

# Varying impacts of cervid, hare and vole browsing on growth and survival of boreal tree seedlings

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**Abstract** The negative impacts of mammalian herbivores on plants have been studied quite extensively, but typically with only a single herbivore species at a time. We conducted a novel comparison of the browsing effects of voles, hares and cervids upon the growth and survival of boreal tree seedlings. This was done by excluding varying assemblages of these key mammalian herbivores from silver birch, Scots pine and Norway spruce seedlings for 3 years. We hypothesised that the pooled impacts of the herbivores would be greater than that of any individual group, while the cervids would be the group with the strongest impact. Growth of birch seedlings advanced when cervids were excluded whereas growth of seedlings accessible to cervids was hindered. Survival of all seedlings was lowest when they were accessible to voles and voles plus hares, whereas cervids seemed not to influence seedling survival. Our results show that the impact of herbivores upon woody plants can be potent in the boreal forests,

but the mechanism and strength of this link depends on the tree and herbivore species in question. Risk of abated stand regeneration appears highest for the deciduous birch, though there is need for seedling protection also in coniferous stands. The clear cervid-mediated growth limitation of birch also indicates potential for a trophic cascade effect by mammalian top predators, currently returning to boreal ecosystems.

**Keywords** Exclosure · Forest regeneration · Herbivory · Top-down effects · Trophic interactions

## Introduction

Ecosystems have traditionally been considered essentially bottom-up controlled, but recent studies give strong support to the importance of top-down regulation (Crooks and Soulé 1999; Pace et al. 1999; Johnson et al. 2007; Beschta and Ripple 2009). This regulation occurs through trophic cascades, i.e. when the upper levels of the food web (such as top predators) cause cascading effects on the subsequent trophic levels (such as herbivores and plants) (Polis et al. 2000; Terborgh and Estes 2010). However, many of the trophic cascade studies have been conducted in aquatic ecosystems and research has focused mainly on invertebrate interactions (Pace et al. 1999; Borer et al. 2005). We thus lack knowledge from long-term, wide-scale experimental testing of terrestrial systems, which could provide a more pervasive synthesis of trophic cascades.

Understanding the functioning of the dynamic, often imperceptible trophic cascades necessitates knowledge about the interaction among individual trophic levels. In an ideal case, cascades can be examined as a whole, accompanied by some manipulation targeted at an upper

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level of the cascade. Such manipulation has been induced at a broad scale, for example, by the extensive eradication of top predators, such as wolves (*Canis lupus*) and bears (*Ursus* spp.) (Linnell et al. 2005; Prugh et al. 2009; Strong and Frank 2010; Estes et al. 2011). Nevertheless, alterations of this magnitude are rarely possible to carry out on purpose (e.g. due to ethical and conservational restraints), and in these cases studying individual, adjacent trophic levels within experimental settings is more feasible.

In the terrestrial food webs, conventional wisdom is that large ungulate herbivores may strongly influence plant abundance and species composition (Augustine and McNaughton 1998). For example, in the predator-free areas of the western USA, ungulates have caused substantial changes in woodland ecosystems (Beschta and Ripple 2009). In the boreal regions of Europe, where forests are the dominant biotope, Cervidae such as moose (*Alces alces*), roe deer (*Capreolus capreolus*) and white-tailed deer (*Odocoileus virginianus*) cause damage in young forest stands (Gill 1992a; Heikkilä and Härkönen 1996; Edenius et al. 2002; Bergman et al. 2005; Vehviläinen and Koricheva 2006). Usually less recognised but potentially as important are the “cryptic consumers”, i.e. hares and small rodents (Keesing 2000; Howe et al. 2006). In the boreal areas, these small and medium-size herbivores include vole species of the genera *Microtus* and *Myodes*, and hares of the genus *Lepus* (Gill 1992b; Hjältén et al. 2004; Vehviläinen and Koricheva 2006). Although the browsing effects of all of these mammalian herbivore species have been widely studied, the pooled effects of ungulates, hares and rodents on plant trophic level have remained without rigorous experimental testing.

In order to examine the effects of mammalian herbivores on woody plants, we conducted a large-scale, 3-year experiment in Finland, in northern Europe. To compare the relative importance of individual herbivore groups, varying combinations of voles, hares and cervids were excluded from accessing and browsing on young silver birch (*Betula pendula*), Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). The growth and survival of the seedlings was then used to assess the impacts of different herbivores. We predicted that the pooled effects of all the herbivores (voles, hares and cervids) would cause more severe damage to tree seedlings than that of any individual herbivore group. Additionally, we also wanted to find out whether the long-term effects of large-sized cervids would be more detrimental than the browsing effects caused by the momentarily peaking vole populations. Strong detrimental effects of cervids on seedling growth and survival could indicate cascading impacts from recovering top predators.

## Materials and methods

### Study species

We selected three of the most common tree species in Finnish forests for use in this study: Scots pine, Norway spruce and silver birch. These species are found throughout the country and they are of great economic importance in forestry (Ylitalo 2011). All of these species also suffer from browsing by herbivores, especially at a young age (Huitu et al. 2009).

