vol. 155, no. 6 the american naturalist june 2000

The Logic and Realism of the Hypothesis of Exploitation Ecosystems

Lauri Oksanen* **and Tarja Oksanen**

Department of Ecology and Environmental Sciences, Umeå University, S-901 87 Umeå, Sweden

Submitted June 24, 1998; Accepted December 29, 1999

abstract: Hypotheses on trophic dynamics in terrestrial ecosystems fall into two major categories: those in which plants are assumed to be invulnerable to their consumers and those in which the build-up of plant biomass is assumed to require top-down control of folivores. The hypothesis of exploitation ecosystems (EEH) belongs to the latter category and focuses particularly on the consequences of the high energetic costs of maintenance of endotherms. Carnivorous endotherms require relatively high prey densities in order to break even. Moreover, they are dependent on folivorous prey during the limiting season, at least at high latitudes. The endotherm branch of the grazing web is thus predicted to collapse from three-link trophic dynamics (carnivores → folivores → plants → inorganic resources) to two-link dynamics (folivores → plants → inorganic resources) along gradients of decreasing primary productivity. Consequently, the vegetation of cold and unproductive areas is predicted to be under intense winter grazing pressure, which prevents the accumulation of aboveground plant biomass and excludes erect woody plants. In the most extreme habitats (e.g., polar deserts and their high alpine counterparts), even folivorous endotherms are predicted to be absent, and the scanty vegetation is predicted to be structured by preemptive competition. Within temperature-determined productivity gradients, EEH is corroborated by biomass patterns, by patterns in the structure and dynamics of carnivore, folivore, and plant communities, and by experimental results. The general idea of top-down trophic dynamics is supported for other autotroph-based systems, too, but the relevance and sufficiency of the energy constraint in explaining patterns in trophic dynamics appears to be variable. Moreover, critical empirical evidence for or against the capacity of folivorous insects to regulate plant biomass has not yet been obtained. Another open question is the ability of boreal and temperate browsers, evolved in productive environments with intense predation pressure and abundance of forage, to prevent the regeneration of the least palatable tree species. There are, thus, many open questions waiting to be answered and many exciting experiments waiting to be conducted.

Keywords: herbivory, mammals, primary productivity, trophic cascades, vegetation, predation.

In the current debate on trophic dynamics in terrestrial ecosystems, two main views can be distinguished. One emphasizes defenses themselves or the diversity of defensive strategies in herbivores and plants and maintains that strong, cascading trophic interactions are uncommon in species-rich terrestrial ecosystems (Murdoch 1966; White 1978; Hunter and Price 1992; Strong 1992; Polis and Strong 1996; Polis 1999). If anything, consumers are seen as factors that might change the behavior of their resources or the composition of resource guilds (Haukioja and Hakala 1975; Rhoades 1985; Leibold 1989, 1996; Abrams 1992, 1993, 1996; Pastor and Cohen 1997). In order to structure the discussion, the above view will be referred to as the defense diversity hypothesis (DDH). A diametrically opposite view of trophic dynamics was outlined by Elton (1927) and is more rigorously presented in the green world hypothesis (HSS) of Hairston et al. (1960). According to HSS, plants are vulnerable to folivores but are nevertheless seldom severely defoliated because the collective density of folivores (grazers, browsers, and folivorous insects) is regulated by the collective action of carnivorous and insectivorous animals. The hypothesis of exploitation ecosystems of Oksanen et al. (1981; to be referred to as EEH) converges with HSS with respect to productive areas (forests and their successional stages, productive wetlands). According to EEH, however, the control of folivorous endotherms by predators fails in unproductive ecosystems (tundras, high alpine areas, steppes, and semideserts), which are characterized by intense natural folivory.

Considering the time elapsed since the formulation of the two main alternatives, relatively few critical experiments have been conducted. Differences in approach and terminology have probably contributed to this situation. The DDH is focused on individual populations (e.g., Ehrlich and Birch 1967; Polis and Strong 1996), while HSS and EEH deal with guild-level dynamics of plants, folivores, and carnivores. These guilds have been referred to as trophic levels, which is conceptually debatable. Nev-

---

* To whom correspondence should be addressed; e-mail: lauri.oksanen@eg.umu.se.

Am. Nat. 2000. Vol. 155, pp. 703–723.

ertheless, they are identifiable units, created by adaptational constraints and even reflected in taxonomy. Moreover, the conjecture that individual folivore populations display density-vague dynamics (Strong 1986) is entirely compatible with the conjecture of Hairston et al. (1960) that the collective standing crop of folivores is regulated by the collective action of carnivores.

The purpose of this article is, first, to explain why we regard both DDH and HSS as incomplete; second, to reanalyze the 1981 model of EEH with focus on endotherms, relaxing unnecessarily specific assumptions of the original model, and replacing graphics with explicit analysis; third, to provide an up-to-date review of relevant empirical evidence; and finally, to outline a research strategy on trophic dynamics.

The Productivity Connection

For us living at high latitudes, the shared point of de parture of DDH and HSS—rarity of severe folivory—appeared unrealistic. In the early 1970s, we saw Norwegian lemmings destroy the moss cover of the tundra (Kalela 1971; Kalela and Koponen 1971). Simultaneously, subarctic forests were dying over enormous areas. The main trunks had been killed after recurrent defoliation by a geometric moth, and the basal recovery shoots were consumed by mammals (Kallio and Lehtonen 1975). Moreover, the profound impact of reindeer and gray-sided voles on the vegetation of the heathlands was easy to see (Oksanen 1978; Callaghan and Emanuelsson 1985; Oksanen and Virtanen 1995). Except for the insect outbreak, the strong impacts were not caused by exceptionally high numbers. Densities of microtine rodents were lower in typical tundra than in productive habitats (willow thickets), where no dramatic changes in vegetation were observed (Oksanen and Oksanen 1981). The winter reindeer density in the area where forests were changing to tundra was about three animals or 200–250 kg km^{-2}, excluding a period of mass starvation in the mid 1970s (L. Oksanen et al. 1995). This density is only twice as high as the average density of barren-ground caribou in northwestern mainland Canada (Crête 1999). Higher standing crops of cervids are commonplace at lower latitudes, but impacts on the vegetation are weaker, and mass starvation is unknown (Cederlund and Markgren 1987; Nygren 1987; Crête 1999). Fretwell's (1977) paper on the impact of primary productivity on trophic dynamics provided a potential solution for the arctic enigma of strong folivory but relatively low folivore densities. However, Fretwell's considerations contained logical gaps and opened more questions than they answered—as is typical for innovative contributions. To answer these questions has been the main theme of our work during the past 2 decades, starting from the 1981 model of EEH.

The independent variable of EEH is potential productivity, defined as the maximum primary productivity of the habitat, when its nutrient pool is fully available, when leaf area index has reached its optimal value, but before the accumulation of heterotrophic stem tissues. In terrestrial ecosystems, this value depends primarily on evapotranspiration and secondarily on nutrient pool (Lieth 1975). Belowground production is included because grazing can dramatically change community-level allocation patterns between roots and shoots (Tilman 1988; Hambäck 1998). For herbaceous vegetation and low scrublands, actual net primary production is a good index for potential productivity. For woodlands, potential productivity should ideally be measured in the early stages of secondary succession. Values for mature forests must be corrected for respiration of stem tissues. In northern ecosystems, primary productivity is even influenced by indirect effects of secondary succession (Sirén 1955), which can be prevented (Zimov et al. 1995) or accelerated (Pastor and Naiman 1992; Pastor et al. 1993) by folivory. However, feedbacks caused by biotic factors cannot be included in the independent variable, which must derive from the properties of the physical environment.

The intention of the simple model of EEH was to produce a parsimonious hypothesis on trophic dynamics along broad biogeographical gradients, where potential productivity varies by orders of magnitude. Unfortunately, the 1981 model includes two unnecessary assumptions: logistic growth in plants and Type II functional response in consumers. Moreover, the team was divided on two central issues. The American part (S. Fretwell and J. Arruda) wanted to retain the integrity of trophic levels, whereas the Finnish part (L. Oksanen and P. Niemelä) preferred to restrict the model to endotherms (Oksanen et al. 1981, p. 257). Moreover, the Finns preferred to model secondary carnivory as diffuse intraguild predation (Oksanen et al. 1981, p. 250). The formal analyses presented in the paper were based on the American alternative. In the verbal part, the paper glided confusingly between the two views. Below, we will reanalyze the model, relaxing superfluous assumptions and consistently applying the Finnish approach. Unless otherwise stated, we will interpret the model as referring to the vegetation and to the guilds of folivorous and carnivorous endotherms. Extensions to other systems will be discussed separately.

A Generalized Version of the 1981 Model of EEH

The EEH builds on a plant equation in which the expansion of aboveground plant biomass is assumed to be an autocatalytic process; that is, growth rate depends on the

Table 1: Definitions of parameters and functions used in equations (1)–(3)

Expression	Definition
$r = \lambda_1 G$	The maximum per biomass unit expansion rate of plants.
$g(P, K)$	A function describing how this rate decreases with increasing plant biomass; g is assumed to have the following four properties: first, $g(0) = 1$; second, g is a monotonically decreasing function of P; third, there is a $K > 0$, such as $g(K) = 0$; and finally, $K = \lambda 2G$.
a	The searching efficiency of folivores.
$\mathrm{f}(P)$	The impact of plant biomass on foraging efficiency and foraging motivation of folivores. The function is unspecified but assumed to have the following property: $a\mathrm{f}(P)P \rightarrow w$ when $P \rightarrow \infty$, where w is a positive constant.
m	The energetic costs of maintenance of folivores and their per capita mortality in the absence of forage.
k	The assimilation efficiency of folivores.
α	The searching efficiency of carnivores.
$\phi(H)$	The impact of folivore biomass on foraging effectivity and motivation of carnivores. The function is unspecified but assumed to have the following property: $\alpha\phi(H)H \rightarrow \omega$ when $H \rightarrow \infty$, where ω is a positive constant.
μ	The energetic costs of maintenance of carnivores and their per capita mortality in the absence of prey.
κ	The assimilation efficiency of carnivores.
i	The guild-level net loss imposed by intraguild predation at unit density of carnivores.

amount of foliage in the system. This assumption is debatable in a short time interval because plants can then sprout from subterranean reserves. However, EEH focuses on long-term, near-equilibrium dynamics, and in that context, growth rate must depend on leaf-area index. The other assumptions are as follows: First, the maximum growth rate of plants and the maximum amount of heterotrophic plant tissues that can be sustained are directly proportional to potential productivity. Second, the kinetics of trophic exploitation follow the principles of mass action (Rosenzweig 1971, 1973, 1977). Third, the vegetation and the guilds of folivorous and carnivorous endotherms can be treated as homogeneous units. Fourth, there is no population dynamically significant interference among folivores. And finally, encounters between carnivores have a fixed probability to lead to intraguild predation, which is a net loss on the guild level and can, thus, be modeled as a negative second-order term in the carnivore equation.

The above assumptions translate to the following differential equations:

$$dP/dt = rPg(P, K) - a\mathrm{f}(P)PH \tag{1}$$

$$= \lambda_1 Gpg(P, \lambda_2 G) - a\mathrm{f}(P)PH,$$

$$dH/dt = -mH + ka\mathrm{f}(P)PH - \alpha\phi(H)HC, \tag{2}$$

$$dC/dt = -\mu C + \kappa\alpha\phi(H)HC - iC^2, \tag{3}$$

where P, H, and C are the standing crops of plants, folivorous endotherms, and carnivorous endotherms, respectively, and G is potential productivity. Definitions of functions and parameters are provided in table 1. Notice that the functions for density dependence in plants and functional responses in consumers are unspecified, except that biologically reasonable boundary conditions are assumed. For instance, we assume the existence of λ_2 such that $g(\lambda_2 G) = 0$, and we assume the existence of the saturation constants w and ω such that $a\mathrm{f}(P)P \rightarrow w$ when $P \rightarrow \infty$ and $\alpha\phi(H)H \rightarrow \omega$ when $H \rightarrow \infty$.

