

Plant defences to no avail? Responses of plants of varying edibility to food web manipulations in a low arctic scrubland

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ABSTRACT

Background: According to the Green World Hypothesis of Hairston, Smith, and Slobodkin, all plants are edible for some herbivores. Hence, the copious abundance of plant biomass, typical for terrestrial ecosystems, depends on the collective regulatory action of predators on the herbivore guild. According to the counterarguments of Polis and Strong, the defensive traits of terrestrial plants attenuate terrestrial trophic cascades to species-specific trickles, so elimination of predators might lead to increased abundance of inedible plants but will not influence community-level plant biomass.

Question: Does the elimination of predators from a low arctic scrubland, with high-quality forage plants and poorly edible evergreen ericoids, lead to a reduction of community-level plant biomass or to an increased abundance of well-defended evergreen ericoids?

Methods: In 1991, we introduced grey-sided voles (*Myodes rufocanus*) to islands, initially harbouring dense scrubland vegetation, and established permanent plots there. In 2000, we transplanted vegetation blocks from a large three-trophic-level island with voles and predators, to two-trophic-level islands with introduced voles but without resident predators, and also to vole-free one-trophic-level islands, and back to the three-trophic-level island. Vole densities were monitored by semi-annual live trapping. Vegetation was monitored by the point-frequency method.

Results: In the absence of predators, vole densities increased 3.7-fold and the community-level plant biomass was decimated. The least palatable plant group, evergreen ericoids, suffered especially heavily, whereas palatable herbaceous plants increased in abundance. However, all three functional plant groups responded positively to the elimination of grey-sided voles.

Conclusions: Our results corroborate the Green World Hypothesis, indicating that in the absence of predators, plant defences do not prevent runaway consumption of the vegetation.

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The fate of plants in predator-free systems with browsing vertebrates depends primarily on the accessibility of each plant during the limiting season. Evergreen ericoids then form the most sensitive functional group.

Keywords: arctic, food web dynamics, herbivory, *Myodes rufocanus*, plant defences, tolerance, trade-offs.

INTRODUCTION

In their Green World Hypothesis (GWH), Hairston *et al.* (1960) proposed that the regulatory action of predators on herbivores is a necessary condition for the persistence of ‘green worlds’ – that is, habitats where plant biomass abounds, erect woody plants prevail, and the vegetation is structured by plant–plant competition. This argument was derived from the observation that detritus, with low concentrations of nutrients and soluble carbohydrates, is consumed everywhere where water and oxygen are available (Slobodkin, 2009). Therefore, the qualitatively superior foliage of living plants ought to be edible. Hairston *et al.* (1960) also pointed out that, after the extirpation of big predators, the forests of the USA have become intensely browsed, demonstrating the importance of predation for herbivore–plant dynamics (see also Terborgh *et al.*, 2001, 2006; Beschta, 2003; Ripple and Beschta, 2003, 2006; Ripple *et al.*, in press).

In modern terms, GWH implies that terrestrial ecosystems form community-wide trophic cascades (Carpenter *et al.*, 1985). This view was vigorously challenged by Polis and Strong (1996; see also Strong, 1992), who argued that plant defences reduce terrestrial trophic cascades to species-specific ‘trophic trickles’, in which elimination of predators could lead to replacement of edible species by inedible ones but would not influence community-level plant biomass. This conjecture appears to be supported by experimental evidence (Schmitz *et al.*, 2000; Halaj and Wise, 2001; Shurin *et al.*, 2002, 2006; Borer *et al.*, 2005). However, almost all terrestrial food web experiments have focused on folivorous insects and their predators. Inferences to mammalian herbivores are thus uncertain (see Shurin and Seabloom, 2005).

The potential of herbivorous mammals to deplete plant biomass has ramifications for the evolutionary ecology of the slowly growing plants of arctic, alpine, and arid regions. The vegetation of unproductive areas cannot sustain herbivore densities high enough to yield positive energy balance for predators. Applying the logic of GWH to such habitats, Fretwell (1977) and Oksanen *et al.* (1981) thus predicted that their plants are living under chronically intense herbivory (see also Grime, 1979; Oksanen, 1990; Oksanen and Virtanen, 1997; Oksanen and Oksanen, 2000; Oksanen *et al.*, 2008). In contrast, the hypothesis of Polis and Strong (1996) implies that there are no natural terrestrial systems where plants would need to tolerate heavy grazing and browsing.

To test GWH, Hambäck *et al.* (2004) introduced grey-sided voles (*Myodes rufocanus*) to four islands in a big tundra lake, Iešjávri, Norwegian Lapland, in 1991–1992, creating replicated two-trophic-level systems in a relatively productive scrubland habitat, which is regularly exploited by predatory mammals on the mainland (Aunapuu *et al.*, 2008). The common vascular plants of these scrublands (Table 1) can be divided into three functional groups: edible herbs; edible, deciduous woody plants; and inedible or marginally edible evergreen ericoids (Aleksandrova *et al.*, 1964). Hambäck *et al.* (2004) estimated the cascading impact of predators on plants by studying changes on permanent plots established on these two-trophic-level islands and on reference plots, established in corresponding mainland habitats.