In our experiment, we controlled the access of wood-browsing mammalian herbivores to planted tree seedlings. Small voles, especially abundant field (*Microtus agrestis*) and bank (*Myodes glareolus*) voles, periodically cause the most damage to young trees in Finnish forests (Huitu et al. 2009). The former can effectively destroy entire newly established seedling stands of both coniferous and deciduous trees via browsing on seedling bark in winter under the snow cover (Gill 1992b; Uotila and Kankaanhuhta 2003; Poteri 2008). This can cause notable monetary losses, as stands need to be replanted. During summers, field voles can also debark silver birch in hay-abundant areas (Uotila and Kankaanhuhta 2003). In turn, the bank vole is more specialised in feeding on the buds of coniferous seedlings, often causing patchy timber-quality defects (Gill 1992b; Uotila and Kankaanhuhta 2003). It also occasionally damages the bark of pine and birch (Uotila and Kankaanhuhta 2003; Poteri 2008). Bark damage exposes seedlings to pathogens, and full girdling usually kills the seedlings (Roll-Hansen and Roll-Hansen 1980; Gill 1992c; Uotila and Kankaanhuhta 2003). Vole populations in the study region express widely synchronous, high-amplitude, 3-year cyclic fluctuation (Hanski et al. 2001; Korpimäki et al. 2005 and unpublished data). Most of the damage induced by vole browsing on seedlings occurs during winters that follow an increase phase of the vole cycle (Gill 1992b; Norrdahl et al. 2002; Huitu et al. 2009).

The mountain hare (*Lepus timidus*) is a forest species abundant throughout Finland, while the European hare (*Lepus europaeus*) resides only in southern and central Finland (Björvall and Ullström 2011). These medium-sized species typically feed on young pines and deciduous trees, damaging the bark and branches of seedlings and sometimes cutting the main stem (Gill 1992b; Hjältén et al. 2004; Poteri 2008). Especially in cultivated birch stands, hare damage is likely (Uotila and Kankaanhuhta 2003), from early spring to summer (Poteri 2008). The number of mountain hares in Finland has been decreasing (Wikman 2010). Though the species is a popular game species among hunters, the reasons for the population decline are most likely related to climate change, competition with the European hare and the current forest practises, in which

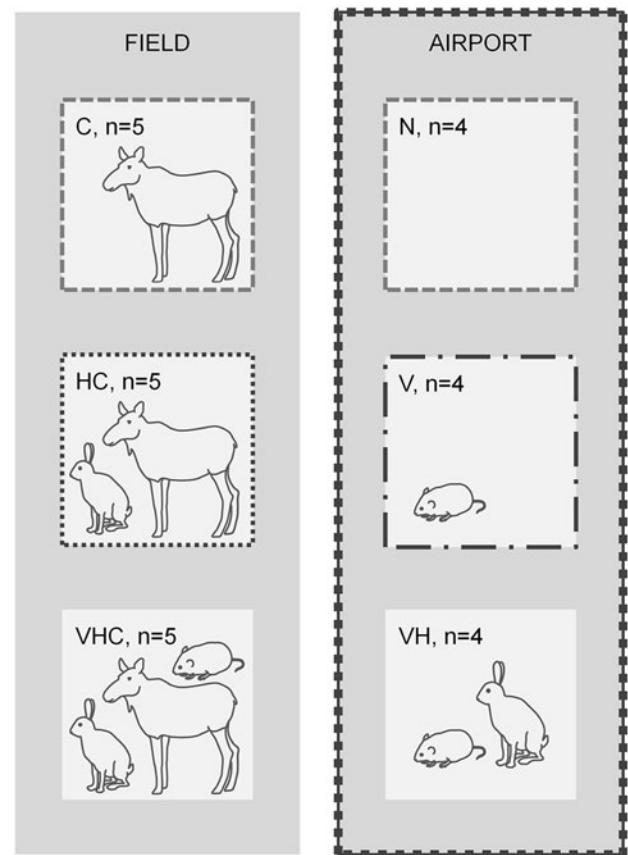
coppices are removed effectively (Kauhala and Helle 2007; Nylander 2012). In contrast, the population of European hare is increasing (Wikman 2010).

The moose is a large-sized, common herbivore in the forest stands of Finland (Björvall and Ullström 2011). Young pine, usually larger than 50 cm in height, and deciduous trees are a major part of the moose diet (Jalkanen 2001; Poteri 2008). This herbivore is also prone to breaking the main stems of fairly large seedlings while feeding on their top shoots (Jalkanen 2001). The Finnish moose population is regulated quite strongly by hunting (Luoma et al. 2001).

In contrast to moose, roe deer and introduced white-tailed deer have rapidly expanded their ranges while their annual game bag quotas have remained only moderate (Nylander 2012). These smaller cervid species also damage trees mainly at early stages of stand development (Heikkilä and Härkönen 1996; Bergman et al. 2005), essentially in southern and central Finland (Poteri 2008; Björvall and Ullström 2011). Similarly to moose, roe and white-tailed deer prefer to browse on pine seedlings, though smaller than 50 cm in height, and additionally damage spruce seedlings (Poteri 2008). Birches are not a favoured deciduous food source but are also browsed by smaller cervids (Gill 1992a; Poteri 2008). Cervid-induced damage on coniferous trees occurs mostly during winters (Uotila and Kankaanhuhta 2003), starting in autumn following the planting of trees (Poteri 2008). In contrast, deciduous trees are often browsed upon in summer as well (Gill 1992a; Poteri 2008).