The equations for 0 isoclines (actually: isosurfaces) for plants, folivores, and carnivores can be derived from equations (1)–(3) by setting the time derivatives equal to 0, which yields the following equations for plant (4), folivore (5), and carnivore (6) isoclines, respectively:

$$H = \frac{r}{a}\frac{g(P, K)}{\mathrm{f}(P)} = \frac{\lambda_1 G}{a}\frac{g(P, \lambda_2 G)}{\mathrm{f}(P)}, \tag{4}$$

$$C = \frac{ka\mathrm{f}(P)P - m}{\alpha\phi(H)}, \tag{5}$$

$$H = \frac{\mu + iC}{\kappa\alpha\phi(H)} \Leftrightarrow C = \frac{\kappa\alpha\phi(H)H}{i} - \frac{\mu}{i}. \tag{6a}$$

The assumption of intraguild predation makes the technical analysis more complicated than in the 1981 model. However, the saturation of the functional response of the folivores and the consequent bending of the folivore isocline largely eliminates the impact of intraguild predation on equilibrium biomass patterns. For the purpose of predicting biomass patterns, we can thus set $i \approx 0$, which simplifies the expression for carnivore isocline to

$$H^* \approx \frac{\mu}{\kappa\alpha\phi(H^*)}. \tag{6b}$$

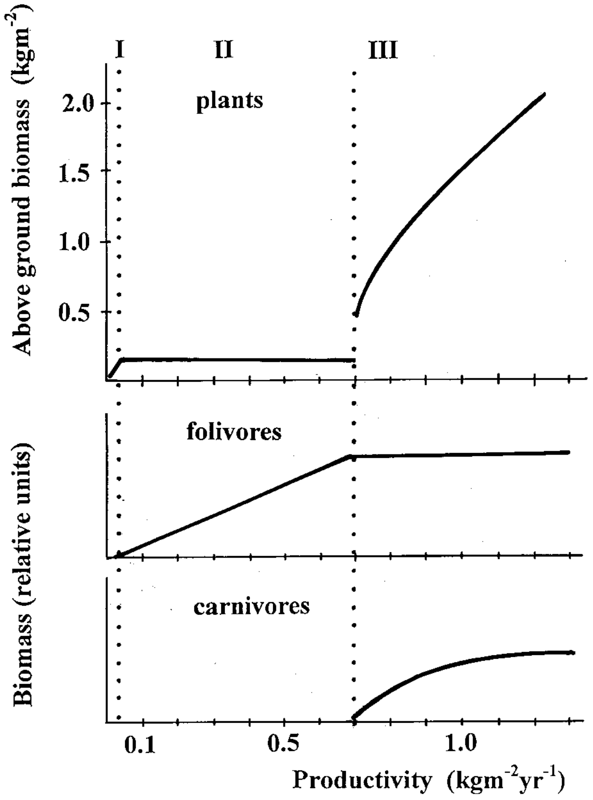

Figure 1: Patterns in aboveground plant biomass, in biomass of folivorous endotherms, and in biomass of carnivorous endotherms predicted by EEH, assuming functional responses that saturate at moderate resource densities. Roman numbers refer to predicted zones with different trophic dynamics (*I*, one-link dynamics; *II*, two-link dynamics; *III*, three-link dynamics). Patterns at the transition from zone II to zone III depend on specific assumptions. The perfectly flat relationship between folivore biomass and potential productivity in zone III presupposes that there is no intraguild predation. Intraguild predation will create a weak, positive relationship between folivore biomass and potential productivity, even in the beginning of zone III, where folivores are not saturated.

In the absence of carnivores, folivores act purely as predators of plants and equation (5) is reduced to

$$P^* = \frac{m}{ka\mathrm{f}(P^*)}. \tag{7}$$

If potential primary productivity is so low that $\lambda_2 G = K < P^*$, folivorous endotherms will be absent. In these "one-link ecosystems" the scanty plant biomass is predicted to be at carrying capacity (fig. 1, zone I). When $K > P^*$, we enter "two-link ecosystems," where equilibrium plant biomass will be fixed at P^* (fig. 1, zone II). In corresponding seasonal systems, late-summer biomasses will increase with increasing potential productivity, as resident endotherms cannot track the seasonal pulse of plant growth (L. Oksanen, unpublished data).

Equilibrium biomass of folivorous endotherms is obtained by substituting $P = P^*$ into equation (4) so that

$$H = \frac{r}{a}\frac{g(P^*, K)}{\mathrm{f}(P^*)}. \tag{8}$$

Recall that $\mathrm{f}(P^*)$ is constant and that $g(P^*, K) \approx 1$ when $P^* \ll K$. Moreover, $r = \lambda_1 G$. Thus, the equilibrium biomass of folivorous endotherms is predicted to increase approximately linearly with increasing primary productivity in the productive end of zone II. For less productive systems, the pattern depends on the forms of $g(P)$ and $\mathrm{f}(P)$ functions. In systems where folivores have Type II functional response (e.g., because all plant biomass is available for folivores), increasing potential productivity is destabilizing (Rosenzweig 1971) and leads to violent folivore-plant cycles. Systems with two-link trophic dynamics can even be destabilized by seasonality, especially if the dominating folivores have high reproductive capacity (L. Oksanen 1990*a*).

The presence of a carnivore guild requires that the folivore density at the folivore-plant equilibrium (eq. [8]) exceeds H^* (see eqq. [6a], [6b]), which yields inequality

$$\frac{\mu}{\kappa\alpha\phi(H^*)} < \frac{r}{a}\frac{g(P, K)}{\mathrm{f}(P)} = \frac{\lambda_1 G}{a}\frac{g(P, \lambda_2 G)}{\mathrm{f}(P)}. \tag{9}$$

Even with an unstable folivore-plant equilibrium, a carnivore-folivore-plant equilibrium emerges as an alternative attractor at potential productivity only slightly higher than implied by inequality (9) (Rosenzweig 1973; Abrams and Roth 1994*a*). Systems without mobile predators can remain trapped in the cyclic folivore-plant attractor (Abrams and Roth 1994*a*, 1994*b*). However, where mobile avian predators abound—as they seem to do in the boreal zone (Korpimäki and Norrdahl 1989, 1991*a*, 1991*b*; Hörnfeldt et al. 1990; Norrdahl and Korpimäki 1996)—their impact will push the system into the domain of attraction of the carnivore-folivore-plant equilibrium.

When the threshold represented by inequality (9) is passed, we enter the green worlds of "three-link ecosystems" (fig. 1, zone III). The standing crop of folivores is predicted to stay put at $H = H^*$, and plant biomass is predicted to increase with increasing potential productivity. At the transition, specific assumptions count and singularities may emerge. With further increase in potential productivity, the predicted response of aboveground plant biomass to increasing potential productivity is almost linear because $P^* \approx K = \lambda_2 G$.

The predicted collective response of carnivores to enrichments can be studied by substituting $H = H^*$ into the equation of the herbivore isocline (eq. [5]), which yields

$$C = \frac{kaf(P)P - m}{\alpha\phi(H^*)}. \tag{10}$$

The denominator is a constant. The term $af(P)P$ in the numerator is the functional response of the folivores, which approaches the saturation constant, (w), when plant biomass increases. In systems with high plant biomasses, the right-hand side of equation (10) consists entirely of constants. Hence, the predicted relationship between primary productivity and carnivore standing crop is asymptotic. In highly productive terrestrial ecosystems, increased primary productivity should thus be retained by plants and, in the end, funneled into the detritus web.

The stability of the enriched three-link ecosystems depends on details. With Type II functional response, the equilibrium will be destabilized by enrichment (Abrams and Roth 1994*a*), whereas it can remain stable if predators have Type III functional response, supposedly typical for generalists (Andersson and Erlinge 1977; Hanski et al. 1991; Hanski and Korpimäki 1995). However, this requires nonoptimal foraging (preferred prey are ignored at low densities) and nondepletable alternative resources, which is inconsistent with EEH and debatable even in principle. Generalists exploiting different species of folivores will only synchronize guild-level dynamics. A more plausible source of stability is provided by intraguild predation, imposing direct density dependence on the predator guild (Wollkind 1976). Conversely, setting $i = 0$ in equation (6a), a mechanism for sustained carnivore-folivore cycles is obtained. This is plausible for systems dominated by small carnivores, which are in the role of victims in intraguild predation and should, thus, display laissez-faire dynamics in areas where they and their prey are protected against larger carnivores. (Unable to protect their prey against larger competitors, they are unlikely to have evolved territorial defense of resource supply against conspecifics, see Oksanen et al. 1985). In the boreal zone, such protection is offered by the long-lasting snow cover (Hansson and Henttonen 1985). Occurrence of cycles of small predators and their prey in productive, boreal habitats is, thus, a straight forward consequence of the basic premises of EEH, combined with the splitting of the folivore and carnivore guilds by the impact of the long, snowy winter.

In the simple model of EEH, the three-link trophic cascade is predicted to embrace all plants growing in productive terrestrial ecosystems. A different variant on the same theme was proposed by Oksanen (1992) by including evolutionary trade-offs between capacity to exploit low-quality forage and ability to escape predation. In this evolutionary variant of EEH, the parameter α (searching efficiency of carnivores) decreases along gradients of increasing potential productivity because of increasing elusiveness of folivores. Hence, folivore standing crop (H^*) will increase monotonically with increasing potential productivity. Due to the trade-offs, the least palatable plants are predicted to be lifted outside the trophic cascade in productive areas. Removal of carnivorous endotherms is predicted to first lead to decimation of palatable plants, then to increased standing crops of unpalatable plants. First in evolutionary timescale or after the invasion or introduction of folivores from unproductive areas with two-link trophic dynamics, the standing crops of all plants should be reduced to the P^* of the simple model of EEH. Both variants of EEH derive from the same approach, but they are nevertheless so different that they must be regarded as two separate hypotheses.

In the 1981 model of EEH, the spatial scale of the model is not specified. Holt (1984, 1985) discovered that the predictions of EEH cannot hold in small-scale habitat complexes with suboptimal habitat selection. Inspired by her snow-tracking results, T. Oksanen (Henttonen et al. 1987; Oksanen and Henttonen 1996) extended the argument to embrace even three kinds of optimal behavior, differing from the Ideal Free model of Fretwell (1972) and from Charnov's (1976) marginal value theorem. First, socially inferior individuals and individuals belonging to the smallest species in the guild must weigh the advantages of high prey density against the risk of aggression and intraguild predation (T. Oksanen 1990). Second, all predators become habitat generalists in the crash phase of the prey cycle, when between-habitat differences in prey density disappear (T. Oksanen et al. 1992*a*). Third, it pays to attack a prey encountered during transit movements (T. Oksanen et al. 1992*b*). Hence, EEH can be expected to apply to trophic dynamics in the dominating habitat of the landscape and, with minor reservations, to dynamics in more productive habitats. Conversely, if a patch of barren habitat lies in a productive landscape or if it is juxtaposed at a rich marine environment (Polis and Hurd 1996), dynamics in the barren habitat will be driven by spillover predation.

Realism of EEH along Gradients from Cold Barrens to Warm and Productive Regions

Biomass Patterns in Plants

Plant biomass patterns predicted by EEH (fig. 1) clearly diverge from the null hypothesis of linear relation between potential productivity and aboveground standing crop. According to EEH, there is a wide productivity interval (fig. 1, zone II) where the regression of aboveground plant biomass versus potential productivity is flat (annual minima) or has shallow slope (annual maxima).

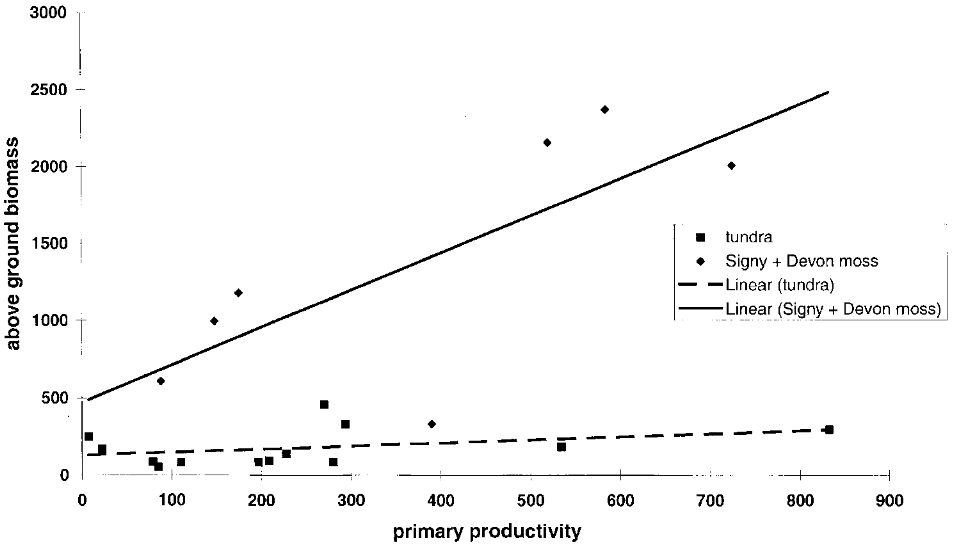

Figure 2: Relation between aboveground plant biomass (gm^{-2}) and annual primary productivity (gm^{-2} yr^{-1}) in the tundra areas with folivorous endotherms (Barrow, Alaska; Hardangervidda, Norway; and ridge and slope sites on Devon Island, Nunavuk) and in the polar areas without folivorous endotherms capable of using the site in winter (Signy, Maritime Antarctic, and mossy bottomlands of Devon Island). Regression for the tundra is $y = 127 + 0.20x$, $R^2 = 0.135$, $n = 13$. Regression for the folivore-free polar areas is $y = 470 + 2.41x$, $R^2 = 0.544$, $n = 7$.

