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Evolution of exploitation ecosystems
I. Predation, foraging ecology and population dynamics in herbivores

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Summary

The hypothesis of exploitation ecosystems was reanalysed using the model of Armstrong (1979) which simultaneously deals with population dynamics and evolution. The results indicate that the prediction of Oksanen *et al.* (1981) of strict predation limitation of herbivores in productive ecosystems does not hold for coevolved systems. Depending on the nature of herbivore–carnivore coevolution, herbivore biomass may level off at a threshold productivity value or increase monotonously with increasing primary productivity, though at a strongly reduced rate in productive ecosystems. Under both circumstances, increasing primary productivity is predicted to be accompanied by gradual replacement of genuine folivores by semi-granivores and true granivores. The dominating guild members are predicted to show some degree of resource-limitation, although only granivores are predicted to be chiefly resource-limited even in the most productive ecosystems. Data on arctic-to-temperate patterns in the community structure of herbivorous vertebrates conform to the implications of the analysis.

Keywords: coevolution; community structure; granivores; herbivores; predation; productivity

Introduction

According to the hypothesis of exploitation ecosystems (Fretwell, 1977, 1987; Oksanen *et al.*, 1981; Oksanen, 1988, 1990a, b), trophic dynamics in relatively productive 'three-link' ecosystems (annual dry matter production over 700 g m^{-2}) conform to the HSS-theory (Hairston *et al.*, 1960; Slobodkin *et al.*, 1967), stating that plants and carnivores are resource limited and herbivores are regulated by predation. Increasing primary productivity is predicted to lead to increased biomass in plants and carnivores but not in herbivores.

In more barren 'two-link ecosystems' (annual dry matter production 30–700 g m^{-2}, e.g. typical arctic and alpine tundras, arid steppes and semideserts), efficient carnivores are predicted to be absent except as temporary visitors exploiting herbivore outbreaks. Consequently, grazers are strictly resource-limited and plants live under intense natural grazing pressure. Increasing primary productivity is predicted to lead to increased herbivore biomass, whereas above-ground plant biomass is predicted to remain constant.

Extremely barren 'one-link' ecosystems (annual dry matter production under 30 g m^{-2}, e.g. polar deserts, high-alpine boulder fields, extreme arid deserts) in turn, do not sustain any grazers at all. Thus plants are predicted to be again strictly resource-limited and plant biomass is predicted to increase linearly with increasing primary productivity.

These changes in trophic dynamics are restricted to vertebrates, large, mobile arthropods

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(e.g. grasshoppers) plus their predators. Within the subcommunity of small arthropods, the hypothesis of Hairston *et al.* (1960) should also apply to barren areas (see Oksanen, 1988).

The model of Oksanen *et al.* (1981) is, in essence, a re-analysis of Rosenzweig's (1971) 'Paradox of Enrichment' with three-dimensional exploitation models (Rosenzweig, 1973a; Wollkind, 1976). As pointed out by C. C. Smith (unpublished observations) and Abrams (1984, and unpublished observations), it can be regarded as a null model of how the structure and dynamics of the grazing chain would respond to changing primary productivity, assuming *laisser-faire* exploitation, spatial homogeneity and no feedback impacts of evolution or behaviour on trophic dynamics. If there is interference competition (as seems reasonable), the zones of constant biomass should be replaced by zones where biomass increases with increased primary productivity, but at a low rate. Spatial heterogeneity, in turn, enhances stability and may change entirely the nature of local trophic dynamics within barren areas adjacent to large pieces of productive habitat (T. Oksanen, 1990).