### Study design

The study was conducted in Kauhava, western Finland (63°7'N, 23°3'E) in 2008–2011. Two separate sites were established at the study location: one within an airport area and one on an adjacent field, ca. 300 m away. Both study sites are dominated by grassy vegetation and surrounded by willow scrub and mainly deciduous forest. The airport site is surrounded with a 2.3-m-high fence that prevents cervids from entering while smaller mammals are able to pass through. The unfenced field site is open to all herbivores. To further manipulate the selection of herbivore species present, three groups of exclusion plots were established in both study sites, on which different treatments were applied (Fig. 1). The following letters are used to indicate species groups which were allowed inside the 10 × 10-m plots in each treatment: vole (V), hare (H), cervid (C), and none allowed (N). Plots in the first group in both sites were surrounded by 1-m-high hardware cloth with 12.7-mm mesh to prevent access of hares and small rodents. In the airport site, this resulted in a treatment where no herbivores were allowed (N), whereas in the field site, cervids alone were allowed (C). Plots in the second group in the fenced airport



**Fig. 1** A schematic presentation of the experimental design containing six different types of treatments, three in both study sites ( $n$  the number of replicates). The field site (*left*) was open to all herbivores whereas the airport site (*right*) was surrounded by a ca. 2.3-m-high fence, which prevented cervids from entering the site. Further exclusion was done by surrounding some of the 10 × 10-m plots with fences. The same types of fence are indicated by *dashed lines*, whereas *unfenced plots* have no borders. *Letters* indicate the herbivores allowed to enter the treatment plots after fence establishment: V vole, H hare, C cervid, N no herbivores

site prevented access from hares (1-m-high hardware cloth, 40-mm mesh), leaving only voles able to enter the plots (V). Meanwhile, in the unfenced field site the second group prevented small rodents from entering (0.6-m-high hardware cloth, 12.7-mm mesh), maintaining the plots accessible for hares and cervids (HC). The third group in both study sites consisted of unfenced plots. In the airport site, this resulted in plots where hares and voles were allowed (VH), whereas in the field site all herbivores were able to enter the plots (VHC). This experimental setup thus resulted in six different treatments. There were four replicate plots per treatment established in the airport and five replicate plots per treatment in the unfenced field, all set up in a randomised order (total  $n = 27$ ).

To compare the effects of different herbivore species, seedlings of Scots pine, Norway spruce and silver birch

were planted within the plots, in groups of nine. The distance between seedlings was ~1.5 m and the species were positioned randomly in separate corners of the plots. Seedlings were planted into the plots in late May–early June 2008, and before this the ground was harrowed to achieve similar conditions for all seedlings. These practises are typical in forestry, albeit planting densities are usually less than one half of that used in this experiment. Once planted, the seedlings were measured in autumn 2008 and after that, three times per growing season (in spring, summer and autumn) until May 2011. Measurements of height, diameter and number of branches were taken in order to find out whether plants differed in their growth when subjected to different herbivores. The height of the seedlings was measured from ground level up to the tip of the main shoot. The diameter of coniferous seedlings was measured from the base of the stem and the diameter of birch seedlings from 10 cm above ground. Additionally, the condition of the plants was recorded to identify dead seedlings and to classify seedlings according to the signs of browsing: (1) no signs; (2) minor damage; and (3) major, lethal damage. Herbivores responsible for damage were identified from the feeding marks in order to verify the success of exclusion.

In the study area, summer 2008 was an increasing phase of the vole cycle, summer 2009 a decreasing phase and summer 2010 a low phase. Since herbivores often occur in a patchy manner, their presence in the study area was confirmed with observations of tracks and visual sightings. After the fence establishment, the vole exclusion was reinforced by several days of snap-trapping in vole-exclusion plots. However, the built fences did not produce a complete exclusion for all the plots. Treatment C in which only cervids were present, was deemed unsuccessful due to the browsing marks of small mammals found on the seedlings in several plots. The remaining five treatments were all included in the analyses, but five additional plots were removed due to unsuccessful exclusion. This resulted in the following number of replicate plots in the airport site: treatment N three, treatment V three and treatment VH four. In the open field site treatment HC had two plots and VHC five plots.

The advantage of utilising an already fenced airport area was that it was large enough to provide a cervid exclusion that extended beyond the territory size of smaller herbivores. Using small, separate cervid-exclusion plots, though cost effective, could have provided smaller mammalian herbivores with high-quality feeding sites more appealing than the rest of the plots. On the other hand, building several large-scale cervid-exclusion fences would not have been feasible with the limited economic resources of the study. Thus the used study design, where half of the treatments were assigned to one site and half to another, is justified despite the possible pseudoreplication concerning the

cervid exclusion (Oksanen 2001). We find acknowledging site variation a precaution sufficient enough to allow us to address the study questions.

The weather conditions during the initiation of the experiment were exceptional. Warm and dry weather prevailed for weeks (Finnish Meteorological Institute 2008), and thus some spruce seedlings and several pine seedlings died due to drought. The amount of live, edible neighbouring seedlings can affect the amount of browsing upon individual seedlings (Heikkilä and Härkönen 1996; Barbosa et al. 2009). Therefore those pine and spruce seedlings that had died due to the unfavourable conditions were replaced with new ones in autumn 2008. Also during the following summer, some replanting was needed for the same species to compensate for high winter mortality presumably caused by unsuccessful planting. For birch, no replanting was required.

### Statistical analyses

The seedling growth data were analysed using generalized linear mixed models. For all of the features measured (height, diameter, number of branches), we built separate models for each of the tree species due to their physiological differences (e.g. pines generally have a smaller number of branches compared to birches and spruces). This resulted in nine separate growth models (Online Resource 1). The growth variables were observed only from living seedlings. Therefore seedlings identified as dead were excluded from the growth analyses, and the models had a decreasing amount of observations (for model-specific  $n$  values, see Online Resource 1). The supplementary planting batch of autumn 2008 (but not the batch of summer 2009) was omitted from the analysis of the growth traits, since the seasonal timing and the conditions of the planting may have differed from those in the beginning of the experiment (summer 2008).

