

# Spatial Patterns and Dynamic Responses of Arctic Food Webs Corroborate the Exploitation Ecosystems Hypothesis (EEH)

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**ABSTRACT:** According to the exploitation ecosystems hypothesis (EEH), productive terrestrial ecosystems are characterized by community-level trophic cascades, whereas unproductive ecosystems harbor food-limited grazers, which regulate community-level plant biomass. We tested this hypothesis along arctic-alpine productivity gradients at the Joatka field base, Finnmark, Norway. In unproductive habitats, mammalian predators were absent and plant biomass was constant, whereas herbivore biomass varied, reflecting the produc-

tivity of the habitat. In productive habitats, predatory mammals were persistently present and plant biomass varied in space, but herbivore biomass did not. Plant biomass of productive tundra scrublands declined by 40% when vegetation blocks were transferred to predation-free islands. Corresponding transfer to herbivore-free islands triggered an increase in plant biomass. Fertilization of an unproductive tundra heath resulted in a fourfold increase in rodent density and a corresponding increase in winter grazing activity, whereas the total aboveground plant biomass remained unchanged. These results corroborate the predictions of the EEH, implying that the endotherm community and the vegetation of the North European tundra behaves dynamically as if each trophic level consisted of a single population, in spite of local co-occurrence of >20 plant species representing different major taxonomic groups, growth forms, and defensive strategies.

**Keywords:** arctic, herbivory, plant communities, predation, trophic cascades, tundra vegetation.

Hairston et al. (1960) initiated a major controversy by proposing that herbivores as a group are limited by the collective action of predators and that this is a necessary condition for the persistence of biomass-rich terrestrial plant communities. They thus argued that terrestrial food webs are characterized by strong community-level trophic cascades (Carpenter et al. 1985) embracing even seemingly inedible plants (Slobodkin et al. 1967). Contrary to Hairston et al., however, leading arctic experts regarded herbivores as food limited and emphasized the role of natural herbivory as a central plant ecological factor on the tundra (Tihomirov 1959; see also Caughley and Gunn 1993; Zimov et al. 1995). Oksanen et al. (1981; see also Oksanen and Oksanen 2000) tackled this apparent discrepancy by applying Fretwell's (1977) idea that trophic dynamics change along gradients of primary productivity. The result (Oksanen et al. 1981; Oksanen and Oksanen 2000) was the exploitation ecosystems hypothesis (EEH), whose predictions are summarized in figure 1.

The least productive areas are predicted to be devoid of herbivorous endotherms, because the physical environment limits plant biomass at a level that is below the minimum requirements of herbivores ( $P^*$ ). In environ-

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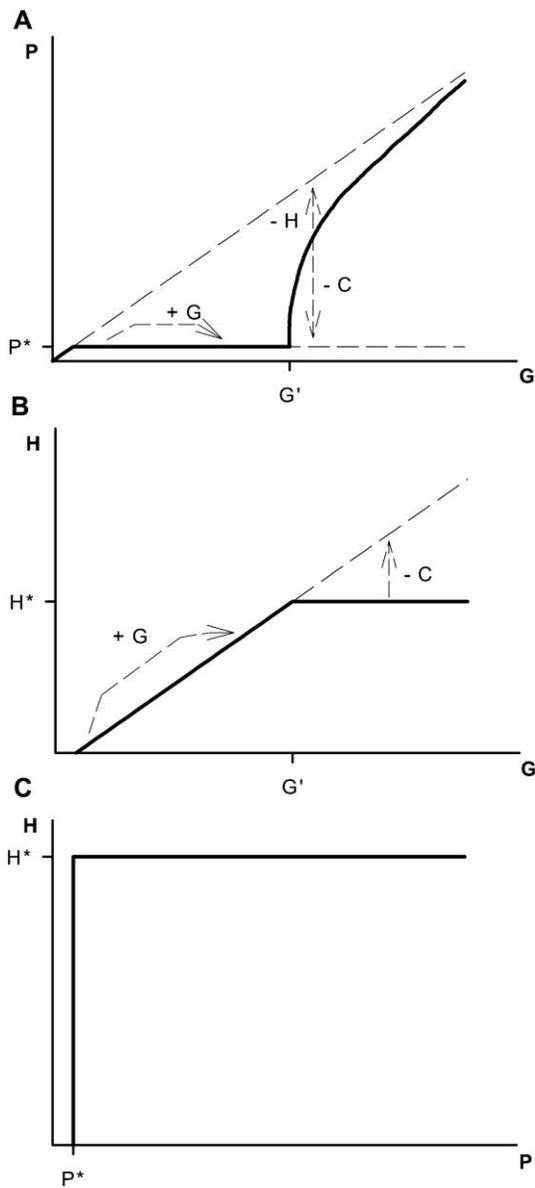
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**Figure 1:** Summary of the predictions of the exploitation ecosystems hypothesis concerning plant ( $P$ , A) and herbivore ( $H$ , B) biomass along gradients of potential primary productivity ( $G$ ) and the predicted relation between plant and herbivore biomass ( $C$ ) inferred from A and B.  $G'$  refers to the predicted threshold between two-trophic-level dynamics and three-trophic-level dynamics;  $P^*$  refers to the equilibrium plant biomass in two-trophic-level systems;  $H^*$  refers to the equilibrium herbivore biomass in systems with three-trophic-level dynamics. The solid lines refer to mainland systems open to herbivores and predators. The straight dashed lines refer to herbivore-free areas (*oblique line* in A) or to predator-free areas (*horizontal line* in A, *oblique line* in B). The distance between the solid line and the horizontal dashed line in A represents the predicted strength of the trophic cascade at a given productivity level. The distance between the solid line and the oblique dashed line in A represents the predicted strength of the direct herbivore effect in the presence of

plants productive enough to support more plant biomass, herbivorous endotherms are predicted to be present, plant biomass is predicted to be locked at  $P = P^*$  (fig. 1A), and herbivore biomass is predicted to increase linearly with increasing primary productivity (fig. 1B). At the next critical productivity threshold ( $G'$  in fig. 1), the biomass of food-limited herbivores reaches the level that predatory endotherms require for positive energy balance ( $H^*$ ). At this threshold, two-trophic-level dynamics, with food-limited herbivores and grazing-controlled vegetation, is predicted to be replaced by three-trophic-level dynamics, with herbivore biomass locked at  $H^*$  (fig. 1B) and plant biomass increasing with increasing productivity. Gradually, the effect of herbivory (the gap between the dashed oblique line and the solid line in fig. 1A) decreases, and the dynamics of the system approach pure Hairston et al. (1960) dynamics.