Successes and shortcomings of the Oksanen *et al.* (1981) model

Despite the oversimplifications of the model, its predictions are in surprisingly good agreement with available data. In tundra communities which are in the productivity interval of two-link trophic dynamics, above-ground plant biomass lies at the level of 100–200 g m^{-2} (dry weight) and does not show a significant positive relation to primary productivity, provided that the area harbours a relatively complete grazer fauna. In areas without moss-eating lemmings, moss biomass is copious (about 1 kg m^{-2} as opposed to about 20 g m^{-2} in areas with lemmings). Removal of lemmings may result in a six-fold increase in moss biomass during a 7-year period (Oksanen, 1983). Thus the low biomasses seem indeed to be a consequence of natural grazing pressure. Above-ground plant biomass in equally barren steppe and semidesert ecosystems also lies at the level of 100–200 g m^{-2} (Oksanen *et al.*, 1981).

McNaughton *et al.* (1989) demonstrated that there is a significant, global positive correlation between herbivore biomass and primary productivity, which seems to contradict the predictions of Oksanen *et al.* (1981). However, a re-analysis of the material shows that this positive relation is critically dependent on the inclusion of data from barren arctic and arid areas. Data points from more productive areas (three-link ecosystems according to Oksanen *et al.*, 1981) hardly show any indication of a positive trend. Grazer biomass reaches the level of 50 kJ m^{-2} already in the high arctic sedge tundra of Truelove Lowland, Devon Island, Canada. Grazer biomasses of the two most productive tropical ecosystems in the material (a grassland and a rain forest) are essentially on the same level (83 and 69 kJ m^{-2}, respectively), despite 25-fold difference in primary productivity.

The data discussed above suggest that the pure exploitation model of Oksanen *et al.* (1981) may pass as a 'reasonable simplification' in the context of global biomass patterns (Rosenzweig, 1977). Nevertheless, the model hardly gives accurate predictions of day-to-day dynamics in productive ecosystems. Intense predation pressure should select for elusive prey. Predators, in turn, do not necessarily have effective countermeasures. Their characteristics represent trade-offs between capture efficiency and other fitness components, and it is not self-evident that the balance shifts in the direction of increased hunting efficiency when prey become more elusive (Abrams, 1986; see also Rosenzweig and Schaffer, 1978). If predators cannot respond to anti-predator adaptations of their prey, increased primary productivity should lead to increased herbivore biomass also in three-link ecosystems (*via* favouring more elusive herbivores and cryptic behaviour; see Abrams, 1984).

The argument of Abrams (1986) is not supported by the above-discussed data. The lack of positive correlation between primary productivity and grazer biomass in productive areas rather argues for the traditional arms race view (e.g. Van Valen, 1973). However, even in that case, evolutionary responses of herbivores are likely to influence community structure and have a feedback impact on day-to-day population dynamics. The scope of the present paper is to analyse these impacts, according to the guidelines of Armstrong (1979) and Oksanen (1981). To facilitate communication, analyses will be presented in two dimensions. However, all analyses have been checked using the more appropriate three-dimensional models (Rosenzweig, 1973a), and cases where the two techniques yielded different results will be commented.

Predation as a selective force

In pure exploitation competition, the winner is always the species (race, genotype) that is able to suppress resources at the lowest level (MacArthur, 1972; Tilman, 1982). The term K-selection (MacArthur and Wilson, 1963) can be used at least metaphorically as a label for such situations. Often, though not always, such selection also increases equilibrium population size (Rosenzweig, 1973b). Intense predation, in turn, favours species (races, genotypes) with maximal ratio of reproductive potential, r to the attack rate of predators a (see Holt, 1977; Armstrong, 1979; Noy-Meir, 1981). As the ratio can be maximized either by having high r or by having low a, adaptation to predation must be regarded as a strategy dimension of its own, outside the $K-r$ strategy axis (as in the case of grazing and plants, see Oksanen, 1990a).