For all the height and diameter models we used a Gaussian error distribution, and for branch models we employed a Poisson error distribution, suitable for count data. Treatment, measurement session (i.e. time) and their interaction were set as fixed explanatory factors. The interaction was omitted when not significant, but the main factors were always retained. Because pine and spruce data contained replaced seedlings, we needed to control for the impact of planting time. Therefore, planting group (two levels) and the original measurement (height, diameter, or number of branches; a continuous covariate), along with the interaction of the two, were fitted in the coniferous growth models. These variables were set as fixed to avoid an excessively complicated random structure. The interaction of planting group and original measurement was omitted when not significant, but the main variables were always



significant and thus retained. Lastly, all nine growth models included plots and individual plants as random factors, the latter as repeated subjects within session with a covariance structure of compound symmetry.

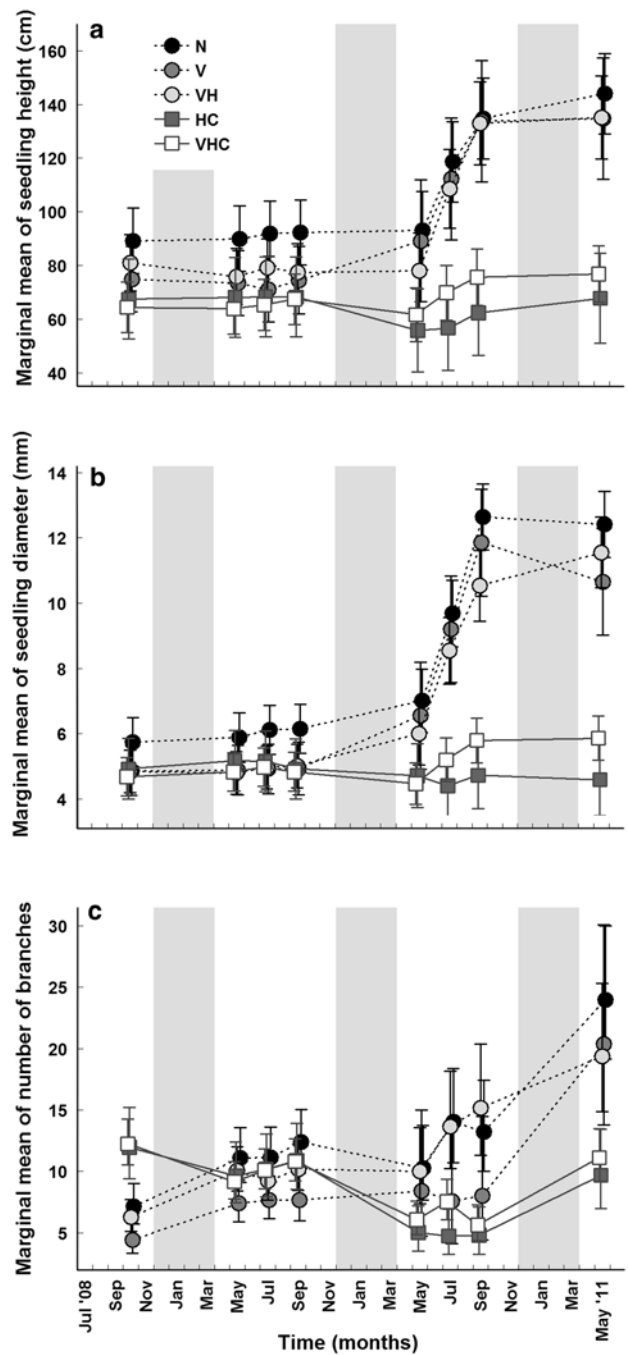
Seedling survival at the end of experiment was analysed with a separate generalized linear mixed model (see Online Resource 1), for which plants were scored according to the browsing damage they had experienced. Seedlings that had records of either minor or major damage and that were dead at the end of the experiment were scored as 1 (=potentially killed by herbivory), whereas those alive at the end of experiment (i.e. in May 2011) were scored as 2 (=survived). Seedlings that evidently had died due to causes not related to herbivory, including those replaced at some point, were excluded. The survival model with binary error distribution incorporated seedling species and treatment as fixed explanatory factors. The interaction of these main factors was not significant and was thus excluded from the final model. Planting group was included as a random factor, which provided a simple random structure while improving the convergence of the model.

All analyses for this paper were generated with the GLIMMIX procedure of SAS/STAT statistical software, version 9.2 of the SAS System for Windows. In the survival model, maximum likelihood was employed with a Laplace approximation. For all growth models, a Kenward–Roger approximation was specified, which applies SE and denominator *df* correction for the fixed effects (Kenward and Roger 1997). Results of pairwise multiple comparisons among treatments in the growth models, although they were conducted with a Tukey–Kramer adjustment, are not given as the same interpretation can be made based on the confidence intervals presented in the figures (Figs. 2, 3, 4). Results of the branch model are transformed back to the original scale of branch count. For the survival model, the estimated marginal means (i.e. the least squares means in SAS) with the 95 % confidence intervals, obtained from the statistical model, are given for each treatment and species. As binary error distribution with a logit link function was used, estimates are transformed back to the probability scale.