Oksanen et al. (1981) thus accepted the general premises of Hairston et al. (1960)—exploitive trophic interactions, functional homogeneity of trophic guilds—but challenged their generality, especially in the case of endotherms. Several other authors have rejected Hairston et al.'s basic premises. According to Strong (1992; see also Polis and Strong 1996; Polis 1999), species-rich terrestrial systems are characterized by such high diversity of plant defenses and antipredator strategies in herbivores that strong community-level trophic cascades cannot exist. Strong's (1992) viewpoint is seconded by the analysis of Hall et al. (2007; see also Shurin et al. 2006), where the strength of trophic cascades is predicted to depend on the digestibility of plants, which is low in most terrestrial ecosystems. Consequently, community-level plant biomass is predicted to increase linearly along gradients of increasing primary productivity. Leibold (1989, 1996; see also Chase et al. 2000) and Oksanen (1992) pursued another idea emphasized by Strong (1992): trophic guilds are functionally heterogeneous because of trade-offs between competitiveness and exploitation tolerance, creating a situation where community-level consequences of trophic cascades are qualitative rather than quantitative. Inducible defenses (Haukioja and Hakala 1975) have a similar net effect on trophic dynamics (Vos et al. 2004). Regardless of whether the average level of resistance increases through changes in species composition or via individual flexibility, such changes create a situation where plant and herbivore biomasses increase monotonically along gradients of increasing primary productivity. Even the theory of ratio-dependent pre-

predators. The dashed lines with arrowheads in A and B refer to the predicted outcomes of predator removal ( $-C$ ) and herbivore removal ( $-H$ ) experiments and the predicted effects of experimental enrichment ( $+G$ ).

dation (Arditi and Ginzburg 1989; Abrams and Ginzburg 2000) predicts that plant and herbivore biomass increase linearly along productivity gradients.

The biomass patterns predicted by the EEH (fig. 1A, 1B) are thus in sharp contrast with the more or less linear, positive relationship of plant and herbivore biomasses to primary productivity predicted by other hypotheses. Unfortunately, primary productivity has turned out to be difficult to estimate in many terrestrial ecosystems (for the tundra, see Kjølvik and Kärenlampi 1975; Rosswall et al. 1975; Wielgolaski 1975b). It is thus practical to convert the biomass-versus-productivity predictions to herbivore biomass-versus-plant biomass predictions by plotting predicted plant and herbivore biomasses against each other. The result is a rectangle, with its vertical side at  $P^*$  and its horizontal side at  $H^*$  (fig. 1C).

Observational studies on spatial patterns are inevitably preliminary, because every pattern can be created by many different processes (Abrams 1993). More conclusive experimental tests can be performed by excluding predators from low-arctic scrublands that are predicted to be slightly above the critical productivity threshold (Oksanen et al. 1981; Oksanen 1983). The EEH predicts that herbivore biomass will increase and plant biomass will be decimated (fig. 1, *dashed lines denoted* “ $-C$ ”). Conversely, exclusion of herbivorous mammals is predicted to initiate an increase in plant biomass (fig. 1A, *dashed line denoted* “ $-H$ ”). On unproductive tundra heaths (with  $G \ll G'$ ), experimental increase in the primary productivity is predicted to lead to increased herbivore biomass and intensification of grazing pressure, preventing an increase in plant biomass (fig. 1A, 1B, *dashed lines denoted* “ $+G$ ”). For food web manipulations ( $-C$  and  $-H$  in fig. 1), the predictions of the ratio-dependent theory (Arditi and Ginzburg 1989) converge with the predictions of the EEH, whereas the other hypotheses outlined above (Leibold 1989, 1996; Oksanen 1992; Strong 1992; Polis and Strong 1996) predict that the effects on community-level biomass are weak. For the fertilization experiment, all competing hypotheses predict an increase in both plant and herbivore biomass. Below, we report three empirical tests of these contrasting predictions.

### The Study System

The study was conducted in the low-arctic tundra landscape of Finnmarksvidda, in northernmost Norway (69°45'N, 23°55'E). The study area consists of two plateaus at different altitudes, the Highland (500–670 m above sea level [asl]) and the Lowland (380–450 m asl). These two nutrient-poor plains, each covering hundreds of square kilometers, are separated from each other by a steep, south-facing escarpment, the Slope, where soils are moist

and nutrient rich. The Lowland is rich in shallow lakes dotted with islands. Most of the landscape is covered by dwarf birch lichen heaths, where 20–25 different plant species co-occur on sample plots of 0.64 m<sup>2</sup>: unpalatable evergreen ericoids and mosses coexisting with palatable deciduous dwarf shrubs, graminoids, and lichens (Oksanen and Virtanen 1995; Bruun et al. 2006; for palatability, see Aleksandrova et al. 1964).

The rodent community includes two species with broad diets and low agility (the Norwegian lemming *Lemmus lemmus* and the gray-sided vole *Clethrionomys rufocanus*), two *Microtus* species, and the agile red vole *Clethrionomys rutilus*, specialized on high-quality forage (Hansson 1985). The prevailing mammalian predators are the stoat (*Mustela erminea*) and the (least) weasel (*Mustela nivalis*); both are specialized on rodents. The generalist American mink (*Mustela vison*) and the red fox (*Vulpes vulpes*) are present in low numbers. The most abundant avian predators are the rough-legged hawk *Buteo lagopus*, a rodent specialist, the long-tailed jaeger *Stercorarius longicaudus*, a generalist, and the merlin *Falco columbarius*, a generalist (Aunapuu 1998).

Our primary study area, referred to as the Joatka research area (16.8 km<sup>2</sup>), spans the escarpment, including pieces of the Highland, the Lowland, and the Slope. Within this study area, we selected 14 smaller areas, called “study sites” (0.2 km<sup>2</sup>; five on the Highland, five on the Lowland, four on the Slope), the criteria being maximal dispersion within each subarea and inclusion of the habitat variation typical for the subarea (see fig. A1 in the online edition of the *American Naturalist*). Three habitats found in our study area—willow thickets, dwarf birch lichen heaths, and palsa bogs—match the focal Fennoscandian tundra habitats studied in detail during the International Biological Programme (IBP; Kjølvik and Kärenlampi 1975; Rosswall et al. 1975). Their primary productivities have been estimated as 780, 270, and 150 g m<sup>-2</sup> year<sup>-1</sup>, respectively. These estimates have been obtained in thermal conditions comparable to those in our Lowland subarea. Primary productivity of tundra habitats with similar soil conditions varies proportionally to the sum of effective temperatures ( $\sum dd > +5^\circ\text{C}$ , where  $dd = \text{degree-days}$ ), obtained by subtracting 5 from daily mean temperatures (in  $^\circ\text{C}$ ) and summing the positive values obtained during a given growing season (Wielgolaski 1975a).

