, and Evgeny Lopatin for providing access to the Ilomantsi research station and facilitating data collection. We also like to thank Therese Bjärstig, Pablo Garrido, Marco Heurich, Rolf Petersen, Johan Månsson, Bill Ripple, and John Vucetich for their inspiring comments to previous versions of the manuscript. This work was supported by the Swedish Research Council Formas (grant number 2011-1737) to Per Angelstam and by the Swedish Institute (grant number 10976/2013) to Marine Elbakidze.

#### LITERATURE CITED

- Abaturov, B. D., and K. A. Smirnov. 2002. Effects of moose population density on development of forest stands in central European Russia. *Alces* 38:S1-S1.
- Ahlén, I. 1975. Winter habitats of moose and deer in relation to land use in Scandinavia. *Swedish Wildlife Research* 9: 45-192.
- Albrechts, L. 2004. Strategic (spatial) planning re-examined. *Environment and Planning B: Planning and Design* 31: 743-758.
- Andersson, K., P. Angelstam, M. Elbakidze, R. Axelsson, and E. Degerman. 2013. Green infrastructures and intensive forestry: need and opportunity for spatial planning in a Swedish rural-urban gradient. *Scandinavian Journal of Forest Research* 28:143-165.

- Andrén, H., and P. Angelstam. 1993. Moose browsing on Scots pine in relation to stand size and distance to forest edge. *Journal of Applied Ecology* 30:133–142.
- Angelstam, P. 2002. Large mammals, people, and the landscape—can trophic interactions be managed? Pages 54–59 in R. Field, R. J. Warren, H. Okarma, and P. R. Sievert, editors. *Wildlife, land and people: priorities for the 21st century*. The Wildlife Society, Bethesda, Maryland, USA.
- Angelstam, P. K., et al. 1997. Biodiversity and sustainable forestry in European forests: How east and west can learn from each other. *Wildlife Society Bulletin* 25:38–48.
- Angelstam, P., P.-E. Wikberg, P. Danilov, W. E. Faber, and K. Nygrén. 2000. Effects of moose density on timber quality and biodiversity restoration in Sweden, Finland, and Russian Karelia. *Alces* 36:133–145.
- Angelstam, P., T. Edman, M. Dönnz-Breuss, and M. F. W. DeVries. 2004. Land management data and terrestrial vertebrates as indicators of forest biodiversity at the landscape scale. *Ecological Bulletins* 51:333–349.
- Angelstam, P., K. Andersson, R. Axelsson, M. Elbakidze, B. G. Jonsson, and J.-M. Roberge. 2011a. Protecting forest areas for biodiversity in Sweden 1991–2010: policy implementation process and outcomes on the ground. *Silva Fennica* 45: 1111–1133.
- Angelstam, P., R. Axelsson, M. Elbakidze, L. Laestadius, M. Lazdinis, M. Nordberg, I. Pătru-Stupariu, and M. Smith. 2011b. Knowledge production and learning for sustainable forest management on the ground: Pan-European landscapes as a time machine. *Forestry* 84:581–596.
- Angelstam, P., M. Grodzynski, K. Andersson, R. Axelsson, M. Elbakidze, A. Khoroshev, I. Kruhlov, and V. Naumov. 2013. Measurement, collaborative learning and research for sustainable use of ecosystem services: landscape concepts and Europe as laboratory. *Ambio* 42:129–145.
- Apollonio, M., R. Andersen, and R. Putman. 2010. *European ungulates and their management in the 21st century*. Cambridge University Press, New York, New York, USA.
- Austrheim, G., E. J. Solberg, and A. Mysterud. 2011. Spatio-temporal variation in large herbivore pressure in Norway during 1949–1999: Has decreased grazing by livestock been countered by increased browsing by cervids? *Wildlife Biology* 17:286–298.
- Balk, D. L., U. Deichmann, G. Yetman, F. Pozzi, S. I. Hay, and A. Nelson. 2006. Determining global population distribution: methods, applications and data. *Advances in Parasitology* 62:119–156 [https://doi.org/10.1016/S0065-308X\(05\)62004-0](https://doi.org/10.1016/S0065-308X(05)62004-0).