Moreover, there must be a sharp transition to a steep, positive relation (zone III). This prediction is corroborated by arctic-boreal data (Oksanen 1983; Oksanen et al. 1992), by alpine-subalpine data (Körner 1999, pp. 253–255) and even by global biomass data (Begon et al. 1996, fig. 18.5). However, the prediction is not unique for EEH. A roughly similar pattern is predicted by the hypothesis that only plants with small shoots can tolerate the environmental stresses of arctic, alpine, and arid environments (Grime 1979) and by the hypothesis that, in unproductive environments, plants compete primarily for soil resources (Walter 1964; Tilman 1988). In principle, the pattern could even be caused by a shift from stable to cyclic folivore-plant dynamics (Abrams and Roth 1994*b*), if the vegetation could recover in a timescale shorter than the period of the cycle. The value of corroboration, thus, hinges on the following additional predictions: first, the flat relationship depends on the presence of folivores; second, the sharp change of biomass trend depends on the presence of carnivores; third, the pattern does not depend on the accumulation of stem wood or, fourth, on change from stable to cyclic dynamics in folivores.

To test the first additional prediction, we have compared biomasses of typical tundra habitats (Kjelvik and Kärenlampi 1975; Wielgolaski 1975; Bliss 1977; Miller et al. 1980) to equally unproductive polar habitats without folivorous endotherms. The maritime Antarctic (Collins et al. 1975) provides such points of reference, as do the mossy bottomlands in those high Arctic areas where moss-eating mammals do not occur (e.g., northern Devon Island; Bliss 1977). Subantarctic islands, in turn, provide information relevant for the second and third additional predictions. Their productivities correspond to or even exceed the productivities of boreal forests, but the vegetation—grasslands, herbfields, and semiherbaceous communities—is totally different. One island—South Georgia—used to have a variant of three-link trophic structure with introduced reindeer hunted by whalers (Lewis Smith and Walton 1975). Another—Macquairie—has folivorous endotherms (introduced rabbits) but no predators (Jenkin 1975). To avoid any biases in favor of EEH, we have excluded stem wood from boreal biomasses (sources: Mälkönen 1974, 1977; Kjelvik and Kärenlampi 1975; Paavilainen 1980; Albrektsson and Lundmark 1991). For moss communities, only the top part of the brown-moss biomass has been regarded as truly living (the ratio of green to live brown biomass is based on Vitt and Pakarinen 1977). The Arctic-Antarctic biomass patterns are presented in figure 2. For areas with folivorous endotherms, the relation between biomass and productivity is flat, whereas the folivore-free habitats are characterized by a positive relation with a steep slope. In figure 3, the productivity gradient is extended to embrace boreal and subantarctic habitats. In these areas, the biomass-productivity relation is positive and has a steep slope, provided that there is

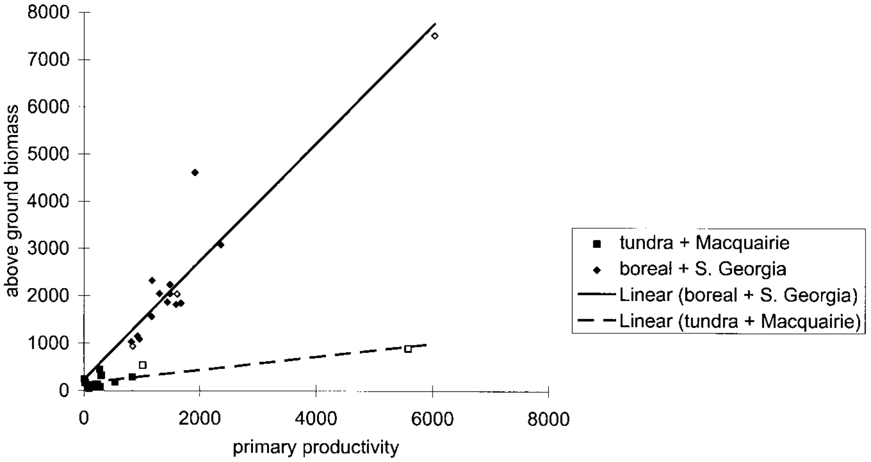

Figure 3: Relation between aboveground plant biomass (gm^{-2}) and annual primary productivity (gm^{-2} yr^{-1}) in areas where EEH predicts folivorous endotherms to be resource-limited and the vegetation to be grazer-controlled (unproductive arctic areas with a complete guild of herbivorous endotherms plus the predator-free subantarctic island Macquairie) and in areas where folivores are predicted to be predator-controlled and plant biomass is predicted to be close to carrying capacity (low-arctic and boreal Fennoscandian habitats with annual primary productivity exceeding 700 gm^{-2} yr^{-1} plus the subantarctic South Georgia before the reindeer eruption). Filled symbols refer to Arctic and boreal data points, open symbols to subantarctic data. Regression for tundra + Macquairie is $y = 156 + 0.14x$; $R^2 = 0.711$, $n = 15$; regression forboreal habitats + South Georgia is $y = 236 + 1.25x$; $R^2 = 0.870$, $n = 16$.

predation or hunting. In the data set obtained combining the arctic tundra and the predation-free Macquairie, the relation is significantly positive, too, but the slope is even more shallow than indicated by the Arctic data alone. Temporal changes are consistent with spatial patterns. On mossy tundra, aboveground plant biomass has increased threefold during 15 yr of grazer exclusion (Virtanen 2000). On subantarctic islands, the introduction of rabbits and the cessation of reindeer hunting have resulted in the total destruction of productive, biomass-rich plant communities (Werth 1928; Leader-Williams 1988). For the fourth additional prediction, see the sections on trophic dynamics.

Notice that many arctic communities are dominated by relatively unpalatable plants. Tannin-loaded, evergreen dwarf shrubs and lichens with high concentrations of lichenic acids abound on ridges (Kalliola 1939; Dahl 1957; Haapasaari 1988; Oksanen and Virtanen 1995), and bottomlands are dominated by mosses, regarded as inedible as a result of lignin-like substances in their cell walls (Prins 1982). Moreover, there is much scatter in the biomass-productivity relation of figure 2 (see also Wegener and Odasz 1998), indicating that plant defenses influence the position of the folivore isocline. However, the defenses are not absolute. Even the unpalatable mosses and cushion plants are eaten by brown/Norwegian lemmings and rock ptarmigans, respectively. All plants contain reduced carbon and nutrients. Where the fitness of folivores depends on their ability to handle low-quality forage, evolution appears to create animals with a sufficiently large and complex digestive system to handle even the poorest forage.

Biomass Patterns in Folivores

For unproductive ecosystems (fig. 1, zone II), EEH predicts that the standing crop of folivorous endotherms rises linearly with increasing potential productivity. This prediction has, however, little diagnostic value. The critical prediction is the flat relation between potential productivity and folivore biomass in productive ecosystems (fig. 1, zone III). For data sets including both categories of systems, the regression of folivore biomass against potential productivity should have a positive slope and a positive *y*-intercept. Moreover, a logarithmic regression with a built-in flattening at high *x* values should fit the data better than a linear regression. Notice that these predictions cannot be tested with logarithmically transformed data. Thus, the work of McNaughton et al. (1989) cannot be regarded as a critical test of EEH. The reanalysis by Moen and Oksanen (1991) is a critique of McNaughton et al. (1989) rather than a test of EEH. The raw data are presented in figure 4. For the temperate data points, the premise of reasonably natural carnivore-folivore dynamics is not even approximately satisfied (Crête 1999), and in several temperate studies, endotherms have not been included at all. As temperate data points are nonrandomly distributed along the productivity axis, there is a risk of spurious patterns. The only

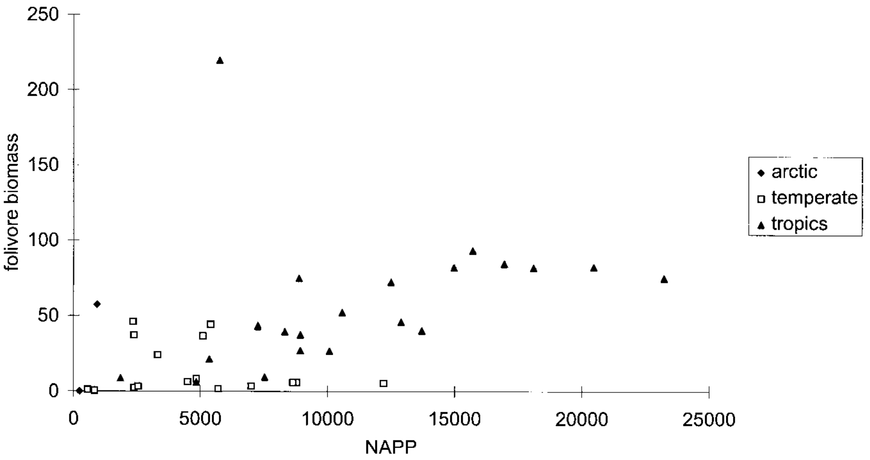

Figure 4: Folivore biomasses (kJm^{-2}), plotted against net aboveground productivity (NAPP, kJm^{-2} yr^{-1}) in the material of Moen and Oksanen (1991). The data were derived from the references of McNaughton et al. (1989). Units: kJm^{-2} for folivore biomass and kJm^{-2} yr^{-1} for net aboveground productivity. With an allocation ratio of 1 : 3 between aboveground and belowground organs, the productivity threshold of 700 gm^{-2} yr^{-1} corresponds to NAPP of 3,500 kJm^{-2} yr^{-1}. Excluding temperate data, the linear regression for the biomass-productivity regression is $y = 24.7 + 0.0029x$, $R^2 = 0.152$. The logarithmic regression is $y = -91.5 + 16.335 \log x$, $R^2 = 0.159$, $n = 25$. For the data points above the above-productivity threshold, the regression is $y = 36.7 + 0.0020x$, $R^2 = 0.052$, $n = 21$.

firm conclusion that we can draw from these data is that the highest folivore biomasses are remarkably constant within different productivity intervals. Regressions computed without temperate data are consistent with EEH, but even this data set contains so many questionable points that the corroboration has little value.

For big folivores, more dependable material has been recently compiled by Crête (1999) and Crête and Manseau (1996). The biomasses of cervids increase along the latitudinal productivity gradient from high-arctic to low-arctic Canada. In the boreal zone, the increasing trend stops. Close to the Canada-U.S. border, where wolves become rare, cervid biomasses increase again. Within the currently wolf-free United States, cervid biomasses increase profoundly with increasing potential productivity. These spatial patterns conform to the predictions of the simple model of EEH. The ongoing reestablishment of wolves in the United States provides a rare opportunity to make predictions about the more distant future. According to EEH, the current high cervid biomasses of the productive southeastern states will be reduced to the level prevailing in the Canadian taiga when wolves reach resource limitation.

Patterns in Occurrence and Abundance of Carnivorous Endotherms

The EEH differs from Fretwell's (1977) verbal food chain hypothesis, where carnivores are assumed to form a continuum from carrion feeders to efficient killers and food chain length is a subtle issue. In EEH, trophic guilds are discrete and the equilibrium standing crop of carnivorous endotherms is predicted to be 0 in unproductive ecosystems (fig. 1, zones I and II). Scavengers can be present everywhere because they can have essentially lower costs of maintenance than true carnivores. The EEH thus requires that the difference between scavengers and carnivores be easy to infer from natural history, including social organization (e.g., lone wolves are scavengers, wolf packs are carnivores). In EEH, the idea of carnivores being physically present but dynamically absent can only refer to systems with a locally unstable folivore-plant equilibrium, generating violent folivore-plant cycles. In these systems folivore peaks are likely to cross the carnivore isocline, creating a niche for outbreak croppers. These "visiting carnivores" should be characterized by extreme nomadism or by a strategy where outbreaks are used for breeding, while survival resources are in other systems.