Table 1. Mean biomasses (dry weight) of dominant plants (species representing more than 99% of total vascular plant biomass) of the scrubland on the three-trophic-level island

Scientific name	Common name	Functional group	Palatability	Height (cm)	Biomass (g · m ⁻²)
<i>Andromeda polifolia</i>	Bog rosemary	Evergreen ericoid	Poisonous	10–20	4
<i>Betula nana</i>	Dwarf birch	Deciduous	Moderate	10–70	152
<i>Cornus suecica</i>	Dwarf cornel	Herbaceous	Moderate	3–8	3
<i>Empetrum nigrum</i>	Crowberry	Evergreen ericoid	Very low	3–12	131
<i>Rubus chamaemorus</i>	Cloudberry	Herbaceous	High	5–20	34
<i>Vaccinium microcarpum</i>	Small cranberry	Evergreen ericoid	Low	1–2	3
<i>Vaccinium myrtillus</i>	Bilberry	Deciduous	High	5–25	82
<i>Vaccinium uliginosum</i>	Arctic blueberry	Deciduous	Moderate	3–30	10
<i>Vaccinium vitis-idaea</i>	Lingonberry	Evergreen ericoid	Low	3–10	65

Note: Height represents typical shoot heights in the study area, exclusive of inflorescences. Assessment of palatability is based on Kalela (1957), Aleksandrova *et al.* (1964), Skjenneberg and Slagsvold (1968), Emanuelsson (1984), Ericson and Oksanen (1987), and Moen *et al.* (1993a).

Fenced exclosures were used as controls. They found that in the absence of predators, woody plants were decimated regardless of their edibility, as predicted by GWH.

Encouraged by the results of this pilot experiment, we designed a new experiment, where the impacts of initial differences in species composition were eliminated and where all plants shared the same grazing history. We did this by using transplanted vegetation, originating from a large three-trophic-level island with both voles and predators. Moreover, we decided to conduct all plant studies on wind-exposed outer islands, thus controlling the experiment for the impacts of differences in snow melt, which often occurs earlier on wind-exposed islands than in corresponding mainland habitats, creating a risk of shoot desiccation (Dahl, 1957; Kullman, 1989). Because fences might ameliorate this stress factor by accumulating snow, we decided to use vole-free one-trophic-level islands as representatives of zero-level herbivory. To extend the time horizon, we also continued to record the vegetation of the unfenced island plots established by Hambäck *et al.* (2004).

To distinguish the impacts of predation from the ‘Krebs effect’ [i.e. the supposed consequences of arrested dispersal on vole dynamics (Krebs *et al.*, 1969; Boonstra and Krebs, 1977)], we decided to study vole dynamics on replicated mainland reference grids and on the three-trophic-level island. If dispersal problems accounted for aberrant vole dynamics on the two-trophic-level islands, voles of the three-trophic-level island should follow suit. If these differences were due to differences in predation pressure, dynamics on the three-trophic-level island should match dynamics on the mainland reference grids.

STUDY SYSTEM

The study area (location: 69°45′N, 24°30′E) belongs to the hemiarctic zone (Oksanen and Virtanen, 1995) – that is, the landscape is dominated by seemingly low arctic tundra habitats, but relatively productive scrublands prevail in moist habitats and patches of mountain birch (*Betula pubescens* ssp. *czerepanovii*) woodland occur in sites with warm microclimate. The climate is continental, with dry, calm, and cold winters [winter precipitation < 100 mm (Anonymous, 1978; Lippstad, 2007)]. The snow-melt normally occurs in early June; the break-up of

Iešjávri's ice takes place about 2 weeks later. The growing season ends in early September. Persistent snow cover is usually established by the end of September. The freezing of Iešjávri starts in late September and is completed by early November. From early November to late June, the islands are thus embedded in an ice field, which dispersing voles can easily cross but which may be intimidating due to the lack of cover.

The flat, Pre-Cambrian bedrock of this area is covered by north–south oriented glaci-fluvial ridges, which jut into Iešjávri as peninsulas and rise here and there as elongated islands. Large parts of the outermost islands lie close to the water table and are thus occupied by productive scrublands, with dense, multi-layered vegetation. The shrub layer (height 30–70 cm) consists of palatable, deciduous species, primarily of the dwarf birch, *Betula nana*. The field layer (height 5–15 cm) consists of palatable herbs, palatable deciduous dwarf shrubs, and evergreen ericoids, which range from poorly edible to poisonous (see Table 1 for details). On the ice-scoured shores, there are patches of species-rich meadow vegetation.