- Bergeron, D. H., P. J. Pekins, H. F. Jones, and W. B. Leak. 2011. Moose browsing and forest regeneration: a case study in northern New Hampshire. *Alces* 47:39–51.
- Bergqvist, G., R. Bergström, and M. Wallgren. 2014. Recent browsing damage by moose on Scots pine, birch and aspen in young commercial forests—effects of forage availability, moose population density and site productivity. *Silva Fennica* 48:1–13.
- Bergström, R., and O. Hjeljord. 1987. Moose and vegetation interactions in northwestern Europe and Poland. *Swedish Wildlife Research* 1:213–228.
- Björstig, T., C. Sandström, S. Lindqvist, and E. Kvastegård. 2014. Partnerships implementing ecosystem-based moose management in Sweden. *International Journal of Biodiversity Science, Ecosystem Services & Management* 10:228–239.
- Brazaitis, G., K. Pēteliš, R. Žalkauskas, O. Belova, D. Danusevičius, V. Marozas, and G. Narauskaitė. 2014. Landscape effect for the Cervidae *Cervidae* in human dominated fragmented forests. *European Journal of Forest Research* 5:857–869.
- Breitenmoser, U. 1998. Large predators in the Alps: the fall and rise of man's competitors. *Biological Conservation* 83: 279–289.
- Breitenmoser, U., D. P. Mallon, von Arx M., and C. Breitenmoser-Wursten. 2008. *Lynx lynx*. The IUCN Red List of Threatened Species. Version 2014.2. [www.iucnredlist.org](http://www.iucnredlist.org)
- Brown, J. H. 1995. *Macroecology*. University of Chicago Press, Chicago, Illinois, USA.
- Cederlund, G., and R. Bergström. 1996. Trends in the moose – forest system in Fennoscandia, with special reference to Sweden. Pages 265–281 in R. M. DeGraaf and R. I. Miller, editors. *Conservation of faunal diversity in forested landscapes*. Chapman and Hall, London, UK.
- Cederlund, G., H. Ljungqvist, G. Markgren, and F. Staffelt. 1980. Foods of moose and roe-deer at Grimsö in central Sweden. Results of rumen content analyses. *Viltrevy* 11:169–244.
- Center for International Earth Science Information Network—CIESIN—Columbia University, International Food Policy Research Institute—IFPRI, The World Bank, and Centro Internacional de Agricultura Tropical—CIAT. 2011. *Global Rural-Urban Mapping Project, Version 1 (GRUMPv1): Population Density Grid*. NASA Socioeconomic Data and Applications Center (SEDAC), Palisades, New York, USA.
- Chapron, G., et al. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* 346:1517–1519.
- Chiot, D. 1989. *The origins of backwardness in Eastern Europe: economics and politics from the Middle Ages until the early twentieth century*. University of California Press, Berkeley, California, USA.
- Curry-Lindahl, K. 1972. *The Brown Bear (Ursus arctos) in Europe: decline, present distribution, biology and ecology*. International Conference on Bear Research and Management 2:74–80.
- Danell, K., R. Bergström, L. Edenius, and G. Ericsson. 2003. Ungulates as drivers of tree population dynamics at module and genet levels. *Forest Ecology and Management* 181:67–76.
- Danell, K., R. Bergström, P. Duncan, and J. Pastor. 2006. *Large herbivore ecology, ecosystem dynamics and conservation*. Cambridge University Press, New York, New York, USA.
- Danilov, P. 1987. Population dynamics of moose in USSR (literature survey, 1970–1983). *Swedish Wildlife Research* 1:503–523.
- Diamond, J. 1986. Overview: laboratory experiments field experiments and natural experiments. Pages 3–22 in J. M. Diamond and T. J. Case, editors. *Community ecology*. Harper and Row, New York, New York, USA.
- Edenius, L., M. Bergman, G. Ericsson, and K. Danell. 2002. The role of moose as a disturbance factor in managed boreal forests. *Silva Fennica* 36:57–67.
- Elbakidze, M., K. Andersson, P. Angelstam, G. W. Armstrong, R. Axelsson, F. Doyon, M. Hermansson, J. Jacobsson, and Y. Pautov. 2013. Sustained yield forestry in Sweden and Russia: How does it correspond to sustainable forest management policy? *Ambio* 42:160–173.