### Methods

#### *Estimating Primary Productivity and Biomasses of Plants, Rodents, and Predators*

To be able to use the productivity estimates presented above and Wielgolaski's (1975a) inferences, we mapped

the vegetation of the study area, using a Landsat 7/ETM+ satellite image (track 195/frames 11–12) taken on July 27, 2000 (see fig. A1), and traditional mapping techniques (e.g., by matching limits between vegetation units against identifiable topographic features and by triangulation). On the basis of Wielgolaski's (1975a) productivity estimates from corresponding habitats, we divided each subarea into (1) productive habitats, (2) intermediate habitats, and (3) unproductive habitats. In the Lowland, the productivity ranges of these habitat categories are  $\approx 750$ ,  $300\text{--}750$ , and  $<300\text{ g m}^{-2}\text{ year}^{-1}$ , respectively. On the basis of abundance relationships between habitat types, we estimated that the mean primary productivity of habitat categories 2 and 3 in the Lowland was  $525$  and  $230\text{ g m}^{-2}\text{ year}^{-1}$ , respectively. For the Highland and the Slope, we corrected the productivity estimates by multiplying them by  $\sum dd_H / \sum dd_L$  for the Highland and  $\sum dd_S / \sum dd_L$  for the Slope, where  $\sum dd_i$  refers to the sums of effective temperatures for of subarea  $i$ . We computed the sums of effective temperatures for the growing seasons of 1991–1999, using mean temperatures from the nearest weather stations and correcting for altitude and for the inclination of the slope, in accordance with the standard technique of the Norwegian Meteorological Institute (<http://www.met.no>; see appendix in the online edition of the *American Naturalist* for details). We estimated the mean primary productivity for each study site as a weighted average of productivity estimates for each habitat category, using the abundances of the habitat categories as weighting factors. From the values obtained for the 14 study sites, we estimated average productivities of the Highland, the Lowland, and the Slope. These estimates are presented in table 1.

When estimating the plant biomass of each study site, we used two methods. First, from the Landsat image mentioned earlier, we computed the normalized difference vegetation index (NDVI, an index for the photosynthetically active plant biomass; see Chen and Brutsaert 1998) for entire study sites of  $0.2\text{ km}^2$ . Second, we estimated plant biomass in rodent-trapping grids by harvesting stratified

plots within the mapped habitats in 2003, when voles were near their long-term average density (for problems created by cyclic dynamics, see Abrams and Roth 1994). The four main layers (tree, bush, field, and bottom) were harvested using different subplot sizes ( $100$ ,  $1.0$ ,  $0.1$ , and  $0.01\text{ m}^2$ , respectively). The numbers of plots used for the Slope, the Lowland, and the Highland were 14, 9, and 15, respectively. We sorted the harvested material by species and dried it in the lab at  $60^\circ\text{C}$  for 48 h. Vascular plants were aggregated into three functional categories: shrubs and trees, high-quality forage plants (graminoids, forbs, and bilberry twigs), and the rest (mainly evergreen ericoids).

To quantify the biomass of rodents, we established live-trapping grids of  $100\text{ m} \times 50\text{ m}$  in central parts of each study site, covering local productivity gradients from hill-ocks to depressions. On the Slope, where the scale of local habitat variation was larger, the grids were enlarged to  $160\text{ m} \times 50\text{ m}$ . In each grid, we placed lemming variants of Ugglan Special live traps (Grahnb, Sweden) permanently in a  $10 \times 10\text{-m}$  network. The traps were activated in spring and autumn for 96 h, every second line at a time. Herbivore biomass was computed as the sums of the weights of rodents trapped in autumn (Oksanen et al. 1999; T. Oksanen, Ü. Rammul, M. Schneider, and M. Aunapuu, unpublished data).

Because of the large home ranges of predators, their biomass could be estimated only for entire subareas. We did this by counting breeding avian predators and their nestlings, and we converted the postfledging numbers into biomass, using the body weights from Cramp and Simmons (1980, 1983). Moreover, we live-trapped stoats (*Mustela erminea*), weasels (*Mustela nivalis*), and minks (*Mustela vison*) every autumn (August–September) with 50–60 Erlinge live traps spread over all three subareas (Aunapuu 1998). Estimates of mustelid biomass were based on the numbers and weights of trapped individuals.

To estimate predator activity within individual study sites, we counted the years when stoats or weasels were tracked or trapped within each trapping grid. To avoid

**Table 1:** Sums of effective temperatures for 1991–1999 and proportions of habitats with favorable, intermediate or unfavorable local conditions for plant growth, along with their estimated primary productivity, and estimated mean primary productivity of each subarea

	Mean sum of effective temperatures ( $\sum dd > +5^\circ\text{C}$ )	Favorable habitats		Intermediate habitats		Unfavorable habitats		Estimated average primary productivity
		Productivity	Share of area (%)	Productivity	Share of area (%)	Productivity	Share of area (%)	
Highland	$324 \pm 11$	640	.1	430	1.8	190	98.1	195
Lowland	$394 \pm 2$	780	.4	525	11.8	230	87.8	270
Slope	$436 \pm 8$	865	20.0	580	72.5	255	7.5	615

Note: The sum of effective temperatures ( $\sum dd$  [degree-days]  $> +5^\circ\text{C}$ ) is obtained by subtracting 5 from daily mean temperatures and summing the positive values obtained during a given growing season. Productivity estimates are rounded to nearest integer divisible by 5 and are expressed in units of  $\text{g m}^{-2}\text{ year}^{-1}$  (dry weight). For details of the productivity estimation process, see the appendix.

bias, each grid had two mustelid traps, and mustelid tracks were recorded only on 100 × 50-m pieces of Slope grids (see Aunapuu and Oksanen 2003). The activity of red foxes (*Vulpes vulpes*) was estimated on the basis of overturned vole traps (Oksanen et al. 1999).