Consequences of intense predation (r/a-selection) have been analysed by Holt (1977), Armstrong (1979) and Noy-Meir (1981). Holt focused on situations where the alternative prey types do not share resources. Conversely, Armstrong assumed perfect competition (identical resource bases and nested feeding niches), while Noy-Meir covered the middle ground. Armstrong's approach is ideal for a micro-evolutionary study where the alternative prey types are races of a single species or guilds of closely related species. Thus my formal analyses will entirely build on his modelling techniques, although I will discuss the limitations of my results in the light of the results of Holt (1977, 1984, 1987) and Noy-Meir (1981).

The core of Armstrong's technique is to construct curves where the per capita reproductive potential of a prey type, scaled with its sensitivity to predation, is plotted against its density. The relationship between these 'Armstrong curves' and standard prey isoclines can be illustrated as follows. Consider a normal predator–prey system where the rate of change in the prey population obeys equation:

$$\mathrm{d}H/\mathrm{d}t = rHg(H) - af(H)HC \qquad (1)$$

where H is prey density, C is predator density, r is the Malthusian parameter of the prey, $g(H)$ represents the density-dependence of prey reproduction ($g(H)$ is decreasing and > 0 if and only if H is smaller than a positive constant K), a is the attack rate of unsaturated, actively hunting carnivores and $f(H)$ represents the impact of prey density on attack rate (i.e. $aHf(H)$ is the functional response of the predator).

Setting $\mathrm{d}H/\mathrm{d}t = 0$ and solving for C, we get equation:

$$C = \frac{r}{a} \cdot \frac{g(H)}{f(H)} \qquad (2)$$

which stands for the prey isocline in the predator–prey phase space. Multiplying by $f(H)$, we obtain the equation for an Armstrong curve:

$$C' = Cf(H) = \frac{r}{a}g(H) \qquad (3)$$

where C' stands for the density of actively hunting predators.

Thus Armstrong curves represent prey isoclines where the impact of changing predator behaviour (predator saturation, various types of activity thresholds; see Abrams, 1982) has been scaled away. The vertical axis now stands for the density of actively hunting predators, while the remaining part of the predator population does not appear in the model. This change of axis is technically helpful when curves for several alternative prey are superimposed on each other, but there are two limitations to be remembered. First, the re-scaling deprives us of the possibility of performing a stability analysis. This limitation is a minor one: Armstrong curves and standard prey isoclines are so closely related that the existing body of stability theory (e.g. Rosenzweig and MacArthur, 1963; Rosenzweig, 1973a; Tanner, 1975; Wollkind, 1976) can easily be applied. Second, attack rates of alternative prey must be assumed to be frequency independent. In other words, predation must be treated as a blind process in which there are no mechanisms of prey choice (e.g. optimal foraging, search images, microhabitat differences). This limitation is not critical in a strictly microevolutionary analysis (due to the similarity of the alternative prey types) and will be relaxed in 'From guilds to communities' (page 24).

Prey equilibrium can be found by coupling Equation 1 with the standard predator equation:

$$dC/dt = -mC + kaf(H)CH \tag{4}$$

where m stands for the mortality rate of starving predators and k for the efficiency of predators in converting captured prey to resources for maintenance and reproduction (other symbols as in Equations (1)–(3)). Setting $dC/dt = 0$ and solving for H, we obtain the equation for the predator isocline:

$$H = m/(kaf(\hat{H})) \tag{5}$$

where $\hat{H}$ refers to prey density at the predator isocline. The constancy of $\hat{H}$ can be demonstrated by using an explicit $f(H)$ function. For instance, assuming type II functional response, $f(H) = w/(D + H)$ (where w is a constant representing maximum predation rate; and D is the half saturation constant of the functional response curve). Then, Equation 5 can be re-written as equation:

$$H = mD/(kaw - m) \tag{6}$$

Because predator densities do not appear in Equations 5 and 6, the re-definition of the predator axis from C to C' does not influence the predator isocline.