- Elmhagen, B., and S. P. Rushton. 2007. Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? *Ecology Letters* 10:197–206.
- Elmhagen, B., G. Ludwig, S. P. Rushton, P. Helle, and H. Lindén. 2010. Top predators, mesopredators and their prey: interference ecosystems along bioclimatic productivity gradients. *Journal of Animal Ecology* 79:785–794.
- Ericsson, G., and T. A. Heberlein. 2003. Attitudes of hunters, locals, and the general public in Sweden now that the wolves are back. *Biological Conservation* 111:149–159.
- ESRI. 2012. *ESRI ArcGIS Desktop 10.1 ArcInfo Licence*. ESRI, Redlands, California, USA.

- Faludi, A. 2000. The performance of spatial planning. *Planning Practice and Research* 15:299–318.
- Flagstad, Ø., C. W. Walker, C. Vilà, A. K. Sundqvist, B. Fernholm, A. K. Hufthammer, Ø. Wiig, I. Koyola, and H. Ellegren. 2003. Two centuries of the Scandinavian wolf population: patterns of genetic variability and migration during an era of dramatic decline. *Molecular Ecology* 12: 869–880.
- Gangaas, K. E., B. P. Kaltenborn, and H. P. Andreassen. 2013. Geo-spatial aspects of acceptance of illegal hunting of large carnivores in Scandinavia. *PLoS ONE* 8:e68849.
- Gervasi, V., et al. 2012. Predicting the potential demographic impact of predators on their prey: a comparative analysis of two carnivore–ungulate systems in Scandinavia. *Journal of Animal Ecology* 81:443–454.
- Giergiczny, M., M. Czajkowski, T. Żylicz, and P. Angelstam. 2015. Choice experiment assessment of public preferences for forest structural attributes. *Ecological Economics* 119:8–23.
- Gill, R. M. A. 1992a. A review of damage by mammals in north temperate forest: 3. Impact on trees and forests. *Forestry* 65:363–388.
- Gill, R. M. A. 1992b. A review of damage by mammals in north temperate forests: 1. Deer. *Forestry* 65:145–169.
- Gill, R. M. A. 2006. The influence of large herbivores on tree recruitment and forest dynamics. Page 506 in K. Danell, R. Bergström, P. Duncan, and J. Pastor, editors. *Large herbivore ecology, ecosystem dynamics and conservation*. Cambridge University Press, New York, New York, USA.
- Gill, R. M. A., and V. Beardall. 2001. The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. *Forestry* 74:209–218.
- Glommen Skog BA. 2010. Bærekraftig hjorteviltforvaltning i Hedmark. Sluttrapport. Glommen Skog BA, Elverum, Norway [In Norwegian.]
- Good, D. F. 1994. The economic lag of central and eastern Europe: income estimates for the Habsburg successor states, 1870–1910. *Journal of Economic History* 54:869–891.
- Gordon, I. J., and H. H. Prins. 2008. *The ecology of browsing and grazing*. Springer, Berlin, Germany.
- Gössling, S., and J. Hultman, editors. 2006. *Ecotourism in Scandinavia: lessons in theory and practice*. CAB International, Wallingford.
- Graham, K., A. P. Beckerman, and S. Thirgood. 2005. Human–predator–prey conflicts: ecological correlates, prey losses and patterns of management. *Biological Conservation* 122: 159–171.
- Granados-Cabezas, V. 1995. Another mythology for local development? Selling places with packaging techniques: a view from the Spanish experience on city strategic planning. *European Planning Studies* 3:173–187.
- Gren, I.-M., P. Baxter, G. Mikusiński, and H. Possingham. 2014. Cost effective biodiversity restoration with uncertain growth in forest habitat quality. *Journal of Forest Economics* 20:77–92.
- Gunst, P. 1989. Agrarian systems of central and eastern Europe. Pages 53–91 in D. Chirot, editor. *The origins of backwardness in Eastern Europe: economics and politics from the Middle Ages until the early twentieth century*. California University Press, Berkeley, California, USA.