Avian predators do not breed on islands smaller than 5 ha if they are more than 200 m from the shore. Such islands are also too isolated to be regularly utilized by mammalian predators; most of them are practically impossible to find when the ice is covered in snow. They have thus been normally predator free, save for occasional visits of avian predators in spring and fall and some late winter invasions of starving red foxes (*Vulpes vulpes*) after crashes of vole populations on the mainland (see Hambäck *et al.*, 2004; Dahlgren *et al.*, 2007, 2009; Aunapuu *et al.*, 2008). Before the introductions, no voles were recorded from small (< 5 ha) islands further than 200 m from the mainland. Conversely, the large (1 km²) three-trophic-level island had resident voles and regularly harboured mammalian and avian predators in vole years (mainly stoats, *Mustela erminea*, and long tailed jaegers, *Stercorarius longicaudus*).

Except for voles, the islands were practically free of herbivorous vertebrates. Treacherous ice conditions prevent reindeer (*Rangifer tarandus*, which migrate through the area in September–October and May–June) from using these islands. Willow grouse (*Lagopus lagopus*) and snow hares (*Lepus timidus*) occasionally visit even the most isolated islands but occur only in low numbers in the area. Norwegian lemmings (*Lemmus lemmus*) invaded the islands during the outbreak years of 1978 (Oksanen and Oksanen, 1981; Ekerholm *et al.*, 2001) and 2007 (our own unpublished data) but occurred only infrequently during 1991–2003.

The Latin nomenclature used above is based on Lid (1987), Mitchell Jones *et al.* (1999), and DelHoyo *et al.* (1992), except that *Clethrionomys* has been replaced by *Myodes* (Pall.) (see Pavlinov, 2006).

METHODS

During 1997–2003, we estimated vole densities on the two-trophic-level islands, which were covered entirely by trapping grids (for sizes, see Table 2), and on seven reference areas of 0.6 ha, with mammalian and avian predators, located in corresponding scrublands. Four of these, to be referred to as NW reference grids, were at the Joatkanjávri field base (12–10 km from Iešjávri). Two were on the southeastern shores of Iešjávri; these will be referred to as SE reference grids. One was on the three-trophic-level island. For further details, see Table 2 and the online Appendix (evolutionary-ecology.com/data/2473.pdf).

On each trapping grid, we marked a 10 × 10 m network of trap lines, with trapping stations in their intersections. At each station, we placed an Ugglan Special (Grahnbab®)

Table 2. Sizes of the experimental islands (in hectares) and their distances (in metres) from the mainland or from the nearest island, rising at least 10 m above the lake surface

	Island								
	1a	1b	1c	1d	2a	2b	2c	2d	3
Total area	0.02	0.20	1.0	4.2	0.03	0.06	0.15	1.26	105
Habitable area	0.02	0.20	0.15	2.6	0.03	0.06	0.12	0.41	80
Dispersal distance	200	300	250	400	450	250	400	2500	250

Note: The numbers in the island row refer to the number of trophic levels on the island; the letters refer to the Appendix (evolutionary-ecology.com/data/2473.pdf). 'Total area' refers to all habitats that are persistently above the lake surface. 'Habitable area' refers to all habitats where voles are normally trapped; wind-exposed ridges are excluded.

multiple-capture vole trap, which was left in the terrain with its back door open, so that the voles perceived the traps as natural parts of their runways. In spring (immediately after ice break up) and in autumn (2–3 weeks before the freeze began), the traps were baited with crushed oats and activated by closing their back doors (Hambäck and Ekerholm, 1997; Dahlgren *et al.*, 2007). The traps were checked at 8-h intervals for a period of 48 h on islands and for a period of 96 h on the mainland. The average percentage of voles captured at least twice during the same trapping session was 76% (range 68–84%) for mainland reference grids and 78% (range 71–85%) for the two-trophic-level islands, indicating that vole censuses were practically complete. We thus regarded the Minimum Number Known Alive (MNKA) as a sufficiently reliable index of vole densities for the purposes of the present study. The vole-free status of the one-trophic-level islands was ensured by using continuously operating traps.

For each grid, we computed mean autumnal vole densities for 1997–2002 as an index of winter herbivory. Differences between two-trophic-level islands and the two sets of reference grids were analysed by analysis of variance (ANOVA) and Tukey's *post hoc* tests. Values were transformed logarithmically to homogenize variances. As there was only one island with three trophic levels, it was included in SE reference grids in the ANOVA. To illustrate the impact of insularity *per se* on vole densities, we also present the data for the three-trophic-level island separately.

In July 2000, we excavated 80 vegetation blocks (0.7 × 0.7 m; depth > 30 cm) from a scrubland on the three-trophic-level island. This scrubland was located on its outer shore, and thus was as exposed to wind as the treatment islands (see the online Appendix: evolutionary-ecology.com/data/2473.pdf). The blocks were randomly assigned to be transplanted to two-trophic-level islands (8 blocks per island), to one-trophic-level islands (8 blocks per island) or back to the three-trophic-level island (16 blocks; these blocks were transported around the island by boat before being transplanted).