Studies on terrestrial carnivore communities in the Arctic have been reviewed by Oksanen et al. (1996). The bottom line is that the inclusion of terrestrial carnivores in high-arctic food webs reflects considerable stretching of criteria for presence. For instance, only three stray wolves have been recorded by the Canadian International Biological Program (IBP) team along the entire northern coast of Devon Island. Stoats have been only intermittently present and only in trace numbers. Jaegers prey primarily on invertebrates, eggs, and young birds. The only endotherm that is consistently present and that uses other endotherms as its primary resources is the scavenging arctic fox (Pattie

1977; Riewe 1977*a*, 1997*b*). In middle-arctic landscapes characterized by strong lemming outbreaks, jaegers and snowy owls are periodically numerous and do eat lemmings (Batzli et al. 1980). However, these carnivores are typical outbreak croppers, which roam around in the Arctic or move between the tundra and the ocean. In the low Arctic, the predominating barrens are still, by and large, carnivore-free, but the most productive habitats harbor a diverse community of mammalian and avian carnivores (Oksanen and Oksanen 1992; Oksanen et al. 1996, 1997, 1999). Carnivores, thus, emerge as persistent community members in the habitats where the productivity threshold of 700 gm^{-2} yr^{-1} is exceeded, where the biomass trend changes, and where the plant community is for the first time dominated by erect shrubs. The gradient from low-arctic to temperate habitats is characterized by increasing density and diversity of carnivorous endotherms (Erlinge et al. 1983; Korpimäki and Norrdahl 1989, 1991*a*, 1991*b*; Hörnfeldt et al. 1990; Hanski et al. 1991; Korpimäki et al. 1991).

Trophic Dynamics in Unproductive Tundra Areas

The EEH predicts that the plant cover of the tundra is locked in a strong, dynamical interaction with folivorous endotherms. Even this prediction is amply corroborated. During the extended low phase of Norwegian lemmings from 1971 to 1977, moss biomasses of snowy tundra habitats increased by an order of magnitude (Kyllönen and Laine 1980; Oksanen 1983). In crash winters, these habitats are denuded (Tihomirov 1959; Batzli et al. 1980; Oksanen and Oksanen 1981; Černjavskij and Tkačev 1982; Moen et al. 1993). Moreover, the outbreaks of lemmings in arctic and alpine barrens follow the predicted time trajectory of a predator—with long periods of low numbers and sharp peaks, ending in abrupt and very deep crashes (Batzli et al. 1980; Oksanen and Oksanen 1992; Framstad et al. 1993; Ekerholm et al. 2000; Turchin et al. 2000). Even the strong dispersal tendency of lemmings during population peaks (Oksanen and Oksanen 1981; Henttonen and Kaikusalo 1993) fits to the behavior of other species adapted to periodic discrepancy between numbers and food supply (Kalela 1949). Daring cliffs, waves, and hostile habitats gives them a chance. Suicide is committed by lemmings staying behind.

The strength of the interaction between the relatively stable ungulate populations and the tundra vegetation can be inferred from two kinds of data. The relatively recent observational studies known to us bear witness to total resource limitation in arctic ungulates (Reimers et al. 1980; Thomas and Edmonds 1983; Caughley and Gunn 1993; Tyler 1993; Crête and Manseau 1996). The strength of the interaction can be inferred from spatial differences in the vegetation. In areas without reindeer (caribou), dry, low-arctic tundra heaths are covered by continuous, 10–20 cm thick "reindeer moss" carpets (Du Rietz 1925; Dahl 1957). When grazed by reindeer, similar sites have a thin, lichen-moss cover, dominated by entirely different species (Kalliola 1939; Oksanen 1978; Haapasaari 1988; Oksanen and Virtanen 1995). The differences in space correspond to the changes observed in the Canadian low Arctic after the recovery of the barren-ground caribou (Crête and Huot 1993; Crête and Manseau 1996).

The intensity of the folivore-plant interaction of the tundra has been demonstrated experimentally, too. Exclusion of folivorous endotherms has initiated dramatic changes in the vegetation, the winners being shrubs and broad-leaved herbs in relatively benign habitats and robust cryptogams in more extreme sites (Oksanen 1988; Oksanen and Moen 1994; Virtanen et al. 1997*a*; Moen and Oksanen 1998; Virtanen 1998, 2000). The final result for coastal arctic areas is seen on the grazer-free islands in the Norwegian arctic, where sheltered and nutrient-rich sites support herbfields and less favorable sites are occupied by massive moss banks. Typical tundra does not exist at all (Virtanen et al. 1997*b*). The primeval states of the Antarctic and subantarctic islands discussed above are variants on the same theme.

The strength of the folivore-plant interaction on the tundra is not appreciated by all arctic ecologists. Bazely and Jeffries (1997) and Jeffries et al. (1994) regard vertebrate herbivory as generally unimportant in the Arctic, except for salt marshes grazed by snow geese. However, their arguments refer to the fraction of primary production consumed by folivores, which reflects their ability or inability to track plant production rather than the intensity of winter grazing. Moreover, they emphasize the IBP data from the early 1970s, when the muskoxen herd in question was in a period of strong increase (Hubert 1977). In the context of North America, we must remember that, even three decades ago, arctic ungulates were regarded as threatened species as a result of overhunting (Tener 1965; Kelsall 1968). Hence, old North American data are not representative for steady state dynamics.

Trophic Dynamics in Productive Ecosystems at High and Middle Latitudes

Entirely different dynamics are encountered in the most productive low-arctic habitats and in the boreal zone. Small-mammal cycles are wave like, corresponding to the time trajectory of a prey in a predator-prey limit cycle (Krebs 1964; Henttonen et al. 1987; Korpimäki and Norrdahl 1989, 1991*a*, 1991*b*; Hanski et al. 1991, 1993; Korpimäki et al. 1991; Krebs et al. 1992; Oksanen and Oksanen 1992; Hanski and Korpimäki 1995; Hanski and Henttonen

1996; Turchin and Hanski 1997; Turchin et al. 2000). The cross-continental difference in the cycling species (weasels and voles in Europe, lynxes and hares in Canada) conforms to the implication of EEH that the combination of high potential productivity and low intensity of intraguild predation leads to carnivore-folivore cycles. In northern Europe, the crusty snows created by recurrent invasion of Atlantic warm fronts do not protect only voles against generalists and avian predators (Hansson and Henttonen 1985), even weasels enjoy the same protection. The North American geography creates entirely different winter conditions. The impact of Pacific warm fronts is restricted to the western mountains, where weasel-vole cycles occur (Fitzgerald 1977). The rest of North America gets snow primarily with cold fronts. The Canadian taiga is characterized by powdery snow, which leaves weasels exposed to intraguild predation but protects the light, large-footed lynxes against wolves.

By arctic standards, the impact of folivorous mammals on boreal and temperate vegetation is light, except on especially grazing-sensitive plants (e.g., tree seedlings and shrubs, Ericson 1977; Hansson 1985; Oksanen and Ericson 1987; Ericson et al. 1992; Ostfeld and Canham 1993) and the exclusion of folivores makes little difference for the vegetation (Oksanen 1988; Oksanen and Moen 1994; Moen and Oksanen 1998). Conversely, density reductions of carnivorous endotherms have resulted in remarkable increases in survival rates of small folivores (Krebs et al. 1995; Norrdahl and Korpimäki 1995; Reid et al. 1995; Korpimäki and Krebs 1996; Klemola et al. 1997; Korpimäki and Norrdahl 1998). Predator exclosures and predation-free islands are characterized by very high folivore densities and dramatic grazing impacts on the vegetation (Linnman 1971; Ottoson 1971; Soikkeli and Virtanen 1975; Angerbjörn 1981; Häkkinen and Jokinen 1981; Pokki 1981; Oksanen et al. 1987; Hambäck and Ekerholm 1997; Klemola et al. 2000*a*, 2000*b*). Provision of natural food (fertilization leading to increased browse production) does not have any consistent effect on folivore densities, whereas folivores have responded positively to the provision of high-quality food (Henttonen et al. 1987; Krebs et al. 1995). Just giving more food should not help predation-controlled folivores. Conversely, provision of high-quality food allows reduced foraging times and increased vigilance (Abrams 1984; Brown 1992), which reduces the searching efficiency of predators (the parameter α in eq. [3]), thus increasing H^* (see eq. [6b]).

As pointed out by Polis (1999), the widespread extirpation of big predators represents an equivalent of predator-removal experiments for ungulates, provided that man has not himself taken the predator's role. An instructive example is a feral reindeer population established by stray individuals south of the limit of reindeer husbandry in Sweden. In the absence of predation and hunting, the herd erupted, wreaking havoc on the vegetation (Höglund and Eriksson 1973). Similar scenarios have been displayed on boreal islands where predators have been absent or rare (Potvin and Breton 1992; McLaren and Peterson 1994) and in East African preserves, when poaching of folivorous mammals has declined but the design of the preserve has not allowed full protection of carnivores (Talbot 1965; Curry-Lindahl 1968; Vesey-Fitzgerald 1973). The domestication of folivorous mammals and their subsequent protection against predation is a variation on the same theme. In all parts of Eurasia, where climate has allowed extensive year-round, out-of-doors grazing, enormous forest areas have been replaced by secondary grasslands and heathlands. Plant ecologists are in total agreement about the pivotal role domesticated grazers and browsers in these habitat changes (Cajander 1916; Walter 1968; Gimingham 1972; Crawley 1983;).

Trophic Dynamics and Guild Structure in Arctic and Boreal Folivorous Endotherms

Competition theory predicts that resource-limited folivores should be primarily segregated along the axis of food and habitat use in the limiting season. In arctic and alpine areas with uneven snow distribution, this accounts for the coexistence of rodents exploiting snowy habitats and ungulates using upland habitats. Otherwise, body sizes should converge toward an optimal compromise between absolute and relative energy needs. This is what we observe in the Arctic. Rock ptarmigans exploit cushion plants and trailing woody plants on windblown ridges. Reindeer (caribou) forage on lichens and winter-green graminoids of upland habitats. Muskoxen, using similar winter habitats, tend to be geographically segregated from reindeer/caribou, in spite of the differences in their diets. Collared lemmings (in Russia and North America) or grey-sided voles (in Fennoscandia) use dwarf shrubs. Brown or Norwegian lemmings forage on graminoids and mosses in snowy bottomlands. Users of the same winter habitat and resource are allopatric, and there is intense competition even between folivore species with rather different winter niches (Morris et al. 2000).

Coexistence under apparent competition allows convergent food and habitat use but requires divergence along axes relevant to predator-prey interaction (Holt 1977). Body size is such a niche dimension because each carnivore can only effectively exploit a restricted range of prey sizes. Divergence along the body size axis is indeed pronounced in the boreal zone and in the most productive low-arctic habitats. Redback voles, grouses, hares, deer, and moose exploit the same browse but are food for different predators. The body size diversity of boreal folivores had been even more pronounced before the mass extinctions in the end of the Pleistocene (Kurtén 1971). The timing of North American extinctions correlates with the invasion of hunting tribes (Alroy 1999), and even in the Old World, development of human hunting techniques is a plausible explanation for the disproportionate fatality of the most recent transition from glacial to interglacial conditions. In apparent competition, success is determined by the ratio of reproductive rate to loss rate (Holt 1977; Armstrong 1979). When loss rates inflicted by the new generalist started to increase, megaherbivores were doomed by their low reproductive rates.

The consequent reduction of size diversity can largely account for the successes of EEH in explaining current patterns in trophic dynamics. In the past, increasing predation pressure probably caused major shifts in body size diversity, and the guilds of folivorous endotherms were anything but homogeneous blocks. Between the tundra proper, with clean, two-link dynamics, and forests with, three-link, trophic dynamics, there was probably a broad zone where small- and medium-sized folivorous mammals were predation controlled, whereas the larger ones were resource limited. Within this zone, grazing and browsing pressure and the accompanied mechanical injury was probably periodically intense, keeping the landscape savanna-like, as a productive grassland (see Zimov et al. 1995) with only patches of woody vegetation, as shown in the reconstructions of Kurtén (1969).