- Halme, P., et al. 2013. Challenges of ecological restoration: lessons from forests in northern Europe. *Biological Conservation* 167:248–256.
- Hannah, L., J. Carr, and A. Lanerani. 1995. Human disturbance and natural habitat: a biome level analysis of a global data set. *Biodiversity and Conservation* 4:128–155.
- Hansen, M. C., et al. 2013. High-resolution global maps of 21st-century forest cover change. *Science* 342:850–853.
- Hearn, R. 2015. Gains and losses in the European mammal fauna. Pages 193–206 in K. J. Kirby and D. Watkins, editors. *Europe's changing woods and forests: from wildwood to cultural landscapes*. CABI, Wallingford, UK.
- Henttonen, H., M. Stubbe, T. Maran, and A. Tikhonov. 2008. *Alces alces*. The IUCN red list of threatened species. Version 2014.2. [www.iucnredlist.org](http://www.iucnredlist.org)
- Hothorn, T., and J. Müller. 2010. Large-scale reduction of ungulate browsing by managed sport hunting. *Forest Ecology and Management* 260:1416–1423.
- Huntington, S. P. 1997. *The clash of civilizations*. Simon & Schuster UK, London, UK.
- IUCN. 2014. The IUCN red list of threatened species. Version 2014.2. [www.iucnredlist.org](http://www.iucnredlist.org)
- Jarvis, A., H. I. Reuter, A. Nelson, and E. Guevara. 2008. Hole-filled seamless SRTM data V4. International Centre for Tropical Agriculture (CIAT). <http://srtm.csi.cgiar.org>
- Kaczynsky, P., G. Chapron, M. Von Arx, D. Huber, H. Andrén, and J. Linnell. 2012. Status, management and distribution of large carnivores–bear, lynx, wolf & wolverine in Europe. European Commission, Brussels, Belgium.
- Katchanovski, I. 2006. Cleft countries. Regional political divisions and cultures in post-Soviet Ukraine and Moldova. *ibidem-Verlag*, Stuttgart, Germany.
- Kuijper, D. P. J. 2011. Lack of natural control mechanisms increases wildlife–forestry conflict in managed temperate European forest systems. *European Journal of Forest Research* 130:895–909.
- Kumar, P. 2010. *The economics of ecosystems and biodiversity: ecological and economic foundations*. UNEP/Earthprint, London, UK.
- Lavsund, S., T. Nygren, and E. J. Solberg. 2003. Status of moose populations and challenges to moose management in Fennoscandia. *Alces* 39:109–130.
- Lehtinen, A. A., J. Donner-Amnell, and B. Sæther. 2004. Politics of forests: Northern forest-industrial regimes in the age of globalization. Ashgate Publishing Company, Aldershot.
- Liberg, O., R. Bergström, J. Kindberg, and H. Von Essen. 2010. Ungulates and their management in Sweden. Pages 37–70 in M. Apollonio, R. Andersen, and R. Putman, editors. *European ungulates and their management in the 21st century*. Cambridge University Press, Cambridge, UK.
- Lidskog, R., G. Sundqvist, A.-S. Kall, P. Sandin, and S. Larsson. 2013. Intensive forestry in Sweden: stakeholders' evaluation of benefits and risk. *Journal of Integrative Environmental Sciences* 10:145–160.
- Lindbladh, M., A.-L. Axelsson, T. Hultberg, J. Brunet, and A. Felton. 2014. From broadleaves to spruce – the borealization of southern Sweden. *Scandinavian Journal of Forest Research* 29:686–696.
- Lindqvist, S., C. Sandström, T. Bjärstig, and E. Kvastegård. 2014. The changing role of hunting in Sweden—from subsistence to ecosystem stewardship? *Alces: A Journal Devoted to the Biology and Management of Moose* 50:53–66.
- Lovari, S., et al. 2008a. *Cervus elaphus*. The IUCN red list of threatened species. Version 2014.2. [www.iucnredlist.org](http://www.iucnredlist.org)
- Lovari, S., et al. 2008b. *Capreolus capreolus*. The IUCN red list of threatened species. Version 2014.2. [www.iucnredlist.org](http://www.iucnredlist.org)
- Månsson, J., C. Kalén, P. Kjellander, H. Andrén, and H. Smith. 2007. Quantitative estimates of tree species selectivity by moose (*Alces alces*) in a forest landscape. *Scandinavian Journal of Forest Research* 22:407–414.