According to the EEH, the Highland is predicted to have two-level trophic dynamics, the Slope is predicted to have three-level trophic dynamics, and trophic dynamics in the Lowland are predicted to be habitat specific. We therefore decided to divide the Lowland study sites into three-trophic-level and two-trophic-level sites, the criterion being whether predators had been recorded in the site during at least four years. Biomass patterns for the four site categories thus obtained were tested with ANOVA.

#### *Food Chain Manipulations*

In order to standardize physical conditions (snow depth, temperature, isolation), we performed these experiments on the islands of Iešjávri (distance to mainland > 250 m). On one of these islands, called the “three-trophic-level island,” we had earlier trapped predatory mammals and observed breeding avian predators. Of the other islands, four had gray-sided voles; these are called “two-trophic-level islands.” Four islands were vole free and were ensured of staying so by recurrent snap trapping; these are called “one-trophic-level islands.” We tackled the statistical problems of our 1 + 4 + 4 design by testing (with *t*-test) whether the three-trophic-level island was outside the 95% confidence interval for individual values in the other categories.

Starting in 2000, we monitored vole populations by live trapping after the spring breakup (late June to early July) and in fall, before freezing started (late August to early September). We used the same trapping method as in the main study area (above; see also Hambäck and Ekerholm 1997; Hambäck et al. 2004). The habitable area of the largest two-level island (with an uninhabitable, wind-blown central ridge) was estimated on the basis of the innermost traps where resident voles were trapped. (For total areas, habitable areas, and productive scrubland areas of these islands, see table A1 in the online edition of the *American Naturalist*.) To study the consequences of insularity per se for vole dynamics, we also established four mainland reference areas (see fig. A1).

The experiment concerning the effect of food web dynamics on the vegetation was started in July 2000 by excavating 80 vegetation blocks (70 cm × 70 cm, depth > 30 cm) from a scrubland on the three-trophic-level island. These blocks were randomly assigned to the treatments. We transferred eight blocks to each of the two-trophic-level and one-trophic-level islands and transplanted them in a habitat similar to their habitat of origin. Moreover,

we drove 16 blocks around the three-trophic-level island and transplanted them back to their habitat of origin (to maximize the initial homogeneity of the vegetation and to ensure that all plants shared the same grazing and handling history). To monitor changes in the vegetation, we used the point frequency method (Jonasson 1988), with 100 sampling points per block and a pin diameter of 2 mm). We transformed the point frequency data into biomass by conducting separate point frequency censuses in 90 additional plots in July 2003, harvesting all shoots of vascular plants, sorting by species, drying for 48 h at 60°C, weighing, and computing species-specific linear regressions between point frequency scores and biomass. We computed relative biomass changes (RCB) using the formula  $RCB = (B_e - B_s)/B_s$ , where  $B_s$  is biomass at the start and  $B_e$  is biomass at the end.

#### *Enrichment Experiment in the Highland*

For this study, we marked eight circles of 0.25 ha on the Highland lying at least 40 m from any neighboring circle and maximally similar to each other. We then assigned these circles randomly to four treatments and four controls. In July 1991, we fertilized the treatment circles with 80 g m<sup>-2</sup> of granulated fertilizer (13.7% N, 6.0% P, 15.7% K), in accordance with local agricultural norms. This level was sufficient to cause a persistent increase in nutrient pool and primary productivity (Grellmann 2002). In August 1999, we determined the aboveground plant biomass in these circles by harvesting four randomly located subplots of 0.1 m<sup>2</sup> (mosses and lichens were harvested only in two fertilized circles and two controls). The biomass of microtine rodents was determined by live trapping, as above. We studied the effect of rodents on the vegetation of each circle immediately after the snowmelt by mapping the areas where the moss cover was destroyed and/or where >50% of dwarf shrub shoots had been clipped.

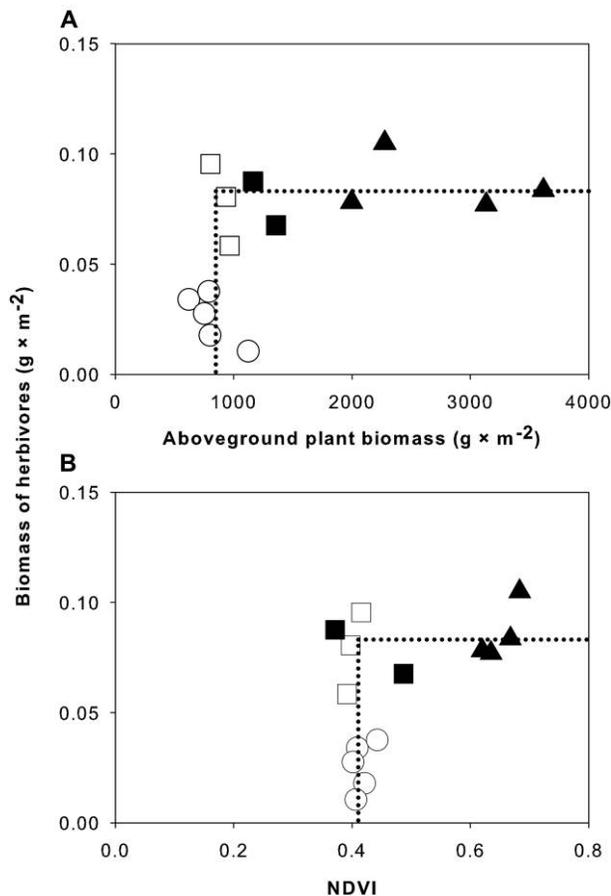
## **Results**

### *Spatial Patterns in Predator Activity and Biomass at Different Trophic Levels*

Within all Slope (S) study sites, we recorded small mustelids during seven or eight years. Within Highland (H) study sites, small mustelids were recorded once or not at all. The numbers of small-mustelid records for the Lowland study sites are 1, 1, 2, 4, and 7. The three Lowland study sites with one or two small-mustelid records we regarded as two-trophic-level study sites (L(2)), whereas the two study sites where small mustelids were recorded during four or seven years we regarded as three-trophic-level study sites (L(3)). When site-specific estimates of

herbivore biomass are plotted against plant biomass estimates, the visual impression is a rectangle (fig. 2) where the two-trophic-level study sites constitute the vertical line and the three-trophic-level study sites define the horizontal line. The statistical significance of this pattern is confirmed by ANOVA. Study site categories with two trophic levels (H, L(2)) differ with respect to rodent biomass, but plant biomass is constant. The converse holds for study site categories with three trophic levels (L(3), S): plant biomass differs but rodent biomass is constant (table 2).