Applicability of EEH to Other Systems

Arid Environments

The logic of EEH does not depend on the ultimate cause of differences in potential productivity, but the factor controlling productivity may also influences the realism of the critical premises of EEH. As for the gradient from temperate and tropical forests to moderately arid plains and semideserts, we cannot see such confounding interactions. The case of real deserts is, however, different. Many desert plants pass the unfavorable season as seeds (Walter 1968), and the high quality of seeds implies a huge increase in the conversion efficiency of plant biomass to assimilated energy (the constant k in eq. [2]). The high efficiency at which primary production is channeled to secondary production in annual-dominated deserts allows even the build-up of relatively dense populations of carnivorous endotherms, posing high predation risks to desert rodents (Kotler et al. 1992). As for desert ungulates, we have another problem. A central premise of EEH is that trophic dynamics obey the principle of mass action, which presupposes random search. In deserts, where water is a limiting resource, this premise is violated. A predator knowing the locations of water holes can sit there and wait for the prey, as leopards seem to do in the Negev (B. Kotler and J. Brown, personal communication). Rather than indicating one-link trophic dynamics, the striking vegetational characteristics of real deserts seem to reflect the return of three-link trophic dynamics.

Dynamics of Folivorous Insects

Due to their low mobility, the larvae of folivorous insects should be vulnerable to their natural enemies, and the same applies to the immobile pupae (Hanski 1987; Tanhuanpää et al. 1999). The experiments performed so far tell that reduced predator density normally leads to increased densities of folivorous insects and increased levels of damage in palatable plants (Schmitz et al. 2000; see also Atlegrim 1989; Spiller and Schoener 1990, 1994; Schmitz 1992, 1994, 1997; Marquis and Whelan 1994; Dial and Roughgarden 1995; Uriarte and Schmitz 1997). However, the observed magnitudes of cascading effects have been modest. The main reason for ambiguity is the short timescale of these experiments. We look forward to experiments in which plants from natural habitats could be enclosed with their folivores in an enemy-free space, large enough for mating and oviposition, for several generations of folivores. Thus far, we have had to use circumstantial evidence, which to our judgment supports the conjecture of trophic cascades. Strong circumstantial evidence for cascades has been obtained, even in the context of gall-builders and root-feeders, which are maximally protected against parasitoids and predators and which are maximally exposed to the chemical environment of the plant (Strong and Larsson 1994; Strong et al. 1996). The relevance of the energy constraint of EEH is less clear. Some data are supportive of EEH, even in the context of folivorous insects (Frazer 1997; Frazer and Grime 1997), while others are not (Oksanen et al. 1997).

Dynamics in Pelagic Systems

Pelagic systems have played a key role in establishing the idea of trophic cascades (Carpenter et al. 1985; Carpenter and Kitchell 1988). Likely contributing factors are the easiness of manipulating trophic structures in small lakes and the short generation times of plankters. This need not imply that cascades were more pronounced in pelagic systems than in systems where plants are more long-lived. Defense against herbivores is probably easier and cheaper for phytoplankters than for terrestrial plants because linking algal cells in long chains amounts to efficient defense against zooplankters (McQueen et al. 1986; Leibold 1989, 1996; Strong 1992; Leibold et al. 1997). The ability of filamentous algae to act as "nutrient sponges" further complicates trophic dynamics (Murdoch et al. 1998). On the other hand, planktivores selectively remove large *Daphnias*, which have relatively good ability to break the filaments (Brooks and Dodson 1965; Hansson 1992). Hence, indirect impacts of trophic cascades can contribute to the apparent inedibility of filamentous algae (Persson et al. 1996).

The ecoenergetic efficiencies of aquatic organisms are high (Humphreys 1979), and we are not aware of the existence of lakes too unproductive to support planktivores. The interesting part of EEH for pelagic ecosystems is the transition from three- to four-link trophic dynamics. In this context, the ontogenic omnivory of piscivores complicates dynamics. The planktivorous prey compete with juvenile piscivores, and adult piscivores prey on their own young. Thus, productive lakes may collapse back to three-link dynamics as a result of the self limitation imposed by cannibalism on piscivores and as a result of competition between planktivores and juvenile piscivores (Persson et al. 1988, 1992; L. Persson and L. Oksanen, unpublished analysis). Moreover, structural complexity covaries with primary productivity and influences interactions between planktivores and juvenile piscivores, providing an alternative explanation for the observed correlation between potential productivity and trophic dynamics (Persson and Eklöv 1995; Persson et al. 1999).

Trophic Interactions in Running Water

In spite of widespread omnivory, trophic cascades occur even in rivers, with three or four functional trophic guilds (Wootton and Power 1993; McIntosh and Townsend 1996; Huryn 1998). However, the energy constraint of EEH seems trivial; the dynamical food chain length is controlled by other factors (Power 1990, 1992; Wootton and Power 1993; Persson et al. 1996). In areas where streams are short and have little contact with each other, the impoverished predator fauna can be unable to break the defenses of herbivores. Consequently, two-link trophic dynamics are found even in productive streams. (Power 1984; T. Oksanen et al. 1995). In other cases, the well-defended herbivore is sensitive to physical disturbance, leading to disturbance-mediated variation in trophic dynamics (Power 1992). Three-link cascades appear to be typical for large, interconnected stream systems, but in the absence of large-mouthed predatory fishes, two-link trophic dynamics can emerge, even in major river systems (Power et al. 1985, 1988; M. E. Power, personal communication).

Littoral and Microbial Systems

In systems based on external inputs of organic material and filtering animals, exploitation of basal organisms does not require adaptations, which would prevent the consumer from being efficient predator of mobile animals, too. Hence, strong interactions can exist between basal organisms and top predators (Paine 1974). In these systems, the positive, indirect interaction between carnivores and basal organisms implied by HSS and EEH is unlikely to occur, and dynamics are likely to conform to the ideas of Menge and Sutherland (1976, 1987). In systems dominated by macroalgae, trophic cascades are found (Estes and Palmisano 1974; Estes and Duggins 1995). The same dichotomy emerges in microbial systems: the perspectives of HSS and EEH are corroborated in autotroph-based systems but not in systems based on external inputs of organic material (Kaunzinger and Morin 1998; Mikola and Setälä 1998; Naaem and Li 1998).

How to Proceed?

The main point emerging from the above review of trophic dynamics in autotroph-based ecosystems is the vulnerability of plants—including the mighty and seemingly invulnerable trees. All trees start as small seedlings, which mammals can consume without noticing. Thereafter, the survivors spend years as small saplings, which can be easily killed by girdling, and decades in the size category where they can be broken by motivated browsers. The widespread heathlands of western Europe and the denuded mountain slopes of Asia strikingly illustrate that trees need protection in order to regenerate. These enormous habitat changes are by far too widespread and encompass too inaccessible habitats to be explained as consequences of direct human impacts. Whether the protecting role of predators is primarily population dynamical (limitation of folivore densities) or evolutionary (giving elusiveness priority over ability to handle low-quality forage) is still difficult to judge. The two browsers that have played a pivotal role in the deforestation of Eurasia are the sheep (initially an alpine browser from the Middle East) and the goat (a domesticated ibex). Both originate from unproductive ecosystems. The famous natural experiment of Aldabra (Merton et al. 1976) has proceeded in evolutionary timescale. On the other hand, theoretical considerations based on optimal foraging (L. Oksanen 1990*b*, Hambäck 1998) and our still largely unpublished island data suggest that strict resource limitation in a seasonal environment, creating periodic starvation in winter, is strikingly damaging even for unpalatable woody plants. The situation can be clarified by additional long-term predator removal experiments, performed in different environments and with focus on different taxa.

For future work, we wish to emphasize two methodological points. First, our hypotheses are judged by a jury of plants and animals, which does not care about persuasive arguments. If we manage to proceed in understanding the dynamics in living nature, we are on the winning side. If we manage to block this process, we are on the losing side and will end up in the company of Lysenko, no matter how persuasive we are in the short run. Second, as pointed out by Levins (1968), ecologists face a trade-off between generality and precision. At their best, general theories can organize our thinking and give directions for more specific ideas, but they will never suffice as comprehensive explanations of dynamics in any system. Our discussions on population cycles serves as an example. The basic ideas have been derived from EEH, but the explanation itself requires relaxation of the assumption that trophic guilds act as homogenous blocks and introduction of system-specific assumptions.

Our collective effort to try to understand the immense diversity of interactions in living nature amounts to an attempt to navigate through a narrow passage between the Scylla of dogmatism and the Charybdis of resignation. We must be critical, see nature as it is, and pursue the limitations of our favorite hypotheses. However, we also need general ideas, showing that everything is not a hopeless maze of special cases. There are even patterns, connected to simple and logical explanations, derived from first principles.

Acknowledgments

We are grateful to the late P. Kallio, who demonstrated the impact of folivorous mammals on the recovery of mountain birches and who prepared the ground for appreciating top-down dynamics in terrestrial ecosystems. P. Pamilo and S.-L. Varvio-Aho helped L.O. to take the first step toward the cascade approach by thoroughly criticizing the traditional bottom-up views. The paradigm change was completed with the guidance of S. D. Fretwell, who was full of exciting ideas and always ready to share them. Much of the practical work has been conducted and many of the new ideas have been given by our past and current graduate students: M. Aunapuu, P. Ekerholm, D. Grellmann, P. A. Hambäck, J. Moen, J. Olofsson, Ü. Rammul, M. Schneider, and R. Virtanen, and numerous field assistants. The help of locals has been indispensable. The ones deserving special thanks are O. Eriksen and the families Johnsen and Romsdal. Our thinking has been sharpened by the arguments of G. Polis and D. Strong, R. Holt, E. Korpimäki, J. Pastor, and M. Power. M. Crête, P. Vanninen, and R. Virtanen helped with new references. Figure 1 was drawn by M. Soininen. This study has been supported by grants from the Swedish Council for Natural Sciences, The Academy of Finland, The Royal Academy of Sweden, and the Swedish Council for Agriculture and Forestry. A great environment for finishing the work was provided by the Centre of Population Biology at Silwood Park. This paper is dedicated to the memory of our friend, Gary Polis, whose immense empirical knowledge, critical attitude, and vigorous pursuit of truth has been a constant source of inspiration for us.

Literature Cited

Abrams, P. 1984. Foraging time optimization in food webs. American Naturalist 124:106–124.

———. 1992 Predators that benefit prey and prey that harm predators: unusual effects of interacting foraging adaptations. American Naturalist 140:573–600.

———. 1993 Effects of increased productivity on abundances of trophic levels. American Naturalist 141: 351–371.

———. 1996. Dynamics and interactions in food webs with adaptive foragers. Pages 113–121 *in* G. A. Polis and K. Winemiller, eds. Food webs: integration of patterns and dynamics. Chapman & Hall, New York.

Abrams, P. A., and J. D. Roth. 1994*a*. The effects of enrichment of three-species food chains with non-linear functional responses. Ecology 75:1118–1130.

———. 1994*b*. The response of unstable food chains to enrichment. Evolutionary Ecology 8:150–171.

Albrektsson, A., and T. Lundmark. 1991. Vegetationens storlek och omsättning inom en barrskog i norra Sverige, samt näring i vegetation och mark i samband med växandet. (Amount and turnover of vegetation in a coniferous forest in northern Sweden, plus nutrients in the vegetation and the soil in the context of growing.) Arbetsrapport 52, Institutionen för skogsskötsel, Sveriges Lantbruksuniversitet, Umeå. [In Swedish.]

Alroy, J. 1999. Putting North America's end-Pleistocene megafaunal extinctions in context. Pages 105–143 *in* R. D. E. McPhee, ed. Extinctions in near time. Kluwer Academic, Dordrecht.

Andersson, M., and S. Erlinge. 1977. Influence of predation on rodent populations. Oikos 29:591–597.

Angerbjörn, A. 1981. Winter food as a limiting factor of dense mountain hare populations on islands. Pages 529–535 *in* K. Myers and C. D. McInnes, eds. Proceedings of the world lagomorph conference, Guelph, Ontario, 1979. University of Guelph Press, Guelph.

Armstrong, R. A. 1979. Prey species replacement along a gradient of nutrient enrichment. Ecology 60:76–84.

Atlegrim, O. 1989. Exclusion of birds from bilberry stands:

impact on insect larval density and damage to the bilberry. Oecologia (Berlin) 79:136–139.

Batzli, G. O., R. G. White, S. F. McLean, Jr., F. A. Pitelka, and B. D. Collier. 1980. The herbivore-based trophic system. Pages 335–410 *in* J. Brown, P. C. Miller, and F. Bunnell, eds. An arctic ecosystem: the coastal tundra at Barrow, Alaska. Dowden, Hutchinson & Ross, Stroudsburg, Pa.