For a system only consisting of the predator and one prey type, to be called H_i, the prey equilibrium (H_i^*) can be found at the intersection between its Armstrong curve and the predator isocline. Coexistence in a system with two alternative prey types, H_1 and H_2, exploiting similar resources, can be studied by superimposing their Armstrong curves on each other (Fig. 1; see also Armstrong, 1979, Figs 5 and 6). If the two prey types only differ in r_i or g_i, the same predator isocline is appropriate for both systems. If a_i:s differ, as assumed in Fig. 1, the two systems have different predator isoclines.

The criterion for coexistence can be derived from invasibility of the two predator–prey systems (see Armstrong, 1979). H_2 can invade a system with predators and H_1, if the equilibrium between H_1 and the predator lies below the isocline of H_2 and vice versa. In the case represented in Fig. 1, the two prey differ in a_i:s and the Armstrong curves happen to cross between the predator isoclines. Thus both one-prey systems can be invaded by the other prey. Consequently, the two prey can coexist on identical resources, as pointed out by Armstrong (1979). Assuming trade-offs between K and a, enrichment should lead to a shift from maximization of K to minimization of a (from K-strategy to g-strategy in the terms of Oksanen, 1990). This general idea can be transformed into a specific, testable hypothesis by studying the specific trade-offs involved.

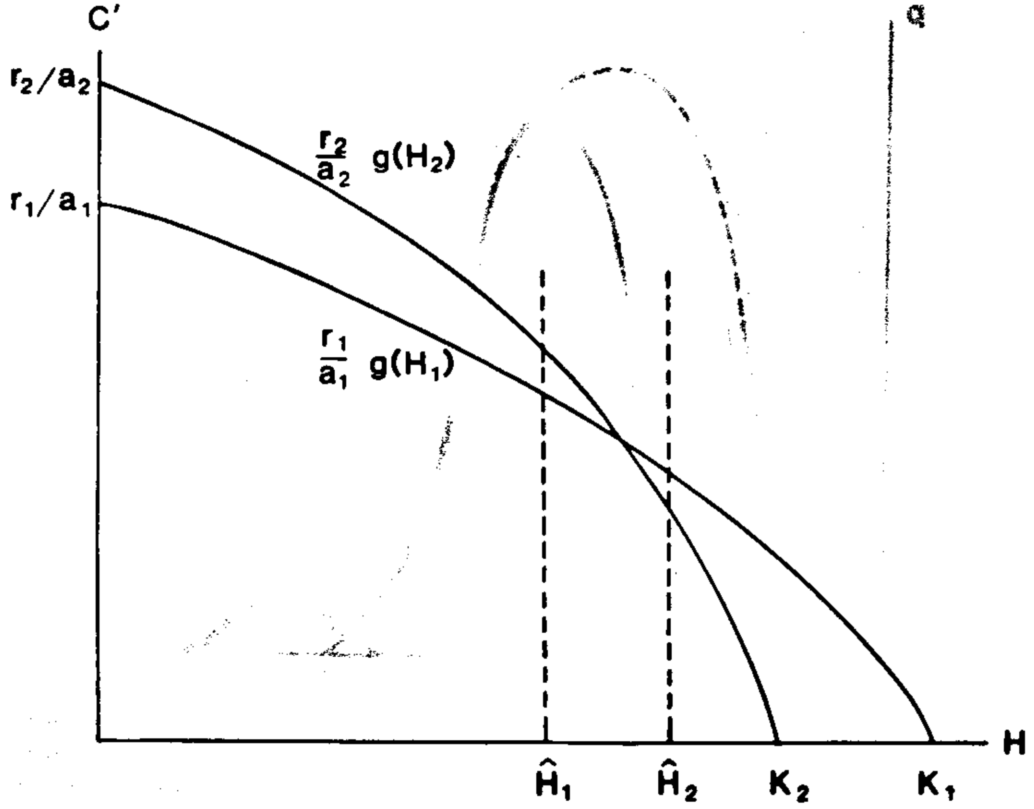

Figure 1. The Armstrong curves or $(r_i/a_i)\,g(H_i)$ functions of two alternative prey types, H_1 and H_2 (entire lines) and predator isoclines for the two alternative prey types (dashed lines, denoted by $\hat{H}_i$). Horizontal axis, prey population density (H); vertical axis, density of actively hunting predators (C'); can also be interpreted as the reproductive output of the prey, scaled by its vulnerability to predation. K_i = carrying capacity of prey i. Owing to the crossing of the Armstrong curves between the predator isoclines, the two prey types will coexist in the system.