## Results

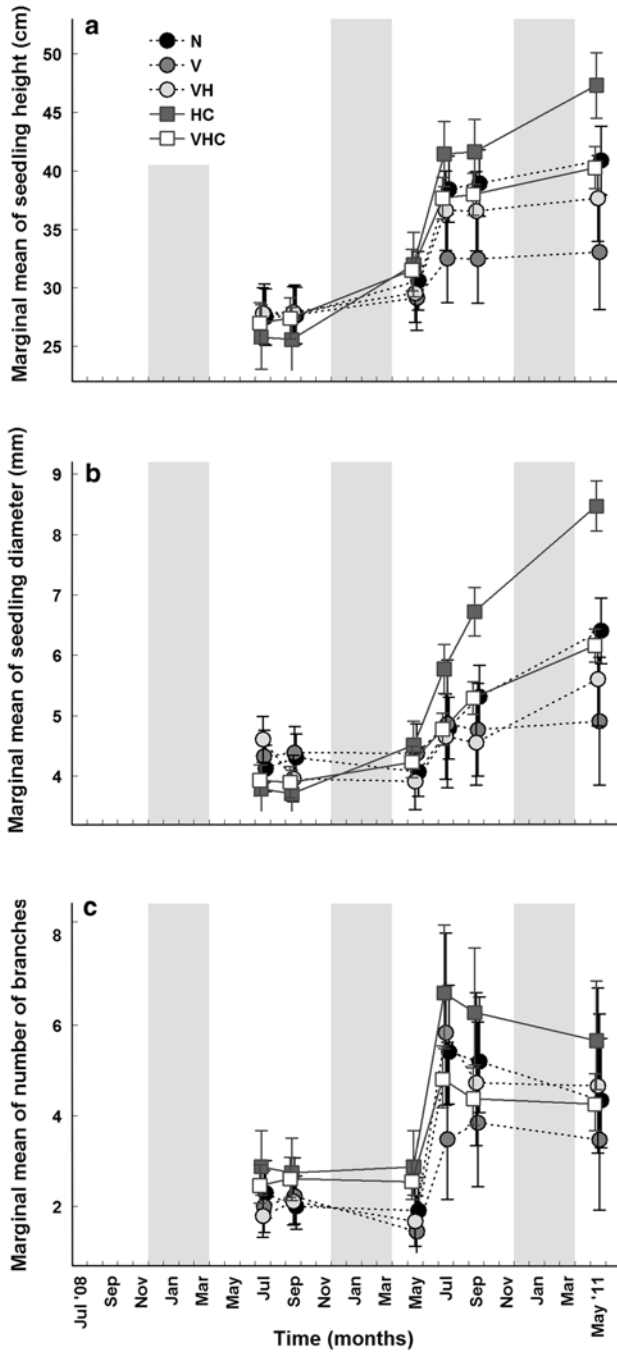
### Birch

Out of the birch seedlings analysed, 74 % experienced some degree of browsing damage during the experiment. The height of the birch seedlings stayed fairly uniform during the first half of the experiment. After the second winter, seedling growth accelerated in the treatments where voles alone (V), voles and hares (VH) or neither (N) were



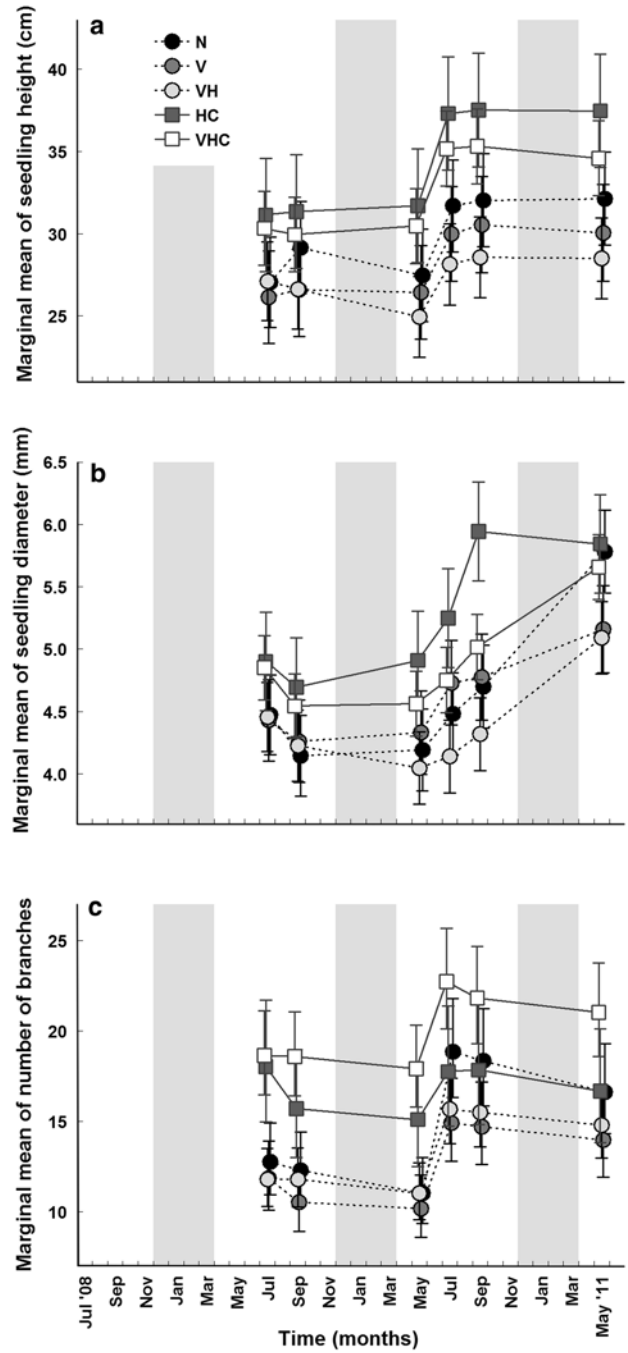
**Fig. 2** Silver birch (*Betula pendula*) seedling **a** height, **b** diameter and **c** number of branches [estimated marginal means and 95 % confidence interval (CI)] in different treatments in the airport (circles) and field site (squares) from October 2008 to May 2011. Letters denote mammalian herbivore groups allowed inside plots. Grey shading delineates winter months when snow cover is typical. For abbreviations, see Fig. 1

allowed to browse on the seedlings. In contrast, in the plots of the unfenced field site, freely accessible either to cervids and hares (HC) or to all herbivores (VHC), seedling growth was hindered (treatment × session  $F_{28, 600} = 7.24$ ,