Bazely, D. R., and R. L. Jeffries. 1997. Trophic interactions in arctic ecosystems and the occurrence of a terrestrial trophic cascade. Pages 183–208 *in* S. J. Woodin and M. Marquiss, eds. Ecology of arctic environments. Blackwell, London.

Begon, M., J. L. Harper, and C. R. Townsend. 1996. Ecology: individuals, populations and communities. 3d ed. Blackwell, London.

Bliss, L. C. 1977. General summary: Truelove Lowland ecosystem. Pages 657–675 *in* L. C. Bliss, ed. Truelove Lowland, Devon Island, Canada: a high arctic ecosystem. University of Alberta Press, Edmonton.

Brooks, J. L., and S. I. Dodson. 1965. Predation, body size and composition of plankton. Science (Washington, D.C.) 150:28–31.

Brown J. S. 1992. Patch use under predation risk. I. Models and predictions. Annales Zoologici Fennici 29:179–182.

Cajander, A. K. 1916. Metsänhoidon perusteet. (Foundations of forestry.) Werner Söderström OY, Porvoo. [In Finnish.]

Callaghan, T. V., and U. Emanuelsson 1985. Population structure processes of tundra plants and vegetation. Pages 399–439 *in* J. White, ed. Population structure of vegetation. Junk, Dordrecht.

Carpenter, S. R., and J. F. Kitchell. 1988. Strong manipulations and complex interactions: consumer control of lake productivity. BioScience 38:764–769.

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience 35:634–649.

Caughley, G., and A. Gunn. 1993. Dynamics of large herbivores in deserts: kangaroos and caribou. Oikos 67: 47–55.

Cederlund, G., and G. Markgren 1987. The development of the Swedish moose population, 1970–1983. Swedish Wildlife Research 1(suppl.):55–62.

Černjavskij, F. B., and A. V. Tkačev. 1982. Populjacionnye cikli lemmingov v arktike: ekologičeskie i endokrinnye aspekty. Nauka, Moscow.

Charnov, E. L. 1976. Optimal foraging: the marginal value theorem. Theoretical Population Biology 9:129–136.

Collins, N. J., J. H. Baker, and P. J. Tilbrook. 1975. Signy Island, maritime Antarctic. Pages 345–374 *in* T. Rosswall and W. O. Heal, eds. Structure and function of tundra ecosystems. Naturvårdsverket, Bulletin 20, Stockholm.

Crawley, M. J. 1983. Herbivory: the dynamics of animal-plant interactions. Blackwell, Oxford.

Crête, M. 1999. The distribution of deer biomass supports the hypothesis of exploitation ecosystems. Ecology Letters 2:223–227.

Crête, M., and J. Huot 1993. Regulation of a large herd of migratory caribou: summer nutrition affects calf growth and body reserves of dams. Canadian Journal of Zoology 7:2291–2296.

Crête, M., and M. Manseau 1996. Natural regulation of cervidae along a 1000 km latitudinal gradient: change in trophic dominance. Evolutionary Ecology 10:51–62.

Curry-Lindahl, K. 1968. Zoological aspects on the conservation of vegetation in tropical Africa. Acta Phytogeographica Suecica 54:25–32.

Dahl, E. 1957. Rondane: mountain vegetation in south Norway and its relation to the environment. Skrifter av den Norske Videnskaps-Akademin. I. Matematisk-Naturvidenskaplig Klasse 1956:1–347.

Dial, R. J., and J. Roughgarden. 1995. Experimental removal of insects from rain forest canopy: direct and indirect effects. Ecology 76:1821–1834.

Du Rietz, E. 1925. Zur Kenntnis der flechtenreichen Zwergstrauchheiden im kontinentalen Südnorwegen. Svenska Växtsociologiska Sällskaps Handlingar 4:1–80.

Ehrlich, P. R., and L. C. Birch. 1967. The "balance of nature" and "population control." American Naturalist 101:97–107.

Ekerholm, P., L. Oksanen, and T. Oksanen. 2000. Long-term dynamics of voles and lemmings in low arctic tundra and above the willow limit as test of theories on trophic interactions. Ecography (in press).

Elton, C. 1927. Animal ecology. Sidgwick & Jackson, London.

Ericson, L. 1977. Influence of voles and lemmings on the vegetation in a coniferous forest during a 4-year period in northern Sweden. Wahlenbergia 4:1–115.

Ericson, L., T. Elmquist, K. Jakobson, K. Danell, and A. Salomonsson. 1992. Age structure of boreal willows and fluctuations in herbivore populations. Proceedings of the Royal Society of Edinburgh 98B:75–89.

Erlinge, S., G. Göransson, L. Hansson, G. Högstedt, O. Liberg, J. Loman, O. Nilsson, I. N. Nilsson, T. von Schanz, and M. Sylvén. 1983. Predation as regulating factor on small rodent populations in southernmost Sweden. Oikos 40:36–52.

Estes, J. A., and D. O. Duggins. 1995. Sea otters and kelp forests in Alaska: generality and variation in community ecological paradigm. Ecological Monographs 65:75–100.

Estes, J. A., and J. F. Palmisano. 1974. Sea otters, their role in structuring near shore communities. Science (Washington, D.C.) 185:1058–1060.

Fitzgerald, B. M. 1977. Weasel predation on a cyclic population of the montane vole (*Microtus montanus*) in California. Journal of Animal Ecology 46:367–397.

Framstad, E., N. C. Stenseth, and E. Östbye. 1993. Time series analysis of population fluctuations of *Lemmus lemmus.* Pages 97–115 *in* N. C. Stenseth and R. A. Ims, eds. The biology of lemmings. Linnean Society Symposium Series 15. Academic Press, London.

Frazer, L. H. 1997. Top-down vs. bottom-up control influenced by productivity in a North Derbyshire, U.K., dale. Oikos 81:99–108.

Frazer, L. H., and J. P. Grime. 1997. Primary productivity and trophic dynamics investigated in a North Derbyshire, U.K., dale. Oikos 80:499–508.

Fretwell, S. D. 1972. Populations in a seasonal environment. Princeton University Press, Princeton, N.J.

———. 1977. The regulation of plant communities by food chains exploiting them. Perspectives of Biology and Medicine 20:169–185.

Gimingham, C. H. 1972. Ecology of heathlands. Chapman & Hall, London.

Grime, J. D. 1979. Plant strategies and vegetation processes. Wiley, Chichester.

Haapasaari, M. 1988. The oligotrophic heath vegetation of northern Fennoscandia and its zonation. Acta Botanica Fennica 135:1–219.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist 94:421–425.

Häkkinen, I., and M. Jokinen 1981. Population dynamics of mountain hare on an island in the outer archipelago of SW Finland. Pages 469–477 *in* K. Myers and C. D. McInnes, eds. Proceedings of the world lagomorph conference, Guelph, Ontario, 1979. University of Guelph Press, Guelph.

Hambäck, P. A. 1998. Seasonality, optimal foraging, and prey coexistence. American Naturalist 152:881–895.

Hambäck, P. A., and P. Ekerholm 1997. Mechanisms of apparent competition in a seasonal environment: an example with vole herbivory. Oikos 80:276–288.

Hanski, I. 1987. Pine sawfly populations: patterns, processes, problems. Oikos 50:327–335.

Hanski, I., and H. Henttonen. 1996. Predation on competing rodent species: a simple explanation of complex patterns. Journal of Animal Ecology 65:220–232.

Hanski, I., and E. Korpimäki. 1995. Microtine rodent dynamics in northern Europe: parametrized models for predator-prey interaction. Ecology 76:840–850.

Hanski, I., L. Hansson, and H. Henttonen. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. Journal of Animal Ecology 60:353–367.

Hanski, I., P. Turchin, E. Korpimäki, and H. Henttonen. 1993. Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos. Nature (London) 364:232–235.

Hansson, L. 1985. Damage by wildlife, especially small rodents, to North American *Pinus contorta* provenances introduced into Sweden. Canadian Journal of Forest Research 15:1167–1171.

Hansson, L., and H. Henttonen. 1985. Gradients in density variations of small rodents: the importance of latitude and snow cover. Oecologia (Berlin) 67:394–402.

Hansson, L. A. 1992. The role of food chain composition and nutrient availability in shaping algal biomass development. Ecology 73:241–247.

Haukioja, E., and T. Hakala. 1975. Herbivore cycles and periodic outbreaks: formulation of a general hypothesis. Reports of Kevo Subarctic Research Station 12:1–9.

Henttonen, H., and A. Kaikusalo 1993. Lemming movements. Pages 157–186 *in* N. C. Stenseth and R. A. Ims, eds. The biology of lemmings. Linnean Society Symposium Series 15. Academic Press, London.

Henttonen, H., T. Oksanen, A. Jortikka, and V. Haukisalmi. 1987. How much do weasels shape microtine cycles in the northern Fennoscandian taiga? Oikos 50: 353–365.

Höglund, N., and B. Eriksson, 1973. Förvildade tamrenarnas inverkan på vegetationen inom Lövhögsområdet. (The impact of feral reindeer on the vegetation within the Lövhög area.) Naturvårdsverket, Stockholm. [In Swedish.]

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12:276–290.

———. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. American Naturalist 124:377–406.

———. 1985. Population dynamics in two patch environments: some anomalous consequences of an optimal habitat distribution. Theoretical Population Biology 28: 181–208.

Hörndfeldt, B., B.-G. Carlsson, O. Löfgren, and U. Eklund. 1990. Effect of cyclic food supply on breeding performance in Tengmalm's owl (*Aegolius funereus*). Canadian Journal of Zoology 68:522–530.

Hubert, B. A. 1977. Estimated productivity of muskox on Truelove Lowland. Pages 467–491 *in* L. C. Bliss, ed. Truelove Lowland, Devon Island, Canada: a high arctic ecosystem. University of Alberta Press, Edmonton.

Humphreys, W. C. 1979. Production and respiration in animal populations. Journal of Animal Ecology 48: 427–454.

Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: bottom-up and top-down forces in natural communities. Ecology 73:724–732.

Huryn, A. D. 1998. Ecosystem-level evidence for top-down and bottom-up control of production in a grassland stream. Oecologia (Berlin) 115:173–183.

Jeffries, R. L., D. R. Klein, and G. R. Shaver. 1994. Vertebrate herbivores and northern plant communities: reciprocal influences and responses. Oikos 71:193–206.

Jenkin, J. F. 1975. Macquairie Island, Subantarctic. Pages 375–397 *in* T. Rosswall and W. O. Heal, eds. Structure and function of tundra ecosystems. Naturvårdsverket, Bulletin 20, Stockholm.

Kalela, O. 1949. Über Fjeldlemming-Invasionen und andere irregulare Tierwanderungen. Annales Zoologici Societatis "Vanamo" 13:1–90.

———. 1971. Seasonal differences in the habitat of the Norwegian lemming, *Lemmus lemmus*, in 1959 and 1960 at Kilpisjärvi, Finnish Lapland. Annales Academiae Scientarum Fenniae A IV "Biologica" 178:1–22.

Kalela, O., and T. Koponen 1971. Food consumption and movements of the Norwegian lemming in areas characterized by isolated fells. Annales Zoologici Fennici 8: 80–84.

Kallio, P., and J. Lehtonen 1975. On the ecocatastrophe of birch forests caused by *Oporinia autumnata*. Pages 174–180 *in* F. E. Wielgolaski, ed. Fennoscandian tundra ecosystems. II. Animals and systems analysis. Ecological Studies 17. Springer, Berlin.

Kalliola, R. 1939. Pflanzensoziologische Untersuchungen in der alpinen Stufe Finnisch-Lapplands. Annales Botanici Societatis "Vanamo" 13:1–321.

Kaunzinger, C. M. K., and P. J. Morin 1998. Productivity controls food chain properties in microbial communities. Nature (London) 395:495–497.

Kelsall, J. P. 1968. The migratory barren ground caribou of Canada. Canadian Wildlife Service, Bulletin 20. Ottawa.

Kjelvik, S., and L. Kärenlampi. 1975. Plant biomass and primary production of Fennoscandian subarctic and subalpine forests and of alpine willow and heath ecosystems. Pages 111–128 *in* F. E. Wielgolaski, ed. Fennoscandian tundra ecosystems. I. Plants and microorganisms. Ecological Studies 16. Springer, Berlin.

Klemola, T., M. Koivula, E. Korpimäki, and K. Norrdahl. 1997. Small mustelid predation slows population growth of *Microtus* voles: a predation reduction experiment. Journal of Animal Ecology 66:607–614.