The local differences in mustelid activity reported above are associated with order-of-magnitude differences in predator biomass between subareas (fig. 3A). The predator communities of different subareas differ even qualitatively. Rodent specialists prevail on the Slope, whereas the pred-



**Figure 2:** Observed relationship of herbivore biomass, plant biomass, and predator activity. Plant biomass is represented by harvested aboveground plant biomass (A) and normalized difference vegetation index (NDVI; B). Study sites are denoted with circles for the Highland, squares for the Lowland, and triangles for the Slope. The number of years in which mustelids were recorded in the grid are indicated as follows: open symbols = 0–2 years; filled symbols = 4–8 years.

**Table 2:** *P* values for Tukey post hoc tests comparing normalized difference vegetation index (NDVI) estimates of plant biomass, harvest-based aboveground plant biomass estimates, and estimates of mean rodent biomass between the Highland, predator-free Lowland sites (L(2)), Lowland sites with predators (L(3)), and the Slope

	Highland	L(2)	L(3)
NDVI:			
L(2)	.927		
L(3)	.961	.790	
Slope	<.001	<.001	<.001
Harvested plant biomass:			
L(2)	.993		
L(3)	.797	.623	
Slope	<.001	.001	.011
Rodent biomass:			
L(2)	.002		
L(3)	.005	.999	
Slope	<.001	.878	.896

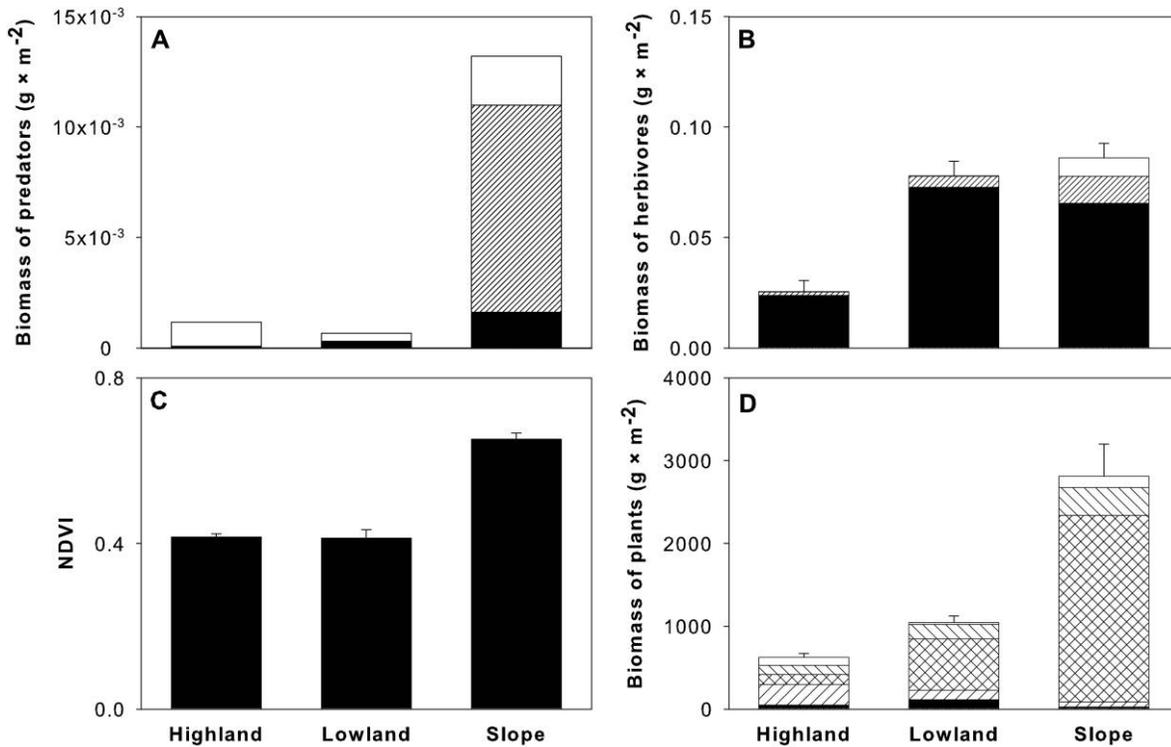
ator communities of the Lowland and the Highland are dominated by opportunistic generalists (jaegers). The biomass of resident small mustelids is by far the highest in the Slope; it is low in the Lowland and almost zero in the Highland. Even the mean index for red fox activity is highest (0.73) for the Slope, lower (0.16) for the Lowland, and zero for the Highland (Oksanen et al. 1999).

Qualitative differences between the rodent communities of different subareas are small. Broadly folivorous and relatively sluggish species prevail everywhere, but more agile and selective species (red voles, root voles) are moderately common in the Slope, whereas the least agile species, the Norwegian lemming, is uncommon in this subarea (fig. 3B; see also Oksanen 1993; Oksanen et al. 1999; Ekerholm et al. 2001).

The NDVI values reflecting green plant biomass on the spatial scale of entire study sites (0.2 km<sup>2</sup>) differ between the Slope and the Lowland (Tukey HSD, *P* < .001) but not between the Highland and the Lowland (fig. 3C). Harvested plant biomasses (from our trapping grids of 0.5 ha) differ in all subareas (Tukey HSD, *P* < .001; fig. 3D). The contribution of the two least palatable plant groups (mosses and evergreen ericoids) to the community-level plant biomass decreases monotonically along the gradient of increasing primary productivity (H > L > S), while the absolute and relative biomass of palatable deciduous woody plants (*Betula*, *Salix*) increases (H < L < S). Biomasses of the most palatable plants are low everywhere but lowest in the Lowland (fig. 3D).