- Månsson, J., H. Andrén, and H. Sand. 2011. Can pellet counts be used to accurately describe winter habitat selection by moose *Alces alces*? *European Journal of Wildlife Research* 57:1017–1023.

- Martikainen, P., L. Kaila, and Y. Haila. 1998. Threatened beetles in white-backed woodpecker habitats. *Conservation Biology* 12:293–301.
- Mathisen, K. M., J. M. Milner, F. M. van Beest, and C. Skarpe. 2014. Long-term effects of supplementary feeding of moose on browsing impact at a landscape scale. *Forest Ecology and Management* 314:104–111.
- Mattisson, J., J. Odden, and J. D. C. Linnell. 2014. A catch-22 conflict: access to semi-domestic reindeer modulates Eurasian lynx depredation on domestic sheep. *Biological Conservation* 179:116–122.
- Mayer, H. 1984. *Wälder Europas*. Gustav Fischer, Stuttgart [In German.]
- McLellan, B. N., C. Servheen, D. Huber, and IUCN SSC Bear Specialist Group. 2008. *Ursus arctos*. The IUCN red list of threatened species. Version 2014.2. [www.iucnredlist.org](http://www.iucnredlist.org)
- Mech, L. D., L. Boitani, and IUCN SSC Wolf Specialist Group. 2010. *Canis lupus*. The IUCN red list of threatened species. Version 2014.2. [www.iucnredlist.org](http://www.iucnredlist.org)
- Melis, C., et al. 2009. Predation has a greater impact in less productive environments: variation in roe deer, *Capreolus capreolus*, population density across Europe. *Global Ecology and Biogeography* 18:724–734.
- Mikusiński, G., and P. Angelstam. 2004. Occurrence of mammals and birds with different ecological characteristics in relation to forest cover in Europe: Do macroecological data make sense? *Ecological Bulletins* 51:265–275.
- Millennium Ecosystem Assessment. 2005. *Ecosystems and human well-being: synthesis*. Island Press, Washington, D.C., USA.
- Milner, J. M., C. Bonenfant, A. Mysterud, J.-M. Gaillard, S. Csányi, and N. C. Stenseth. 2006. Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. *Journal of Applied Ecology* 43:721–734.
- Müller, J., H. Bußler, M. Goßner, T. Rettelbach, and P. Duelli. 2008. The European spruce bark beetle *Ips typographus* in a national park: from pest to keystone species. *Biodiversity and Conservation* 17:2979–3001.
- Mykrä, S., S. Kurki, and A. Nikula. 2000. The spacing of mature forest habitat in relation to species-specific scales in managed boreal forests in NE Finland. *Annales Zoologici Fennici* 37(2):79–91.
- Naumov, V., P. Angelstam, and M. Elbakidze. 2016. Barriers and bridges for intensified wood production in Russia: insights from the environmental history of a regional logging frontier. *Forest Policy and Economics* 66:1–10.
- Nilsson, S. G., U. L. F. Arup, R. Baranowski, and S. Ekman. 1995. Tree-dependent lichens and beetles as indicators in conservation forests. *Conservation Biology* 9:1208–1215.
- Norgaard, R. B. 2010. Ecosystem services: from eye-opening metaphor to complexity blinder. *Ecological Economics* 69:1219–1227.
- Nygrén, T. 1987. The history of moose in Finland. *Swedish Wildlife Research* 1:49–54.
- Oliver, T., and T. Jenkins. 2003. Sustaining rural landscapes: the role of integrated tourism. *Landscape Research* 28:293–307.
- Pasanen-Mortensen, M., M. Pykönen, and B. Elmhagen. 2013. Where lynx prevail, foxes will fail—limitation of a mesopredator in Eurasia. *Global Ecology and Biogeography* 22:868–877.