During 2000–2003, we monitored the cover of photosynthetically active organs of each species in the transplanted blocks and on the plots established by Hambäck *et al.* (2004). We used the point-frequency method (Jonasson, 1988). When estimating community-level plant biomass, we transformed the point-frequency scores to biomass (dry weight) by using regressions obtained from harvested mainland plots (for details, see Aunapuu *et al.*, 2008). Note that this method is conservative because it does not take into account the impact of grazing on stem biomass. We computed treatment effects by the lnRR approach (see Hedges *et al.*, 1999),

now standard in meta-analyses. Species-specific analyses were based directly on point-frequencies.

We focused on those nine common plant species that had been recorded from at least one transplanted block on all islands (see Table 1). For each species, we computed the relative change on each island i as $C_i = F_{i,e}/F_{i,s}$, where $F_{i,s}$ is the initial (year 2000) point-frequency score (hits per 100 holes) of the species, and $F_{i,e}$ is the final (year 2003) point-frequency score. Zeroes were replaced by a dummy value of 0.5 hits. We then computed relative changes as $\ln RR = \ln(C_i/C_{3-tr})$, where C_{3-tr} is the relative change on the three-trophic-level island. Differences between the responses of different species were analysed with ANOVA. Responses of community-level plant biomass were computed in a similar way, except that we then used biomass estimates instead of point-frequency scores. To determine whether different functional groups responded differently to the treatments, we also analysed the results on the functional group level, using species as replicates and their responses, averaged over the islands, as input values. Then, using ANOVA, we examined whether the treatment responses of different functional groups differed.

When analysing vegetation changes on the long-term plots of Hambäck *et al.* (2004), we included all species with a point-frequency score of at least 5 either in 1992 or in 2003 on at least one two-trophic-level island. We then computed island-specific indices of change as $\ln RR = \ln(F_{i,2003}/F_{i,1992})$, where $F_{i,2003}$ and $F_{i,1992}$ are the point-frequency scores for 2003 and 1992 on island i , respectively. In this analysis also, we replaced zeroes by 0.5 hits. Three plots, which had been impacted by ice scouring, were eliminated from this analysis.

On the smallest two-trophic-level island, 2a (Table 2), where the scrubland formed a 40 m long but only 2–7 m broad swath, several herbaceous plants, typical for shoreline meadows, were present on the plots of Hambäck *et al.* (2004) in 1992 or invaded them shortly thereafter. We studied changes in the 16 species with the highest point-frequency scores by computing regressions for the relationship between the numbers of years elapsed since 1991 and logarithmically transformed point-frequency scores. In all analyses, we used the SPSS v. 16-0 for Windows software package.

RESULTS

Mean autumnal vole densities differed significantly between the three areas (ANOVA: $F_{2,8} = 6.938$, $P = 0.018$). The differences between two-trophic-level islands and the SE and NW reference grids were statistically significant (Tukey's *post hoc* test: $P = 0.036$ and $P = 0.027$, respectively). In contrast, the mean autumnal vole densities of SE and NW reference grids did not differ (Tukey's *post hoc* test: $P \approx 1$). The pattern of the vole cycle on the three-trophic-level island matched the pattern on the mainland grids (Fig. 1), and the mean autumnal density on the three-trophic-level island (33.1 voles per hectare) was similar to the average for all six mainland reference grids (34.4 voles per hectare). The corresponding mean for the two-trophic-level islands was 145.6 voles per hectare.

Transfer of vegetation blocks from the three-trophic-level island to the two-trophic-level islands resulted in a 40% decline in estimated community-level plant biomass (the lowermost horizontal line in Fig. 2). But transfer to one-trophic-level islands triggered an equally strong increase (the uppermost horizontal line in Fig. 2).

The responses of most plant species to transfer to one-trophic-level islands (open circles in Fig. 2) by and large followed the community-level response. Nevertheless, ANOVA revealed significant differences between the responses of different plant species ($F_{1,8} = 4.367$,

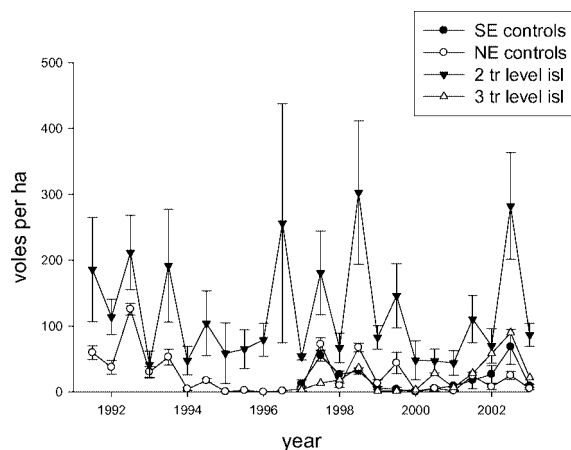


Fig. 1. Vole densities on two-trophic-level islands, on the three-trophic-level island, and in the two control areas on different sides of the lake during 1991–2002. Error bars refer to standard errors.