#### *Island Experiments on Trophic Dynamics in Low-Arctic Scrublands*

Comparisons of vole biomass between mainland reference areas, the three-trophic-level island, and the two-trophic-



**Figure 3:** Biomass patterns in the study area. *A*, Predators: mammalian predators (black), specialist avian predators (hatched), generalist avian predators (white). *B*, Herbivores: nonagile species with a broad diet (*Lemmus lemmus*, *Clethrionomys rufocanus*; black), intermediate species (*Microtus* spp.; hatched), the agile red vole (*Clethrionomys rutilus*; white), which depends on high-quality food. *C*, Normalized difference vegetation index, an index of the density of photosynthetically active plant tissue. *D*, Plants (harvested aboveground): lichens (black), mosses (ascending hatched), *Betula* spp. and *Salix* spp. (cross-hatched), ericoids (descending hatched); high-quality forage (herbs, grasses, *Vaccinium myrtillus*; white). Error bars show standard errors for total rodent and plant biomass ( $n = 5$  for the Highland and the Lowland,  $n = 4$  for the Slope). Predator biomasses are point estimates, as they represent entire subareas.

level islands show a significant treatment effect ( $F = 8.522$ ,  $P = .018$ ; data log transformed in order to standardize variance). Vole biomass on the three-trophic-level island is within the mainland range. On the two-trophic-level islands, vole biomass exceeds the mainland mean by a factor of 4 (fig. 4A). On the one-trophic-level islands, only five rodents were captured.

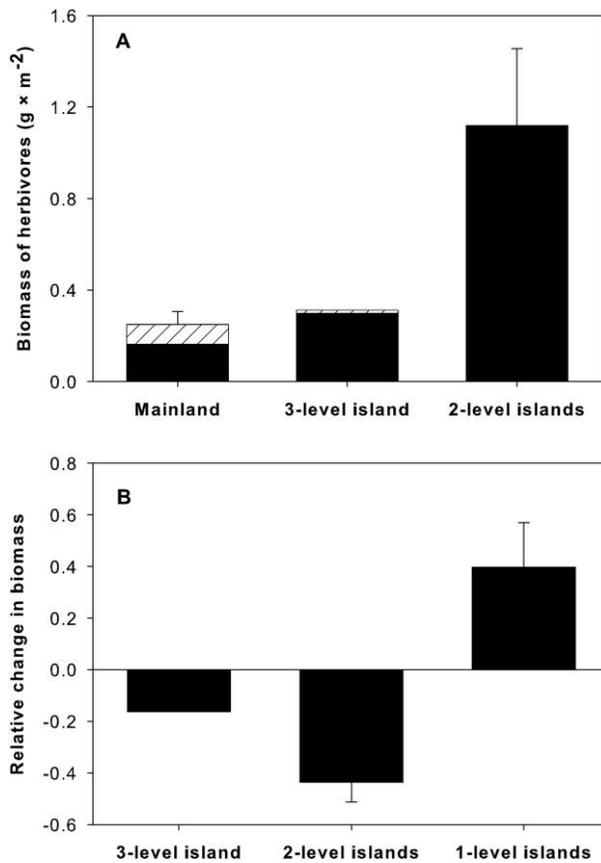
Food chain length has a large (fig. 4B) and statistically significant ( $F = 9.381$ ;  $P = .014$ ) effect on the development of plant biomass. The three-trophic-level island is a statistical outlier (outside the 95% confidence interval) when compared to two-trophic-level islands ( $P = .036$ ) and one-trophic-level islands ( $P = .046$ ). In absolute values, the changes in plant biomass from 2000 to 2003 are as follows: one-trophic-level islands, from 959 to 1,308 g m<sup>-2</sup>; two-trophic-level islands, from 1,045 to 583 g m<sup>-2</sup>; the three-trophic-level island, from 876 to 733 g m<sup>-2</sup>. Island-specific start and end values are presented in table A2 in the online edition of the *American Naturalist*.

#### Responses of Highland Heaths to Fertilization

Fertilization of Highland heaths led to dramatic increases in rodent biomass (fig. 5A;  $P = .019$ ) and the extent of areas devastated by winter grazing (fig. 5B;  $P = .049$ ). The overall response of vascular plant biomass to fertilization was positive ( $P = .001$ ; see fig. 5C). The response of mosses and lichens to fertilization was negative (fig. 5C) and statistically significant ( $P = .012$ ). Data from the circles, where all plants were harvested, yield almost identical community-level plant biomass estimates for fertilized circles ( $599 \pm 43$  g m<sup>-2</sup>) and unfertilized controls ( $584 \pm 13$  g m<sup>-2</sup>).

#### Discussion

Our results indicate that, in the inland tundra, the effective length of the endotherm food chain depends on primary productivity and that the biomass at the trophic level below the effective top trophic level remains constant across pro-

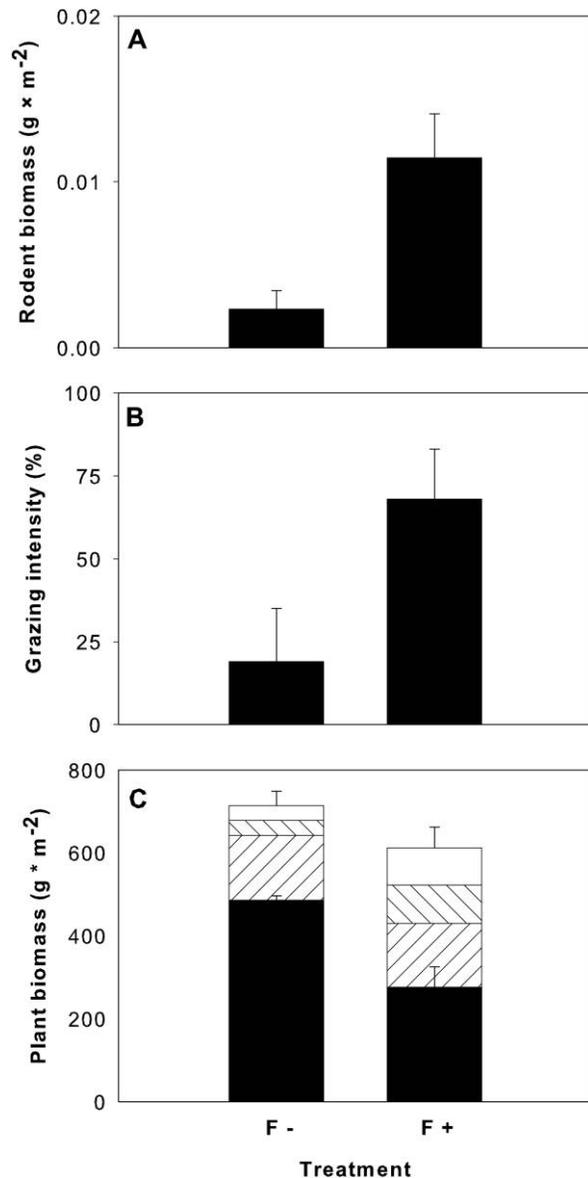


**Figure 4:** Consequence of predator and herbivore manipulation on herbivore and vegetation biomass on the islands of Iešjávri. *A*, Mean autumnal vole biomass ( $\text{g m}^{-2}$ ) during 2000–2003 in mainland reference areas, on the three-trophic-level island, and on the two-trophic-level islands: *Clethrionomys rufocanus* (black), *Microtus oeconomus* (hatched). Error bars show standard errors for total vole biomass;  $n = 4$  for mainland reference areas and two-level islands;  $n = 1$  for the three-level island. *B*, Mean relative change in community-level plant biomass for the treatments and the control from 2000 to 2003 (+1 = doubling, -1 = total disappearance);  $n = 4$  for two-level and one-level islands;  $n = 1$  for the three-level island. Error bars show standard errors.