- Pedersen, S. 2011. Effects of native and introduced cervids on small mammals and birds. Dissertation. Norwegian University of Science and Technology, Trondheim, Norway. <http://www.diva-portal.org/smash/get/diva2:512518/FULLTEXT02>
- Pedersen, S., E. B. Nilsen, and H. P. Andreassen. 2007. Moose winter browsing affects the breeding success of great tits. *Ecoscience* 14:499–506.
- Peterson, R. O., J. A. Vucetich, R. E. Page, and A. Chouinard. 2003. Temporal and spatial aspects of predator-prey dynamics. *Alces* 39:215–232.
- Peterson, R. O., J. A. Vucetich, J. M. Bump, and D. W. Smith. 2014. Trophic cascades in a multicausal world: Isle Royale and Yellowstone. *Annual Review of Ecology, Evolution, and Systematics* 45:325–345.
- Petrosyan, V. G., N. N. Dergunova, S. A. Bessonov, and A. V. Omelchenko. 2012. Modeling the dynamics of population, evaluation and comparative analysis of the demographic parameters of moose in the Russia and Finland using long-term monitoring data. *Mathematical Biology and Bioinformatics* 7:244–256 [In Russian.]
- Putman, R., J. Langbein, P. Green, and P. Watson. 2011. Identifying threshold densities for wild deer in the UK above which negative impacts may occur. *Mammal Review* 41:175–196.
- Rackham, O. 2003. *Ancient Woodland its history, vegetation and uses in England*. Castlepoint Press, London, UK.
- Reinhardt, I., G. Kluth, S. Nowak, and R. Mysłajek. 2013. A review of wolf management in Poland and Germany with recommendations for future transboundary collaboration. BfN Bundesamt für Naturschutz, Bonn, Germany.
- Ripple, W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: Can predation risk structure ecosystems? *BioScience* 54:755–766.
- Ripple, W. J., and R. L. Beschta. 2007. Hardwood tree decline following large carnivore loss on the Great Plains, USA. *Frontiers in Ecology and the Environment* 5:241–246.
- Ripple, W. J., and R. Beschta. 2012. Large predators limit herbivore densities in northern forest ecosystems. *European Journal of Wildlife Research* 58:733–742.
- Ripple, W. J., et al. 2014. Status and ecological effects of the world's largest carnivores. *Science* 343:151–162.
- Ritchie, E. G., B. Elmhagen, A. S. Glen, M. Letnic, G. Ludwig, and R. A. McDonald. 2012. Ecosystem restoration with teeth: What role for predators? *Trends in Ecology and Evolution* 27:265–271.
- Roberge, J.-M., G. Mikusiński, and S. Svensson. 2008b. The white-backed woodpecker: Umbrella species for forest conservation planning? *Biodiversity and Conservation* 17:2479–2494.
- Roberge, J.-M., P. Angelstam, and M.-A. Villard. 2008a. Specialised woodpeckers and naturalness in hemiboreal forests—deriving quantitative targets for conservation planning. *Biological Conservation* 141:997–1012.
- Sand, H., C. Wikenros, P. Wabakken, and O. Liberg. 2006. Cross-continental differences in patterns of predation: will naive moose in Scandinavia ever learn? *Proceedings of the Royal Society B: Biological Sciences* 273(1592):1421–1427 doi: 10.1098/rspb.2005.3447.
- Sand, H., C. Wikenros, P. Ahlqvist, T. H. Strømseth, and P. Wabakken. 2012. Comparing body condition of moose (*Alces alces*) selected by wolves (*Canis lupus*) and human hunters: consequences for the extent of compensatory mortality. *Canadian Journal of Zoology* 90:403–412.
- Sandström, C., J. Pellikka, O. Ratamäki, and A. Sande. 2009. Management of large carnivores in Fennoscandia: new patterns of regional participation. *Human Dimensions of Wildlife* 14:37–50.
- Sandström, C., S. Wennberg Di Gasper, and K. Öhman. 2013. Conflict resolution through ecosystem-based management: the case of Swedish moose management. *International Journal of the Commons* 7:549–570.
- Säterberg, T., S. Sellman, and B. Ebenman. 2013. High frequency of functional extinctions in ecological networks. *Nature* 499:468–470.

- Schönfeld, F. 2009. Presence of moose (*Alces alces*) in Southeastern Germany. *European Journal of Wildlife Research* 55:449–453.