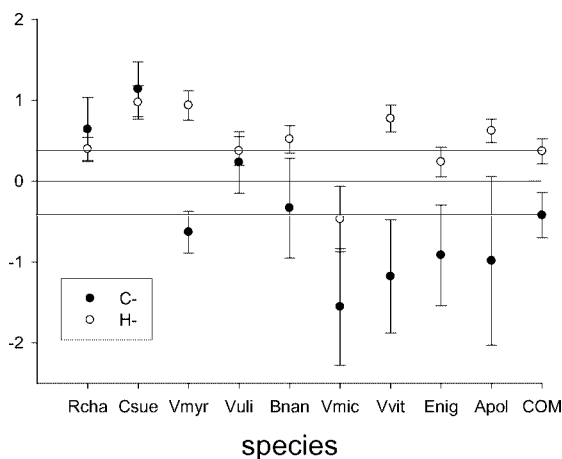


Fig. 2. Responses of the nine common species to transfers from the three-trophic-level island to two-trophic-level islands (C-, solid dots) and to one-trophic-level islands (H-, open circles), expressed as natural logarithms of response ratios (lnRR). Species are ordered in accordance to their palatability. As points of reference, we present the zero-level and the mean responses of the community-level plant biomass (COM) as horizontal lines. Error bars represent standard errors. Rcha = cloudberry, *Rubus chamaemorus*; Csue = dwarf cornel, *Cornus suecica*; Vmyr = bilberry, *Vaccinium myrtillus*; Vuli = arctic blueberry, *Vaccinium uliginosum*; Bnan = dwarf birch, *Betula nana*; Vmic = small cranberry, *Vaccinium microcarpum*; Vvit = lingonberry, *Vaccinium vitis-idaea*; Enig = crowberry, *Empetrum nigrum*; Apol = bog rosemary, *Andromeda polifolia*.

$P = 0.002$), but the only species behaving significantly differently from the others was the trailing small cranberry: it declined on one-trophic-level islands (Fig. 2, Table 3).

The responses of different species to the transfer to two-trophic-level islands were variable (Fig. 2, solid dots). Results of ANOVA revealed significant interspecific heterogeneity ($F_{1,8} = 7.976$, $P < 0.001$), and several interspecific contrasts were statistically significant

Table 3. Probability values for the null hypothesis that the responses of different species to food chain manipulations are equally strong (Tukey's *post hoc* test)

	<i>Rcha</i>	<i>Csue</i>	<i>Vmyr</i>	<i>Vuli</i>	<i>Bnan</i>	<i>Vmic</i>	<i>Vvit</i>	<i>Enig</i>	<i>Apol</i>
<i>Rubus chamaemorus</i>		0.452	0.521	1.00	0.997	0.380	0.882	1.00	0.972
<i>Cornus suecica</i>	0.885		1.00	0.555	0.835	0.002	0.999	0.295	0.995
<i>Vaccinium myrtillus</i>	0.363	0.009		0.631	0.887	0.002	1.00	0.356	0.976
<i>Vaccinium uliginosum</i>	1.00	0.493	0.551		1.00	0.157	0.912	1.00	0.995
<i>Betula nana</i>	0.750	0.046	0.998	0.918		0.059	0.994	0.988	1.00
<i>Vaccinium microcarpum</i>	0.005	0.000	0.464	0.008	0.992		0.008	0.344	0.027
<i>Vaccinium vitis-idaea</i>	0.037	0.000	0.930	0.061	0.853	0.992		0.688	1.00
<i>Empetrum nigrum</i>	0.124	0.000	0.999	0.205	0.205	0.853	0.999		0.927
<i>Andromeda polifolia</i>	0.092	0.000	0.995	0.154	0.154	0.914	1.00	1.00	

Note: Values for transfer to two-trophic-level islands are shown below the diagonal; values for transfer to one-trophic-level islands are shown above the diagonal. Probability values <0.1 are shown in **bold** font.

(Table 3, below the diagonal). The positive response of the herbaceous dwarf cornel differed significantly from the negative responses displayed by all evergreen ericoids and by two deciduous woody plants. The herbaceous cloudberry and the deciduous arctic blueberry handled the impacts of food-limited voles significantly better than the lingonberry and small crowberry.

All three functional groups responded positively to the transfer from the three-trophic-level island to one-trophic-level islands (Fig. 3, open circles), but there was a trend: herbs reacted most positively and evergreen ericoids lagged behind. These differences were at the limit of statistical significance (ANOVA: $F_{2,6} = 4.842$, $P = 0.56$; Tukey's *post hoc* test for the contrast between herbs and evergreen ericoids: $P = 0.51$).