**Fig. 3** Scots pine (*Pinus sylvestris*) seedling **a** height, **b** diameter and **c** number of branches (estimated marginal means and 95 % CI) in different treatments in the airport (*circles*) and field site (*squares*) from July 2009 to May 2011. Letters denote mammalian herbivore groups allowed inside plots. Grey shading delineates winter months when snow cover is typical. For abbreviations, see Figs. 1 and 2

$P < 0.0001$ ; Fig. 2a). The results were comparable for birch diameter (treatment  $\times$  session  $F_{28, 615} = 18.36$ ,  $P < 0.0001$ ; Fig. 2b). The number of branches in the field plots, where cervid browsing was allowed (HC, VHC), never quite



**Fig. 4** Norway spruce (*Picea abies*) seedling **a** height, **b** diameter and **c** branch number (estimated marginal means and 95 % CI) in different treatments in the airport (*circles*) and field site (*squares*) from July 2009 to May 2011. Letters denote mammalian herbivore groups allowed inside plots. Grey shading delineates winter months when snow cover is typical. For abbreviations, see Figs. 1 and 2

surpassed the initial level of the planting. In contrast, in the plots of the airport site, in which only smaller herbivores or no herbivores at all were allowed (V, VH, N), the number of branches increased gradually, resulting in clearly higher

numbers than in the field site (treatment  $\times$  session  $F_{28, 610} = 8.77$ ,  $P < 0.0001$ ; Fig. 2c).

### Pine

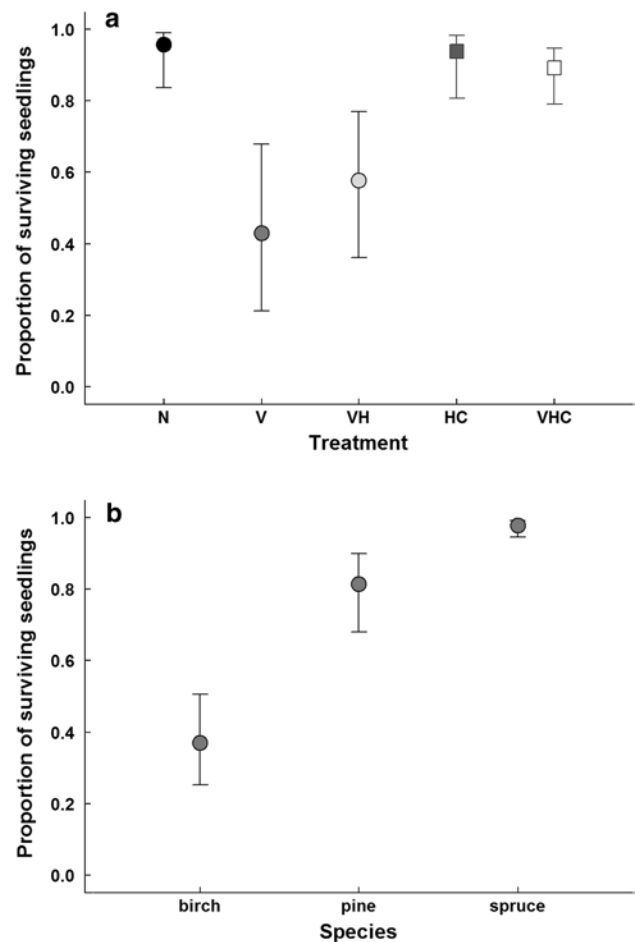
Only 21 % of the analysed pine seedlings showed signs of browsing damage. The height of pine seedlings increased evenly in all of the treatments as the experiment advanced. In the final measurement, only HC plots differed from the others, having the tallest pine seedlings in the experiment (treatment  $\times$  session  $F_{20, 449} = 6.42$ ,  $P < 0.0001$ ; Fig. 3a). Similarly, pine seedling diameter in HC plots was larger than in other plots (treatment  $\times$  session  $F_{20, 523} = 9.49$ ,  $P < 0.0001$ ; Fig. 3b). The number of branches did not obviously differ between treatments in the course of time, and treatment alone affected the number of branches only marginally (treatment  $\times$  session  $F_{20, 425} = 1.32$ ,  $P = 0.1611$ ; treatment  $F_{4, 16} = 2.56$ ,  $P = 0.0784$ ; Fig. 3c).