- Schwartz, C. C., J. E. Swenson, and S. D. Miller. 2003. Large carnivores, moose and humans: a changing paradigm of predator management in the 21st century. *Alces* 39:41–63.
- Seiler, A. 2003. The toll of the automobile: wildlife and roads in Sweden. Dissertation, Swedish University of Agricultural Sciences, Uppsala, Sweden.
- Silva, M., and J. A. Downing. 1995. CRC handbook of mammalian body masses. CRC Press, Boca Raton, Florida, USA.
- Sjölander-Lindqvist, A. 2007. Local identity, science and politics indivisible: the Swedish wolf controversy deconstructed. *Journal of Environmental Policy and Planning* 10:71–94.
- Skaarnæs-Moldestad, A. 2012. Management of moose (*Alces alces*) in Norwegian municipalities—a study of the social aspects of the Norwegian management system. Universitetet for Miljø-Og Biovitenskap, Ås, Norway.
- Solberg, E. J., B. E. Saether, O. Strand, and A. Loison. 1999. Dynamics of a harvested moose population in a variable environment. *Journal of Animal Ecology* 68:186–204.
- Solberg, E. J., C. M. Rolandsen, M. Heim, V. Grøtan, M. Garel, B. E. Sæther, E. Nilsen, G. Austrheim, and I. Herfindal. 2006. Elgen i Norge sett med jegerøyne. En analyse av jaktmaterialet fra overvåkningsprogrammet for elg og det samlede sett elgmaterialet for perioden 1968–2004. NINA Rapport 125:197.
- Spong, G., and L. Hellborg. 2002. Near-extinction event in Lynx: Do microsatellite data tell the tale? *Ecology and Society* 6:15.
- Stighäll, K., J.-M. Roberge, K. Andersson, and P. Angelstam. 2011. Usefulness of biophysical proxy data for modelling habitat of an endangered forest species: the white-backed woodpecker *Dendrocopos leucotos*. *Scandinavian Journal of Forest Research* 26:576–585.
- Strandgaard, S. 1982. Factors affecting the moose population in Sweden during the 20th century with special attention to silviculture (Report 8). Department of Wildlife Ecology Report, Swedish University of Agricultural Sciences, Uppsala, Sweden.
- Sveaskog. 2014. Annual report. Sveaskog, Stockholm, Sweden.
- Sylla, R., and G. Toniolo. 1991. Patterns of European industrialisation: the nineteenth century. Routledge, London, UK.
- Thomas, W. L. 1956. Man's role in changing the face of the earth. University of Chicago Press, Chicago, Illinois, USA.
- Trauger, D. L., B. Czech, J. D. Erickson, P. R. Garretson, B. J. Kernohan, and C. A. Miller. 2003. The relationship of economic growth to wildlife conservation. *Wildlife Society Technical Review* 03-1. The Wildlife Society, Bethesda, Maryland, USA.
- Treves, A., and K. U. Karanth. 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology* 17:1491–1499.
- Treves, A., R. B. Wallace, L. Naughton-Treves, and A. Morales. 2006. Co-managing human-wildlife conflicts: a review. *Human Dimensions of Wildlife* 11:383–396.
- Ueno, M., E. J. Solberg, H. Iijima, C. M. Rolandsen, and L. E. Gangsei. 2014. Performance of hunting statistics as spatio-temporal density indices of moose (*Alces alces*) in Norway. *Ecosphere* 5:13.
- Wabakken, P., H. Sand, O. Liberg, and A. Bjärvall. 2001. The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978–1998. *Canadian Journal of Zoology* 79:710–725.
- Westman, W. E. 1990. Managing for biodiversity. *BioScience* 40:26–33.
- Zablotskaya, L. V., and M. M. Zablotskaya. 2002. Anthropogenic effects on moose populations in the southern Taiga. *Alces* 38(Supplement):S131–S135.
- Zuur, A. F., E. N. Ieno, N. L. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, New York, USA.

## DATA AVAILABILITY

Data associated with this paper have been deposited in Figshare <https://doi.org/10.6084/m9.figshare.4557592.v1>