The differences between the responses of functional groups to the transfer from the three-trophic-level island to two-trophic-level islands (Fig. 3, solid dots) were statistically significant (ANOVA: $F_{2,6} = 11.560$, $P = 0.009$). The profoundly negative response of evergreen ericoids differed significantly from the positive response of herbaceous plants (Tukey's *post hoc* test: $P = 0.008$) and almost significantly from the variable responses of deciduous woody plants (Tukey's *post hoc* test: $P = 0.084$). The difference between the responses of herbs and deciduous woody plants was non-significant ($P = 0.140$).

The changes in vegetation observed on the long-term plots (Fig. 4) by and large corresponded to the responses of the transplanted vegetation blocks. Evergreen ericoids were decimated, whereas herbaceous plants had increased. Trailing woody plants stood their ground or increased, as did the morphologically flexible, deciduous arctic blueberry. The main difference, compared with the transplanted blocks, was the precipitous decline of the deciduous bilberry, whose point-frequency score on the long-term plots in 2003 was only 5% of its score in 1992.

Logarithmically transferred point-frequency scores of herbaceous plants increased linearly with the time elapsed from the start of the experiment (Fig. 5), implying exponential expansion. The only species with a statistically significant ($P = 0.014$), negative second-order term was the preferred and initially abundant cloudberry (Fig. 5A), which was also the only herbaceous species failing to show a net increase on the long-term plots (Fig. 4). Otherwise, there was no obvious relationship between the slopes of the regressions

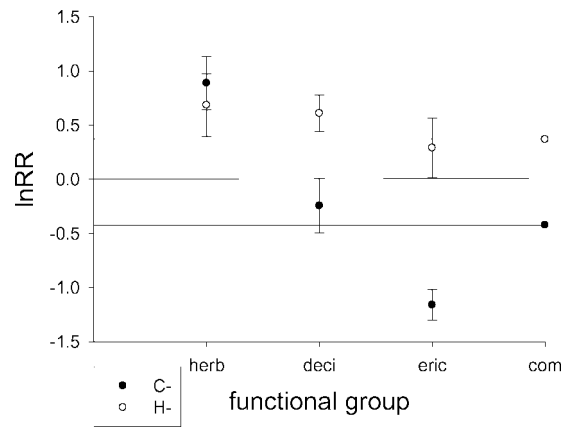


Fig. 3. Responses of different functional groups to transfer from the three-trophic-level island to two-trophic-level islands (C-, black dots) and to one-trophic-level islands (H-, open circles), where herb = herbaceous dicotyledons, deci = deciduous dwarf shrubs, eric = evergreen ericoids, and com = community-level plant biomass; denoted also by horizontal lines. In this analysis, species have been used as replicates and the means of their responses as input values. The responses are expressed as natural logarithms of response ratios. Error bars represent standard errors.

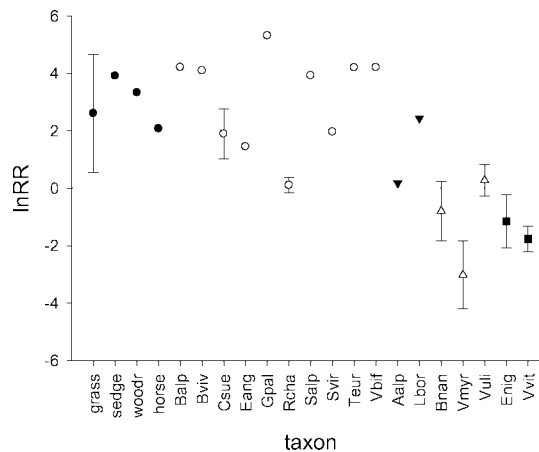


Fig. 4. Net changes in the point-frequency scores of all reasonably common species on the long-term plots of Hambäck *et al.* (2004). Criterion: the plant had a frequency score of 5% (5 hits per 100 holes) on at least one two-trophic-level island in 1992 or 2003. Grasses, sedges, wood rushes, and horsetails have been aggregated, as they could not be reliably identified to species in the early years. Solid dots: silica accumulating plants; open circles: herbs; solid triangles: trailing plants; open triangles: deciduous dwarf shrubs; solid squares: evergreen ericoids. Within each functional group, species are arranged alphabetically. Error bars represent standard errors. grass = Poaceae, sedge = Cyperaceae, woodr = *Luzula* spp., horse = *Equisetum* spp., Balp = *Bartsia alpina*, Bviv = *Bistorta vivipara*, Csue = *Cornus suecica*, Eang = *Epilobium angustifolium*, Gpal = *Galium palustre*, Rcha = *Rubus chamaemorus*, Salp = *Saussurea alpina*, Svir = *Solidago virgaurea*, Teur = *Trollius europaeus*, Vbif = *Viola biflora*, Aalp = *Arctostaphylos alpina*, Bnan = *Betula nana*, Vmyr = *Vaccinium myrtillus*, Vulii = *Vaccinium uliginosum*, Enig = *Empetrum nigrum*, Lbor = *Linnaea borealis*, Vvit = *Vaccinium vitis-idaea*.