### Spruce

When examining the browsing marks on spruce seedlings, 29 % of the analysed seedlings showed signs of browsing. Different treatments affected the observed height of spruce seedlings regardless of time (treatment  $\times$  session  $F_{20, 641} = 1.32$ ,  $P = 0.1560$ ; treatment  $F_{4, 13} = 5.93$ ,  $P = 0.0063$ ; Fig. 4a), as seedlings in all treatments followed a pattern of gradual growth. For spruce diameter, the interaction of treatment and time was significant. However, only VH plots differed with their small-sized seedlings from N, HC and VHC plots. Moreover, this difference was evident only at the end of the experiment (treatment  $\times$  session  $F_{20, 661} = 2.85$ ,  $P < 0.0001$ ; Fig. 4b). Number of branches was high in plots allowing cervid browsing (HC, VHC) at first, but in the course of the experiment, differences between the treatments narrowed so that finally the number of branches was higher only in VHC plots when compared to V and VH plots (treatment  $\times$  session  $F_{20, 647} = 3.19$ ,  $P < 0.0001$ ; Fig. 4c).

### Seedling survival

Differences in seedling survival between tree species were significant (species  $F_{2, 333} = 37.47$ ,  $P < 0.0001$ ; Fig. 5a). For birch seedlings the estimated marginal mean of survival probability was only 0.37 (95 % CI: 0.26–0.49) whereas for pine and spruce it was clearly higher (0.81 and 0.98; 95 % CI: 0.69–0.90 and 0.95–0.99, respectively). When comparing the effects of treatments, survival probability was high in the plots where cervid browsing was allowed (treatment  $F_{4, 333} = 9.94$ ,  $P < 0.0001$ ; Fig. 5b), i.e. treatments HC (0.94; 95 % CI: 0.84–0.98) and VHC (0.89; 95 % CI: 0.82–0.94), and also in treatment N, which



**Fig. 5** Seedling survival **a** in different study species and **b** in different treatments (estimated marginal means and 95 % CI). For abbreviations, see Figs. 1 and 2

allowed no herbivores (0.96; 95 % CI: 0.86–0.99). In contrast, survival was distinctly lower in plots allowing browsing by only small mammals, i.e. treatments V (0.43; 95 % CI: 0.25–0.62) and VH (0.58; 95 % CI: 0.41–0.74).

### Discussion

We used a novel experimental herbivore exclusion to compare the browsing effects of different mammalian herbivore groups upon woody plants. We expected to see clear harmful impacts on tree seedling growth and survival especially when large cervids or herbivores of all sizes together were able to access the seedlings. The harmful effects of pooled hare and cervid browsing were visible in the growth of silver birch seedlings but, for Scots pine and Norway spruce, our experiment provided little evidence of herbivore-induced growth limitation. Nonetheless, we found that all tree species, particularly birch, experienced lowest survival

in the presence of voles only, and voles and hares together. The strength of herbivore impact upon woody plants can be potent but appears to depend on the herbivore and the tree species in question.

The growth of birch seedlings differed little during the first full growing season (2009). However, consistent with the initial hypothesis, throughout the second growing season seedlings showed steady growth in the absence of cervids, whereas in the area where cervids were allowed, seedlings grew very little. The large growth differences between the treatments indicate clear vulnerability to damage caused jointly by cervids and hares. A likely reason for this is that birch seedlings grow fast, and thus during winters they receive relatively little protection from the snow against hares and cervids (Gill 1992b). The lack of sufficient snow cover either leaves seedling tops and branches exposed to browsing, or it facilitates excavation and access to seedlings. Additionally, damage caused during winter typically affects the growth in the following summer (den Herder et al. 2009). We could not directly distinguish between the effects of cervids and hares as the treatment of cervid browsing alone was unsuccessful. Still, birch seedlings which grew well in plots subjected not to cervids but to hares and voles would suggest that cervids cause the most harm for birch growth.

Pine seedling growth during the first summer was likely affected by the harsh planting conditions. Towards the end of the experiment the growth of the seedlings remained quite uniform between different treatments, with only plots that allowed hare and cervid browsing having larger seedlings than other plots. This slight difference likely resulted from a beneficial impact of vole absence and less harsh growing environment in the field site compared to the airport site. The latter was indicated by the considerably lower number of replanted seedlings (field, 29 seedlings replanted; airport, 163 seedlings). Because seedling growth was relatively slow in the no-browsing treatment, we can state that the general lack of differences between the treatments was not due to an overall high level of herbivory. Instead, pine seedlings appear not to be very susceptible to non-lethal browsing injuries. This result was somewhat of a surprise because pine seedlings are known to be a commonly used food resource for mammalian herbivores, especially in winter (Heikkilä and Härkönen 1996; Uotila and Kankaanhuhta 2003; Poteri 2008). One possibility is that the seedlings endured herbivory well by compensating for damage that was not too severe (Edenius et al. 1993). However, only one-fifth of the seedlings showed any signs of browsing, leading to a more plausible explanation that the seedlings were collectively more influenced by the planting conditions of the experiment than by browsing.

The growth of spruce seedlings was minimally affected by the varying herbivore assemblages. A mediocre growth

of seedlings in the plots that allowed browsing by all mammalian herbivores and rather small differences between all treatments suggest low overall browsing, which was also supported by the low number of damaged seedlings. This lack of harmful impacts was unexpected because there is evidence of damage caused to spruce stands e.g. by white-tailed deer and roe deer (Welch et al. 1991; Bergquist et al. 2003; Poteri 2008). Also, seedlings experienced the peak phase of the vole cycle, during which vole damage is most likely to occur (Huitu et al. 2009). We suspect that the lack of damage may have resulted from the abundance of more highly preferred food for herbivores. Perhaps extending the study period or using monocultures of spruce could have produced more pronounced differences for this less-preferred tree species.