Klemola, T., K. Norrdahl, and E. Korpimäki. 2000*a*. Do delayed effects of overgrazing explain population cycles in voles? Oikos (in press).

———. 2000*b*. Experimental tests of predation and food hypotheses for population cycles of voles. Proceedings of the Royal Society of London B, Biological Sciences (in press).

Körner, C. 1999. Alpine plant life: functional plant ecology of high mountain ecosystems. Springer, Berlin.

Korpimäki, E., and C. J. Krebs. 1996. Predation and population cycles of small mammals. BioScience 46: 754–764.

Korpimäki, E., and K. Norrdahl. 1989. Predation of Tengmalm's owls: numerical responses, functional responses, and dampening impacts on population fluctuations of voles. Oikos 54:154–164.

———. 1991*a*. Do breeding nomadic avian predators dampen fluctuations of small mammals? Oikos 69: 504–510.

———. 1991*b*. Numerical and functional responses of Kestrels, Short-eared owls and Long-eared owls to vole densities. Ecology 72:814–826.

———. 1998. Experimental reduction of predators reverses the crash phase of small mammal cycles. Ecology 79:2448–2455.

Korpimäki, E., K. Norrdahl, and T. Rinta-Jaskari. 1991. Responses of stoats and weasels to fluctuating vole abundances: is the low phase of the vole cycle due to mustelid predation? Oecologia (Berlin) 88:552–561.

Kotler, B. P., L. Blaustein, and J. S. Brown. 1992. Predator facilitation: the combined effect of snakes and owls on the foraging behavior of gerbils. Annales Zoologici Fennici 29:199–206.

Krebs, C. J. 1964. The lemming cycle at Baker Lake, Northwest Territories, during 1959–62. The Technical Papers of the Arctic Institute of North America 15:1–104.

Krebs, C. J., R. Boonstra, S. Boutin, M. Dale, S. Hannon, A. R. E. Sinclair, J. N. M. Smith, and R. Turkington. 1992. What drives the snowshoe hare cycle in Canada's Yukon? Pages 886–896 *in* D. M. McCullough and R. Barrett, eds. Wildlife 2001: populations. Elsevier Applied Science, London.

Krebs, C. J., S. Boutin, R. Boonstra, A. R. E. Sinclair, J. N. M. Smith, K. Martin, and R. Turkington. 1995. Impact of food and predation on snowshoe hare cycle. Science (Washington, D.C.) 269:1112–1115.

Kurtén, B. 1969. Istiden. (The ice age.) International Book Production, Stockholm. [In Swedish.]

———. 1971. The age of mammals. Weidenfeld & Nicholson, London.

Kyllönen, H., and K. Laine. 1980. Tunturikasvillisuuden vuotuisista vaihteluista Kilpisjärvellä. (Annual variation in plant biomass, net production, flowering and berry and seed crops in the Kilpisjärvi fjeld area, Finnish Lapland.) Luonnon Tutkija 84:19–23. [In Finnish; English summary.]

Leader-Williams, N. 1988. Reindeer on South Georgia: the ecology of an introduced population. Cambridge University Press, Cambridge.

Leibold, M. A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. American Naturalist 134:922–949.

———. 1996. A graphical model of keystone predators in food webs: regulation of abundance, incidence, and diversity patterns in communities. American Naturalist 142:784–812.

Leibold, M. A., J. Chase, J. B. Shurin, and L. A. Dowding. 1997. Species turnover and regulation of trophic structure. Annual Review of Ecology and Systematics 29: 467–494.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, N.J.

Lewis Smith, R. I., and D. W. H. Walton. 1975. South Georgia, Subantarctic. Pages 399–423 *in* T. Rosswall and W. O. Heal, eds. Structure and function of tundra ecosystems. Naturvårdsverket, Bulletin 20, Stockholm.

Lieth, H. 1975. Primary productivity of the major vegetation units of the world. Pages 203–215 *in* H. Lieth and R. H. Whittaker, eds. Primary productivity of the biosphere. Springer, Berlin.

Linnman, N. 1971. Hararna och skogen på Stora Karlsön. (The hares and the forest on the island Stora Karlsön.) Fauna och Flora 66:221–264. [In Swedish.]

Mälkönen, E. 1974. Annual primary production and nutrient cycling in some Scots pine stands. Metsäntutkimuslaitoksen julkaisuja. Vol. 84, no. 5. Metsäntutkimuslaitos, Helsinki.

———. 1977. Annual primary production and nutrient cycling in a birch stand. Metsäntutkimuslaitoksen julkaisuja. Vol. 84, no. 5. Metsäntutkimuslaitos, Helsinki.

Marquis, R. J., and Whelan, C. J. 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. Ecology 75:2007–2014.

McIntosh, A. R., and C. R. Townsend. 1996. Interactions between fish, grazing invertebrates, and algae in a New Zealand stream: a trophic cascade mediated by fish-induced changes to grazer behavior? Oecologia (Berlin) 108:174–181.

McLaren, B. E., and R. O. Peterson. 1994. Wolves, moose and tree rings on Isle Royale. Science (Washington, D.C.) 266:1555–1557.

McNaughton, S. J., M. Oesterheld, D. A. Frank, and K. J. Williams. 1989. Ecosystem level patterns of primary productivity and herbivory in terrestrial ecosystems. Nature (London) 341:142–144.

McQueen, D. J., J. R. Post, and E. L. Mills. 1986. Trophic relationships in freshwater pelagic ecosystems. Canadian Journal of Fisheries and Aquatic Sciences 43:1571–1581.

Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition and temporal heterogeneity. American Naturalist 110:351–369.

———. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. American Naturalist 130:730–757.

Merton, L. F., D. M. Bourn, and R. J. Hnatiuk. 1976. Giant tortoise and vegetation interaction on Aldabra atoll. I. Inland. Biological Conservation 9:293–304.

Mikola, J., and H. Setälä. 1998. No evidence of trophic cascades in experimental microbial-based soil food web. Ecology 79:153–164.

Miller, P. C., P. J. Webber, W. C. Oechel, and L. Tieszen 1980. Biophysical processes and primary production. Pages 66–101 *in* J. Brown, P. C. Miller, and F. Bunnell, eds. An arctic ecosystem: the coastal tundra at Barrow, Alaska. Dowden, Hutchinson & Ross, Stroudsburg, Pa.

Moen, J., and L. Oksanen. 1991. Ecosystem trends. Nature (London) 353:510.

———. 1998. Long term exclusion of mammals in two arctic-alpine plant communities: a test of the hypothesis of exploitation ecosystems. Oikos 82:333–346.

Moen, J., P. A. Lundberg, and L. Oksanen. 1993. Lemming grazing on snowbed vegetation during a population peak, northern Norway. Arctic and Alpine Research 25: 130–135.

Morris, D. W., D. L. Davidson, and C. J. Krebs. 2000. Measuring ghost of competition: insights from density-dependent habitat selection on the coexistence and dynamics of lemmings. Evolutionary Ecology Research (in press).

Murdoch, W. W. 1966. Community structure, population control, and competition—a critique. American Naturalist 100:219–226.

Murdoch, W. W., R. M. Nisbeth, E. McCauley, A. M. de Roos, and W. S. C. Gurney. 1998. Plankton abundance and dynamics across nutrient levels: test of hypotheses. Ecology 79:1339–1356.

Naaem, S., and S. Li. 1998. Consumer species richness and autotroph biomass. Ecology 79:2603–2615.

Norrdahl, K., and E. Korpimäki. 1995. Effects of predator removal on vertebrate prey populations: birds of prey and small mammals. Oecologia (Berlin) 103:241–248.

———. 1996. Do nomadic avian predators synchronize population fluctuations of small mammals: a field experiment. Oecologia (Berlin) 107:478–483.

Nygren, T. 1987. The history of moose in Finland. Swedish Wildlife Research 1(suppl.):49–54.

Oksanen, L. 1978. Lichen grounds of Finnmarksvidda, northern Norway, in relation to summer and winter grazing by reindeer. Reports of Kevo Subarctic Research Station 14:64–71.

———. 1983. Trophic exploitation and arctic phytomass patterns. American Naturalist 122:45–52.

———. 1988. Ecosystem organization: mutualism and cybernetics or plain Darwinian struggle for existence. American Naturalist 131:424–444.

———. 1990*a*. Exploitation ecosystems in seasonal environments. Oikos 57:14–24.

———. 1990*b*. Predation, herbivory, and plant strategies along gradients of primary productivity. Pages 445–474 *in* D. Tilman and J. Grace, eds. Perspectives on plant consumption. Academic Press, New York.

———. 1992. Evolution of exploitation ecosystems. I. Predation, foraging ecology and population dynamics in herbivores. Evolutionary Ecology 6:15–23.

Oksanen, L., and L. Ericson 1987. Dynamics of tundra and taiga populations of herbaceous plants in relation to the Tihomirov-Fretwell and Kalela-Tast hypotheses. Oikos 50:381–388.

Oksanen, L., and J. Moen. 1994. Species-specific plant responses to exclusion of grazers in three Fennoscandian tundra habitats. Écoscience 1:31–39.

Oksanen, L., and T. Oksanen. 1981. Lemmings (*Lemmus lemmus*) and grey-sided voles (*Clethrionomys rufocanus*) in interaction with their resources and predators on Finnmarksvidda, northern Norway. Reports of the Kevo Subarctic Research Station 17:7–31.

———. 1992. Long-term microtine dynamics in north Fennoscandian tundra: the vole cycle and the lemming chaos. Ecography 15:226–236.

Oksanen, L., and R. Virtanen 1995. Topographic, altitudinal and regional patterns in continental and suboceanic heath vegetation of northern Fennoscandia. Acta Botanica Fennica 153:1–80.

Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemelä. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist 118:240–261.

Oksanen, L., T. Oksanen, A. Lukkari, and S. Sirén. 1987. The role of phenol-based chemical defense in the interaction between tundra populations of the vole *Clethrionomys rufocanus* and the dwarf shrub *Vaccinium myrtillus*. Oikos 50:371–380.

Oksanen, L., J. Moen, and P. A. Lundberg. 1992. The time scale problem in exploiter-victim systems: does the solution lie ratio-dependent exploitation? American Naturalist 140:938–960.

Oksanen, L., J. Moen, and T. Helle. 1995. Timberline patterns in northernmost Fennoscandia: the relative importance of climate and grazing. Acta Botanica Fennica 153:93–105.

Oksanen, L., T. Oksanen, P. Ekerholm, J. Moen, P. A. Lundberg, M. Schneider, and M. Aunapuu. 1996. Structure and dynamics of arctic-subarctic grazing webs in relation to primary productivity. Pages 231–242 *in* G. A. Polis and K. O. Winemiller, eds. Food webs: integration of patterns and dynamics. Chapman & Hall, New York.

Oksanen, L., M. Aunapuu, T. Oksanen, M. Schneider, P. Ekerholm, P. A. Lundberg, P. Armulik, V. Aruoja, and L. Bondestad. 1997. Outlines of food webs in a low arctic tundra landscape in relation to three theories of trophic dynamics. Pages 351–373 *in* A. C. Gange and V. K. Brown, eds. Multitrophic interactions in terrestrial systems. Blackwell, London.

Oksanen, T. 1990. Exploitation ecosystems in heterogeneous habitat complexes. Evolutionary Ecology 4:220–234.

Oksanen, T., and H. Henttonen. 1996. Dynamics of voles and small mustelids in the taiga landscape of northern Fennoscandia in relation to habitat quality. Ecography 19:432–443.

Oksanen, T., L. Oksanen, and S. D. Fretwell. 1985. Surplus killing in the hunting strategy of small predators. American Naturalist 126:328–346.

Oksanen, T., L. Oksanen, and M. Gyllenberg. 1992*a*. Exploitation ecosystems in heterogeneous habitat complexes. II. Impact of small-scale heterogeneity on predator-prey dynamics. Evolutionary Ecology 6:383–398.

Oksanen, T., L. Oksanen, and M. Norberg. 1992*b*. Habitat use of small mustelids in a tundra landscape: a test of the hypothesis of patchy exploitation systems. Ecography 15:237–244.

Oksanen, T., M. E. Power, and L. Oksanen. 1995. Habitat selection and predator resource dynamics. American Naturalist 146:565–585.

Oksanen, T., M. Schneider, Ü. Rammul, and M. Aunapuu 1999. Population fluctuations of voles on the North Fennoscandian tundra: contrasting dynamics in adjacent areas with different habitat compositions. Oikos 86:463–478.