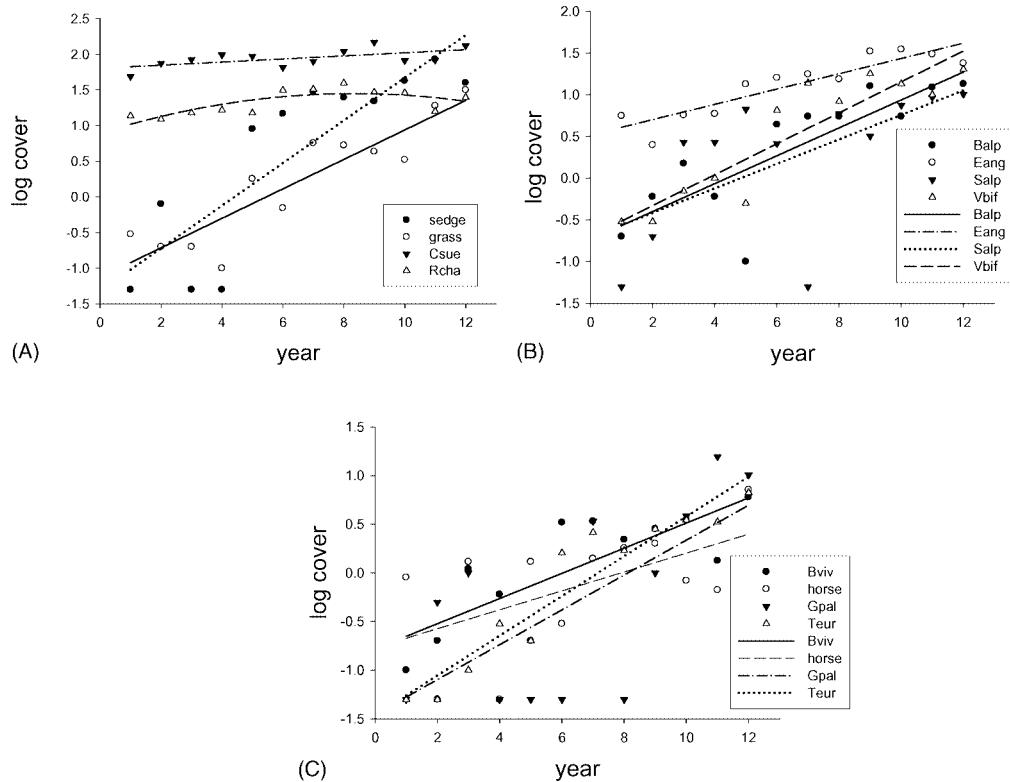


Fig. 5. Logarithmically transformed point-frequencies (log cover) of the 16 most common herbaceous taxa encountered on island 2a as functions of years elapsed since the start of the experiment. The log cover values can be interpreted as 10-based logarithms of percent leaf area cover on the plots ($-1 = 1\%$; $0 = 10\%$; $2 = 100\%$). The regression for horsetails (C) is almost significant ($P = 0.062$); all other regressions are statistically significant ($P < 0.05$). Abbreviations are as in the legend to Fig. 4.

(Fig. 5) or magnitudes of net increase (Fig. 4) and palatability of each species to grey-sided voles.

DISCUSSION

The 3.7-fold difference in autumnal vole densities between our two-trophic-level islands and reference grids, and the similarity of vole densities and fluctuation patterns between the three-trophic-level island and the mainland reference grids, warrant the conclusion that reduced predation pressure accounted for the high vole densities on the two-trophic-level islands. This interpretation is also consistent with other studies emphasizing the importance of predation as a regulating factor of voles living in the boreal zone or in productive low arctic scrublands (Korpimäki and Norrdahl, 1998; Klemola *et al.*, 2000; Ekerholm *et al.*, 2004; see also Hanski *et al.*, 2001; Korpimäki *et al.*, 2005).

The hypothesis that arrested dispersal causes high vole densities is also logically problematic. Dispersal barriers block both immigration and emigration. Therefore, arrested dispersal should not influence population growth, unless the fenced area consists of source habitats (Ostfeld, 1994).

According to our conservative method, which does not take into account the impact of herbivory on the stature of the plants, the elimination of predators resulted in a 40% reduction of community-level plant biomass. Contrary to the arguments of Strong (1992) and Polis and Strong (1996), the impact of reduced predation pressure on voles thus cascaded to the first trophic level, as predicted by GWH, and so did the impact of the elimination of the whole food chain. The latter impact is predicted by the model of Oksanen *et al.* (1981) for habitats barely productive enough to support resident predators (see also Aunapuu *et al.*, 2008).