ductivity gradients. The island experiment shows that food chain length influences the community-level plant biomass. Moreover, unproductive tundra heaths react to enrichment like simple food chains with plants as prey and herbivores as predators (Rosenzweig 1971). These results corroborate the EEH (Oksanen et al. 1981) and contradict alternative hypotheses, implying a positive relationship between biomasses at adjacent trophic levels (White 1978; Arditi and Ginzburg 1989; Leibold 1989, 1996; Oksanen 1992; Polis and Strong 1996; Vos et al. 2004).

At least for northern Fennoscandian inland ecosystems, the results reported above fit a broader pattern. In productive scrublands, rodents are controlled by predation

(Turchin et al. 2000; Ekerholm et al. 2004), and competition between plants is intensive (Olofsson et al. 2002; Olofsson 2004; Sammul et al. 2006). In unproductive tundra areas, the vegetation is periodically devastated by rodents (Oksanen and Oksanen 1981; Moen et al. 1993b),



**Figure 5:** Results of the fertilization experiment in the Highland. *A*, Average biomass of microtine rodents on control ( $F^-$ ) and fertilized plots ( $F^+$ ) during 1991–1999. *B*, Cumulative percentages of study plots devastated by herbivores in 1991–1999. *C*, Aboveground plant biomass in 1999: cryptogams (lichens and mosses; black), *Betula nana* and *Salix* spp. (ascending hatched), ericoids (descending hatched), high-quality forage (herbs, grasses, *Vaccinium myrtillus*; white). Error bars for rodent biomass, grazing effect, and plant biomass show standard errors;  $n = 4$  for both treatments, except for cryptogams, where  $n = 2$ .

and lichen grounds are chronically depleted by reindeer (Johansen and Karlsen 2000). Exclusion of herbivores is followed by changes in vegetation, ecosystem processes, and plant biomass (Oksanen and Moen 1994; Virtanen et al. 1997; Moen and Oksanen 1998; Virtanen 1998, 2000; Olofsson et al. 2002, 2004a, 2004b). Conversely, elimination of putative competitors has no positive effect on plant performance (Virtanen 1998; Callaway et al. 2002; Olofsson et al. 2004b; Sammuli et al. 2006), except for grazer exclosures and grazer-free high alpine barrens (Olofsson et al. 1999, 2002).

While trophic dynamics in northernmost Europe conform to the predictions of the EEH, the connectivity food web, as defined by Cohen et al. (1990) and Pimm (1982, 1991), retains the third trophic link (e.g., jaegers) even in the unproductive areas. The discrepancy between connectivity webs and interaction webs is further illustrated by the Spitsbergen food web of Summerhayes and Elton (1923), where the connectivity web includes arctic foxes as consumers of reindeer. Indeed, this link is not predatory: the strong interaction is between reindeer and plants (Hansen et al. 2007). (For further discussion of discrepancies between connectivity webs and interaction webs, see Pimm 1991, pp. 283–285.)

Similar results have been obtained by ecologists working in other unproductive areas, provided that they are large enough to annul the effect of “spillover predation” from adjacent, more productive habitats (Oksanen 1990; Oksanen et al. 1992) and sufficiently far from the coast to exclude the effect of “marine subsidies” (Sittler 1995; Polis and Hurd 1996; Polis et al. 1997; Sittler et al. 2000; Roth 2003; see also Wilson et al. 1999; Gilg et al. 2003; Gauthier et al. 2004). In inland tundra and steppe areas, herbivorous endotherms are resource limited, responding to changes in primary productivity and to experimental manipulations of food supply (Batzli et al. 1980; Caughley and Gunn 1993; Crête and Huot 1993; Crête and Manseau 1996; Crête 1999; Turchin and Batzli 2001; Zhong et al. 2008), and the natural effect of herbivorous endotherms on the tundra vegetation is strong (Tihomirov 1959; Batzli et al. 1980; Crête and Huot 1993; Zimov et al. 1995; Manseau et al. 1996; Crête and Doucet 1998; Hansen et al. 2007).

Quantitatively, the effects of herbivores on community-level plant biomass documented here do not reach the level documented in aquatic environments (Power et al. 1985, 1988, 1989; Power 1990, 1992; Persson et al. 1992; Wootton and Power 1993; Estes and Duggins 1995; T. Oksanen et al. 1995; Shurin et al. 2002), but the very existence of community-wide terrestrial trophic cascades contrasts with the message of recent meta-analyses (Halaj and Wise 2001; Shurin et al. 2002; Borer et al. 2005). Moreover, contrary to the arguments of Strong (1992; see also Polis and Strong 1996; Persson 1999; Polis 1999; Shu-

rin et al. 2006; Hall et al. 2007), the community-wide trophic cascades occur in an area with heterogeneous and species-rich vegetation containing unpalatable species with high concentrations of secondary chemicals (see “The Study System”; see also Aleksandrova et al. 1964; Oksanen and Virtanen 1995; Bruun et al. 2006). However, even the least palatable arctic plant groups have turned out to be vulnerable to herbivores (Oksanen and Moen 1994; Virtanen et al. 1997; Virtanen 2000; Olofsson et al. 2001, 2002, 2004a; Hambäck et al. 2004; Dahlgren 2006).

Rather than depending on the properties of plants, the vulnerability of the arctic-alpine vegetation depends on the properties of arctic and alpine herbivores. Mosses are “inedible” in temperate lowlands (Prins 1982) but form the main winter resource of brown/Norwegian lemmings and high-arctic reindeer/caribou populations (Batzli 1993; Turchin and Batzli 2001; van der Wal 2006). Rock ptarmigans survive on a winter diet dominated by maximally unpalatable ericoids (e.g., *Loiseleuria procumbens*; see Pulliainen 1970). In unproductive environments, natural selection seems to favor the ability to exploit all reasonably abundant plants. When all plants have their consumers, the dynamics of species-rich terrestrial communities can be as simple as the dynamics of the species-poor microbial food webs studied by Kaunzinger and Morin (1998).