Ostfeld, R. S., and C. D. Canham 1993. Effects of meadow vole population density on tree seedling survival on an old field. Ecology 74:179–801.

Ottoson, J. 1971. Något om skogshararnas inverkan på ön Jungfrun i Kalmarsund. Fauna och Flora 66:229–240.

Paavilainen, E. 1980. Effects of fertilization on plant biomass and nutrient cycle on a drained dwarf shrub pine swamp. Metsäntutkimuslaitoksen julkaisuja. Vol. 98, no. 5. Metsäntutkimuslaitos, Helsinki.

Paine, R. T. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia (Berlin) 15:93–120.

Pastor, J. B., and Y. Cohen. 1997. Herbivores, the functional diversity of plants species, and the cycling of nutrients in ecosystems. Theoretical Population Biology 51:165–179.

Pastor, J. B., and R. J. Naiman. 1992. Selective foraging and ecosystem processes in boreal forests. American Naturalist 139:690–705.

Pastor, J. B., B. Dewey, R. J. Naiman, P. F. McInnes, and Y. Cohen. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. Ecology 74: 770–777.

Pattie, D. L. 1977. Population levels and bioenergetics of arctic birds on Truelove Lowland. Pages 413–436 *in* L. C. Bliss, ed. Truelove Lowland, Devon Island, Canada: a high arctic ecosystem. University of Alberta Press, Edmonton.

Persson, L., and P. Eklöv. 1995. Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. Ecology 76:70–81.

Persson, L., G. Andersson, S. F. Hamrin, and L. Johansson. 1988. Predator regulation and primary production along the productivity gradient of temperate lake ecosystems. Pages 45–68 *in* S. R. Carpenter, ed. Complex interactions in lake communities. Springer, Berlin.

Persson, L., S. Diehl, L. Johansson, G. Andersson, and S. F. Hamrin. 1992. Trophic interactions in temperate lake ecosystems: a test of the food chain theory. American Naturalist 140:59–84.

Persson, L., J. Bengtsson, B. A. Menge, and M. E. Power. 1996. Productivity and consumer regulation—concepts, patterns, and mechanisms. Pages 396–434 *in* G. A. Polis and K. Winemiller eds. Food webs: integration of patterns and dynamics. Chapman & Hall, New York.

Persson, L., P. Byström, E. Wahlström, J. Andersson, and J. Hjelm. 1999. Interactions among size-structured populations in a whole-lake experiment: size- and scale-dependent processes. Oikos 87:139–156.

Pokki, J. 1981. Distribution, demography and dispersal of the field vole, *Microtus agrestis* (L.), in the Tvärminne archipelago, Finland. Acta Zoologica Fennica 164:1–48.

Polis, G. A. 1999. Why are parts of the world green? multiple factors control productivity and the distribution of green biomass. Oikos 86:3–15.

Polis, G. A., and S. Hurd. 1996. Allochtonous inputs across habitats, subsidized consumers, and apparent trophic cascades: examples from the ocean-land interface. Pages 275–285 *in* G. A. Polis and K. Winemiller, eds. Food webs: integration of patterns and dynamics. Chapman & Hall, New York.

Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. American Naturalist 147: 813–846.

Potvin, F., and L. Breton. 1992. Impact du cerf sur la succession végétale après coupe à Anticosti: suivi d'un ensemble d'exclos de 1984 à 1989. Provincial Governement of Québec, Technical Report. Québec City, Québec.

Power, M. E. 1984. Habitat quality and the distribution of algae grazing catfish in a Panamanian stream. Journal of Animal Ecology 53:357–374.

———. 1990. Effects of fish in river food webs. Science (Washington, D.C.) 250:811–814.

———. 1992. Hydrologic and trophic control of seasonal algal blooms in northern Californian rivers. Archiv für Hydrobiologie 125:385–410.

Power, M. E., W. J. Matthews, and A. J. Stewart. 1985. Grazing minnows, piscivorous bass and stream algae: dynamics of a strong interaction. Ecology 69:1448–1456.

Power, M. E., A. J. Stewart, and W. J. Matthews. 1988. Grazer control of attached algae in an Ozark mountain stream: effects of short-term exclusion. Ecology 69: 1894–1989.

Prins, H. H. T. 1982. Why are mosses eaten in cold environments only? Oikos 38:374–380.

Reid, D. G., C. J. Krebs, and A. Kenney 1995. Limitation of collared lemming population growth at low densities by predation mortality. Oikos 387–394.

Reimers, E., L. Villmo, E. Gaare, V. Holthe, and T. Skogland. 1980. Status of rangifer in Norway including Svalbard. Pages 774–785 *in* E. Reimers, E. Gaare, and S. Skjenneberg, eds. Proceedings of the 2d international reindeer/caribou symposium, Röros, Norway. Direktoratet for vilt og ferskvannfisk, Trondheim.

Rhoades, D. F. 1985. Offensive-defensive interactions between herbivores and plants: their relevance in herbivore population dynamics and ecological theory. American Naturalist 125:205–238.

Riewe, R. R. 1977*a*. Mammalian carnivores utilizing Truelove Lowland. Pages 493–500 *in* L. C. Bliss, ed. Truelove Lowland, Devon Island, Canada: a high arctic ecosystem. University of Alberta Press, Edmonton.

———. 1977*b*. The utilization of wildlife in the Jones Sound region by the Grise Fjord Inuit. Pages 623–644 *in* L. C. Bliss, ed. Truelove Lowland, Devon Island, Canada: a high arctic ecosystem. University of Alberta Press, Edmonton.

Rosenzweig, M. L. 1971. Paradox of enrichment: the destabilization of exploitation ecosystems in ecological time. Science (Washington, D.C.) 385–387.

———. 1973. Exploitation in three trophic levels. American Naturalist 107:275–294.

———. 1977. Aspects of biological exploitation. Quarterly Review Biology 52:371–380.

Schmitz, O. J. 1992. Exploitation in model food webs with mechanistic consumer-resource dynamics. Theoretical Population Biology 39:100–114.

———. 1994. Resource edibility and trophic exploitation in an old field food web. Proceedings of the National Academy of Sciences of the USA 91:5364–5367.

———. 1997. Press perturbations and predictability of ecological interactions in a food web. Ecology 78:55–69.

Schmitz, O. J., P. A. Hambäck, and A. P. Beckerman. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removal on plants. American Naturalist 155:141–153.

Sirén, G. 1955. The development of spruce forests on raw humus sites in northern Finland and its ecology. Acta Forestalia Fennica 62:1–363.

Soikkeli, M., and J. Virtanen 1975. Ulkosaariston huipputiheät jäniskannat. (The extraordinarily dense hare populations of the outer archipelago.) Metsästys ja Kalastus 64:16–19. [In Finnish.]

Spiller, D. A., and T. W. Schoener. 1990. A terrestrial field experiment showing the impact of eliminating top predators on foliage damage. Nature (London) 374:469–472.

———. 1994. Effects of top and intermediate predators in a terrestrial food web. Ecology 75:182–196.

Strong, D. R. 1986. Density vagueness: abiding the variance in the demography of real populations. Pages 257–268 *in* J. Diamond and T. Case, eds. Community ecology. Harper & Row, New York.

———. 1992. Are trophic cascades all wet? differentiation and donor-control in speciose ecosystems. Ecology 73: 747–754.

Strong, D. R., and S. Larsson. 1994. Is the evolution of herbivore resistance influenced by parasitoids? Pages 261–276 *in* B. Hawkins and W. Sheenan, eds. Parasitoid community ecology. Oxford University Press, Oxford.

Strong, D. R., J. L. Maron, and P. G. Connors. 1996. Top down from underground? the unappreciated influence of subterranean food webs on above-ground ecology. Pages 170–175 *in* G. A. Polis and K. Winemiller, eds. Food webs: integration of patterns and dynamics. Chapman & Hall, New York.

Talbot, L. N. 1965. A survey of past and present wildlife research in East Africa. East African Wildlife Journal 3: 61–85.

Tanhuanpää, M., K. Ruohomäki, P. Kaitaniemi, and T. Klemola. 1999. Different impact of pupal predation on populations of *Epirrita autumnata* (Lepidoptera; Geometridae) within and outside the outbreak range. Journal of Animal Ecology 68:562–570.

Tener, J. S. 1965. Muskoxen in Canada: a biological and taxonomical review. Canadian Wildlife Service Monograph Series 2. Canadian Wildlife Service, Ottawa.

Thomas, D. C., and J. Edmonds. 1983. Rumen contents and habitat selection of Peary caribou in winter. Arctic and Alpine Research 15:97–105

Tihomirov, B. A. 1959. Vzajmosvjazizivotnogomira i rastiteånogo pokrova tundry. Trudy Botaniceskij Institut V. L. Komarova. Akademija Nauk SSSR, Moscow.

Tilman, D. 1988. Plant strategies and the structure and dynamics of plant communities. Princeton University Press, Princeton, N.J.

Turchin, P., and I. Hanski. 1997. An empirically based model for latitudinal gradient in vole population dynamics. American Naturalist 149:842–874.

Turchin, P., L. Oksanen, P. Ekerholm, T. Oksanen, and H. Henttonen. 2000. Lemmings: prey or predators. Nature (London) (in press).

Tyler, N. 1993. Svalbardsrein. (The Svalbard reindeer.) Ottar (Tromsö museum) 93:51–58. [In Norwegian.]

Uriarte, M., and O. J. Schmitz. 1997.Trophic control across a natural productivity gradient: verification of the exploitation hypothesis with sap-feeding herbivores. Oikos 82:552–560.

Vesey-Fitzgerald, D. F. 1973. Animal impact on vegetation and plant succession in Lake Nanyara National Park, Tanzania. Oikos 24:314–324.

Virtanen, R. J. 1998. Impact of grazing and neighbour removal on a heath plant community transplanted onto a snowbed site, NW Finnish Lapland. Oikos 81:359–367.

———. 2000. Effects of grazing on above-ground biomass on a mountain snowbed, NW Finland. Oikos (in press).

Virtanen, R. J., H. Henttonen, and K. Laine 1997*a*. Lemming grazing and structure of a snowbed plant community—a long-term experiment at Kilpisjärvi, Finnish Lapland. Oikos 79:155–166.

Virtanen, R. J., P. A. Lundberg, J. Moen, and L. Oksanen. 1997*b*. Topographic and altitudinal patterns in plant communities on European arctic islands. Polar Biology 17:95–113.

Vitt, D. H., and P. Pakarinen 1977. The bryophyte vegetation, production and organic components of Truelove Lowland. Pages 225–244 *in* L. C. Bliss, ed. Truelove Lowland, Devon Island, Canada: a high arctic ecosystem. University of Alberta Press, Edmonton.

Walter, H. 1964. Die Vegetation der Erde in öko-physiologischer Betrachtung. I. Die tropischen und subtropischen Zonen. Gustav Fischer, Jena.

———. 1968. Die Vegetation der Erde in öko-physiologischer Betrachtung. II. Die gemässigten und arktischen Zonen. Gustav Fischer, Jena.

Wegener, C., and A.-M. Odasz. 1998. Do Svalbard reindeer regulate standing crop in the absence of predators: a test of the "exploitation ecosystems" model. Oecologia (Berlin) 116:202–206.

Werth, E. 1928. Überblick über die Vegetationsgliederung von Kerguelen sowie von Possession-Eiland (Crozet-Gruppe) und Heard-Eiland. Pages 300–326 *in* E. von Drygalski, ed. Deutsche Südpolar-Expedition 1901–1903. Teil 8. de Gruyter, Berlin.

White, T. C. R. 1978. The importance of a relative shortage of food in animal ecology. Oecologia (Berlin) 3:71–86.

Wielgolaski, F. E. 1975. Primary productivity of alpine meadow communities. Pages 121–128 *in* F. E. Wielgolaski, ed. Fennoscandian Tundra Ecosystems. I. Plants and microorganisms. (Ecological Studies 16.) Springer, Berlin.

Wollkind, D. J. 1976. Exploitation in three trophic levels:

an extension allowing intraspecies carnivore interaction. American Naturalist 110:431–447.

Wootton, J. T., and M. E. Power. 1993. Productivity, consumers, and the structure of a river food chain. Proceedings of National Academy of Sciences of the USA 90:1384–1387.

Zimov, S. A., V. I. Chuprynin, A. P. Oreshko, F. S. Chapin, J. F. Reynolds, and M. C. Chapin 1995. Steppe-tundra transition: a herbivore-driven biome shift at the end of the Pleistocene. American Naturalist 146:765–794.

Associate Editor: Robert D. Holt