There were large between-species differences in the seedling survival. The high proportion of surviving spruce seedlings suggests very low susceptibility to lethal damage caused by browsing, or at least low preference for herbivores. This supports earlier perceptions of low palatability of spruce to mammalian herbivores when other food is available (Hjältén et al. 2004), and is also in line with the findings of the growth models. For pine, we conclude that roughly four fifths of the analysed seedlings survived regardless of herbivores, suggesting a minor susceptibility to herbivory. In earlier studies, the palatability of pines has varied greatly, likely depending on the herbivore species studied (Heikkilä and Härkönen 1996; Rao et al. 2003; Hjältén et al. 2004). Of the analysed birch seedlings, less than half survived through the tree-year experiment, which demonstrates a clear susceptibility to herbivore browsing, supported also by earlier studies (Gill 1992a; Baxter and Hansson 2001; Hjältén et al. 2004). We find it probable that such high mortality, together with the growth limitations mentioned earlier, impair regeneration in birch stands. Adverse impacts of herbivory on forest regeneration have previously been shown, for example, with studies conducted on voles and ungulates (Ostfeld et al. 1997; Randall and Walters 2011).

Comparison of seedling survival between different treatments provided puzzling results. Unexpectedly the effects of individual treatments were parallel regardless of the tree species. Survival was lowest when only voles or both voles and hares were present, and higher in the other plots, notably also in the treatment which enabled all herbivore groups to browse on the seedlings. This could suggest that voles are more harmful to seedling survival than cervids. Nonetheless, this detrimental impact of voles was not as strong in the field site unfenced from cervids as it was in the airport site where cervids were excluded. Such prominent survival differences through competition or disturbance seem improbable. A better explanation could be that there were differences in vegetation consistency, which



influenced the food preference and densities of herbivores. Because only the presence of herbivores but not their abundance was observed during the experiment, we cannot state this for certain.

All in all, the impact of mammalian herbivores on conifer growth appears weak at least in mixed forest stands, where more preferred food is available. As starvation is not a dominating cause of mortality among cervids in Finland, our results do not rule out the possibility that human activities account for the steady growth of conifers accessible for cervids. Besides the impact of hunting, also the bottom-up effect of human-modified plant composition is likely to count (Muhly et al. 2013). In our system, with lots of palatable secondary growth trees and shrubs, pines and spruces were rarely used. By contrast in Scotland, where heather is the only alternative winter forage, introduced spruces are preferred over heather (Welch et al. 1991). Yet, it is noteworthy that the survival and recruitment of Scots pine and Norway spruce seem to be negatively affected by voles and hares. The amount of cervid-induced (Ylitalo 2011) and vole-related damage (Huitu et al. 2009, 2012) has for long been the major concern in Fennoscandian forests. Our results suggest that hare populations should also be taken into closer account while anticipating damage in pine-dominated stands.

In contrast to conifers, we found clear growth limitations on silver birch induced especially by cervids. This indicates that cervids browse on the top parts of the birch seedlings, rarely killing the entire plant, though they may instead hamper its growth or cause forking and offshoot growth (Gill 1992a; Heikkilä and Löyttyniemi 1992). On the other hand, voles and hares have a higher tendency to gnaw or cut the entire seedling from the bottom, thus resulting in the likely death of the plant (Gill 1992b; Baxter and Hansson 2001), which was seen in our study too. This information is important for forest management, because the damage induced by mammalian herbivores, though not necessary lethal, can severely degrade the monetary value of timber, e.g. via growth deformations (Heikkilä and Löyttyniemi 1992), and cause added monetary costs due to replanting. As damage on birch appears to result from the co-actions of all the key mammalian herbivores, relying on reducing ungulate populations is not enough to prevent damage—smaller herbivores also need to be controlled.

When extending the results of the cervid-birch link to the framework of food webs, we can hypothesise that it provides support for a boreal trophic cascade. After all, top predators have been shown to limit cervid populations (McLaren and Peterson 1994; Boutin 2005; Ripple and Beschta 2012), and at the same time, the browsing effects of herbivores on plants in predator-free systems have also become apparent (Tremblay et al. 2005; Dahlgren et al. 2009). Recovering large predators could benefit

forest stands if they reduced the browsing pressure through decreased herbivore numbers or altered herbivore behaviour (Wolff and Van Horn 2003; Dussault et al. 2005). However, we stress that the impacts of top predator comeback upon plants seem clearly dependent on the tree species in question.

Top predator recovery will probably affect mesopredators as well (Elmhagen and Rushton 2007; Levi and Wilmers 2012), and different herbivore species are likely to respond varyingly to this mesopredator suppression. For example, voles are an important food resource for a particularly wide selection of mesopredators in North Europe, e.g. for red fox (*Vulpes vulpes*) and stoat (*Mustela erminea*) (review in Korpimäki and Norrdahl 1997). In contrast, medium-sized hares likely experience predation both from top predators and mesopredators. Given that mesopredators are currently quite numerous their response to top predator return is very relevant when anticipating any cascading impacts upon herbivores and woody plants.

## Conclusion

This landscape-level experimental study provides new insight on the food webs of boreal woodlands. Information about the interactive roles of herbivores in the boreal food webs is important and may well have increasing value in the future. As populations of mammalian top predators are currently recovering and returning to boreal ecosystems (Wikman 2010), our results of herbivory effects can help to anticipate the forthcoming ecosystem changes and aid in both wildlife and forest management. Most importantly, our results supplement earlier studies conducted on the impacts of herbivores, by showing that ungulates are more influential on the growth of boreal tree seedlings than smaller mammalian herbivores, whereas voles particularly have an impact on the survival of the seedlings.

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