In productive environments at lower latitudes, herbivorous endotherms appear to be controlled by predators if these have not been extirpated (Erlinge et al. 1983; Krebs et al. 1995; Crête and Manseau 1996; Korpimäki and Norrdahl 1998; Klemola et al. 2000; Hanski et al. 2001; Terborgh et al. 2001), and ungulate biomass depends on the presence or absence of large predators, not on primary productivity (Crête 1999). This result indicates that inclusion of areas without large predators might account for the positive relationship between primary productivity and herbivore biomass detected by McNaughton et al. (1989) and Moen and Oksanen (1991). While herbivore biomass seems to be regulated at a constant level, the characteristics of herbivores change along the gradient from the tundra to temperate deciduous forests. Broadly folivorous and relatively clumsy northern herbivores (lemmings, gray-sided voles, reindeer/caribou) are replaced by more selective and agile species (bank voles, deer; see Hansson 1985; Henttonen et al. 1987; Oksanen 1993; Crête and Manseau 1996; Crête et al. 2001; Hörnfeldt et al. 2006).

These qualitative changes in the composition of the herbivore community might attenuate trophic cascades to species-specific trickles because of trade-offs between the ability to exploit low-quality forage and the ability to elude predators (Holt 1977; Oksanen 1992). However, the evidence against community-wide terrestrial trophic cascades is based on invertebrate studies (Halaj and Wise 2001; Shurin et al. 2002; Borer et al. 2005), and the size of the

herbivore is important for the strength of trophic cascades (Shurin and Seabloom 2005). We thus cannot know whether the contrast between our results and the results obtained in more productive areas reflects differences between arctic-alpine and temperate herbivores or differences between mammals and invertebrates. Another confounding issue is seasonality. In seasonal environments, resident herbivores are saturated during the growing season, and in winter (or dry season), the perennating organs of herbaceous plants are inaccessible, leading to attenuation of herbivore effects (Norrdahl et al. 2002). Studies on terrestrial trophic cascades have primarily focused on herbaceous communities (see Chase et al. 2000), whereas community-wide trophic cascades are, a priori, most likely to embrace plants with perennial shoots, and herbivory should culminate in the nongrowing season, as has been the case in our study system as well.

According to the EEH, vegetation changes initiated by predator removal in forested regions should thus mimic the deforestation processes triggered by large-scale grazing systems in Eurasia, where hundreds of thousands of square kilometers are covered by seminatural "pastoral vegetation" (heath, meadow, alvar, garrigue, maquis, etc.) and individual trees and forest patches may occur in inaccessible sites, but where the continuous forests vanished long ago and reforestation requires control of herbivorous mammals (Tansley 1926, 1939; Godwin and Tansley 1941; Walter 1964, 1968; Gimingham 1972; Rosén 1982; Crawley 1983; Ellenberg 1988; Prösch-Danielsen and Simonsen 2000; Bjune 2005). This prediction is in sharp contrast with the prediction of contesting hypotheses (Pastor and Naiman 1992; Strong 1992; Leibold 1996; Polis and Strong 1996; Hall et al. 2007), according to which the exclusion of predators and hunters should eliminate palatable second-growth trees and speed up the growth of unpalatable climax trees.

In accordance to the predictions of the EEH, the absence of wolves from Yellowstone and the consequent increase in ungulate densities have resulted in eliminating aspen and poplar saplings at the arid timberline. Without recruitment, the aspen and poplar forests have thinned out into sparse parklands, where the field layer is dominated by *Artemisia* steppe vegetation ("sagebrush"; see fig. 1 of Beschta 2003 and fig. 1 of Fortin et al. 2005). After the return of wolves, saplings of poplar and aspen have started to abound again (Beschta 2003; Larsen and Ripple 2003; Ripple and Beschta 2003; Fortin et al. 2005). Similarly, the combined effect of the reindeer and the autumnal moth has influenced the birch forests forming the arctic-alpine timberline in northernmost Europe (Kallio and Lehtonen 1975; L. Oksanen et al. 1995; Cairns and Moen 2004). However, these timberline forests are, in essence, mono-

cultures of palatable deciduous trees, making inferences to more species-rich forests ambiguous.

Studies conducted in species-rich boreal habitats show that the short-term effect of low predation pressure is the selective elimination of palatable species (Pastor and Naiman 1992; Potvin and Breton 1992; McLaren and Peterson 1994; Chouinard and Fillion 2005; Hebblewhite et al. 2005; Vehviläinen and Koricheva 2006), but the least palatable species, such as spruces, need not be invulnerable. In the planted spruce monocultures of Scotland, deer browse leader shoots of saplings, which respond by becoming bushy and more palatable (Welch et al. 1991; see also Danell et al. 1985). Browsers can thus take advantage of the internal heterogeneity of trees and of their lack of adaptation to intense browsing. The preferences of rodents are partial at best (Ostfeld and Canham 1993; Vehviläinen and Koricheva 2006), and even the most toxic plants can be eliminated by food-limited rodents (Moen et al. 1993a; Rammul et al. 2007).

Strong community-level effects of predator exclusion on woody vegetation have been observed in the tropics, too. When the construction of an impoundment led to the formation of predator-free islands, herbivore densities increased, the community-level density of tree saplings crashed, and even full-size trees became heavily defoliated (Terborgh et al. 2001, 2006). Unfortunately, political problems terminated the fieldwork before critical parameters (e.g., leaf biomass) could be quantified, and the whole natural experiment is now over because a severe drought has caused a partial draining of the lake.

Our study lends support to the EEH in the context of arctic-alpine ecosystems and suggests that the endotherm branches of terrestrial food webs form community-level trophic cascades in productive low-arctic and subarctic habitats. Whether community-level trophic cascades remain strong even in more productive areas, where natural selection has favored agility rather than the ability to exploit nutrient-poor and heavily defended plants, remains to be seen. Available empirical evidence is open to several interpretations (Pace et al. 1999; Chase 2000). Progress will therefore require experimental studies addressing the dynamics in the endotherm food webs of productive boreal, temperate, and tropical ecosystems.

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