Elimination of predators also had a strong, cascading impact on abundance relationships between different plant species and functional groups, but these impacts were diametrically opposite to the changes predicted by Leibold (1989, 1996), Strong (1992), and Polis and Strong (1996). Instead of favouring well-defended evergreen ericoids, the absence of predators was especially detrimental to them. Ericoids had comparatively low rates of shoot mortality (Hambäck and Ekerholm, 1997), but this advantage was apparently offset by the greater impact of each lost shoot for the evergreens, which do not translocate their resources from shoots to rhizomes in fall.

The strong seasonality of our study area probably contributed to the vulnerability of plants that rely on chemical defences (Hambäck, 1998). Searching is costly when the ground is covered by a dense snow pack, and high searching costs favour broad diets (Krebs and Davies, 1991). However, similar replacements of unpalatable woody plants and tall, poisonous herbs by more palatable low herbs or graminoids have also been observed in predator-free tropical systems and in greenhouse experiments (Merton *et al.*, 1976; Moen *et al.*, 1993a; Rammul *et al.*, 2007; Bond, in press; Oksanen *et al.*, in press). Strong seasonality thus cannot be a necessary condition for the occurrence of community-wide terrestrial trophic cascades in terrestrial ecosystems. Seasonality probably only amplifies the cascading impacts of predation on woody plants and ameliorates those impacts on herbaceous plants (Norrdahl *et al.*, 2002).

Within each functional group, differences in palatability did count. Among the herbs, the preferred cloudberry responded less positively than other species. The preferred bilberry declined more profoundly than other deciduous woody plants. Moreover, as predicted by several authors (Leibold, 1989, 1996; Pastor and Naiman, 1992; Chase *et al.*, 2000; Howe *et al.*, 2006; Schmitz, 2006), the well-defended evergreen ericoids thrived best on the three-trophic-level island, with substantial herbivore pressure. When transferred to one-trophic-level islands, evergreen ericoids did not increase as fast as their competitors, and the smallest evergreen ericoid, the small cranberry, declined. Leibold's (1989, 1996) trade-off model thus correctly predicted the responses of different kinds of plants to the elimination of vole herbivory but failed to predict their responses to the elimination of predators.

To understand the successes and failures of Leibold's (1989, 1996) trade-off model and other ideas emphasizing the role of plant defences (Pastor and Naiman, 1992; Strong, 1992; Polis and Strong, 1996), consider the qualitative difference between the behaviour of predation-controlled and food-limited herbivores. In the presence of predators, herbivores are alert (Fortin *et al.*, 2005) and minimize their exposure to predation by choosing those plants that yield the most nutrients and energy per unit of foraging time. When food is running out and predators are absent, herbivores do not face such constraints. They start to use marginal food sources, such as the phloem, which can result in large-scale girdling and high shoot mortality (Hansson, 1985). Moreover, food-limited voles may clip ericoid shoots just because they are in the way, leaving them dying on the ground (our own observations).

For well-defended evergreen ericoids, moderate grazing pressure, exerted by predation-controlled herbivores, thus seems to be optimal. It keeps more palatable competitors at bay,

but does not result in heavy losses for ericoids. In contrast, palatable herbaceous plants flourish when herbivores are absent, allowing undisturbed competition, and, when herbivores are food limited, allowing herbaceous plants to capitalize on their relative inaccessibility in winter. The latter situation is especially favourable for those herbaceous species that are not directly preferred by the herbivore in question and that have ruderal characteristics, making them quick to invade disturbed sites (Moen *et al.*, 1993a; Rammul *et al.*, 2007).

Low palatability is thus an excellent way of minimizing the rate of tissue loss in areas with predator-controlled herbivores, especially in nutrient-poor northern habitats, where the costs of accumulating carbon-based secondary chemicals are low (Bryant *et al.*, 1983; Oksanen, 1990; Dahlgren *et al.*, 2009). Consequently, evergreen ericoids abound in the boreal zone and along the southern fringes of the tundra (Kujala, 1926; Hämet-Ahti, 1963; Haapasaari, 1988; Oksanen and Virtanen, 1995). On the tundra proper, with food-limited herbivores (Aunapuu *et al.*, 2008; Oksanen *et al.*, 2008), the strategy of evergreen ericoids is successful only in habitats with shallow and tightly packed snow, creating difficult grazing conditions (Oksanen and Virtanen, 1995). In habitats with deeper snow, the vegetation is recurrently devastated by lemmings, which is disastrous for ericoids and for layer-forming mosses, thus favouring graminoids and vertically growing mosses (Moen *et al.*, 1993b; Virtanen *et al.*, 1997; Virtanen, 1998, 2000; Aunapuu *et al.*, 2008).

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