The *K* vs *r*/*a* trade-off in herbivores

Specialization to high-quality forage yields a dual advantage in dealing with predation. Consumers of low-quality food must process large quantities of forage rapidly through the gut and thus be burdened by low ecoenergetic efficiencies and long foraging times (Barkley *et al.*, 1980). Conversely, specialists of high-quality forage get the necessary nutrients from smaller amounts of food and can spend longer times hiding. Moreover, handling low-quality forage requires a bulky digestive apparatus and elaborated mechanisms for re-cycling gut microflora (Sperber *et al.*, 1983) which reduce the fleetness of the animal. In systems where the ability to use marginal forage is never tested while ability to escape predators is essential for daily survival, natural selection will thus favour specialization to high-quality forage.

A detailed analysis on the trade-offs between *r*/*a* and *K* requires knowledge of the abundance relationships between different kinds of plants and on the relation between foraging ecology and elusiveness. Most terrestrial ecosystems are characterized by at least moderate abundance of 'brown biomass' with very low digestibility: moss and lichen thalli, old grass and bark. Another

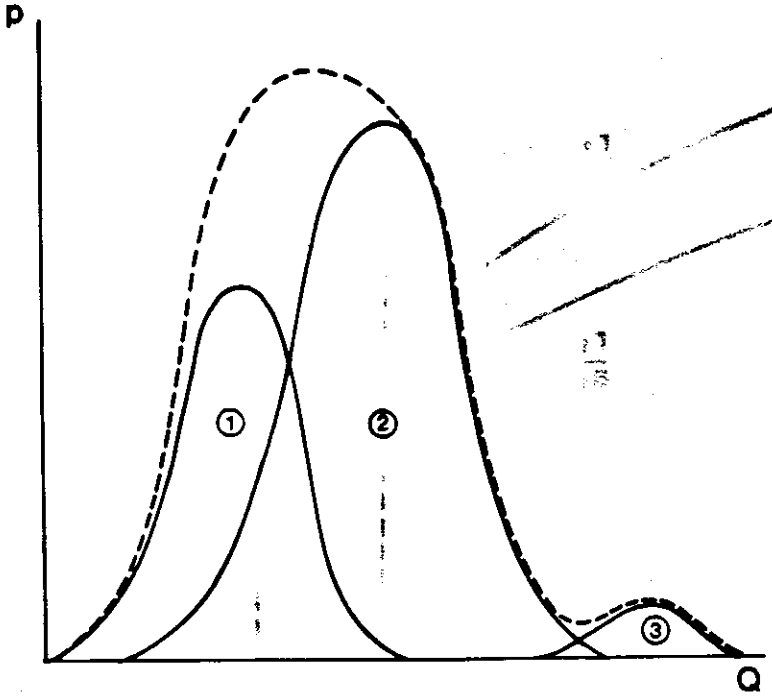

Figure 2. Schematized distribution of forage quality in a boreal old field ecosystems, according to Stenseth *et al.* (1977). Q = quality, p = abundance of forage with a given quality. Entire lines: distributions for 'brown biomass' (1), 'green biomass' (2) and 'white biomass' (3). Dashed line: pooled quality distribution for all forage types.

major component can be called 'green biomass': foliage, buds and rhizomes, richer in soluble carbohydrates and amino acids than the brown biomass, but nevertheless containing so much fibre that a consumer needs a fairly large digestive apparatus to be able to extract energy or nutrients from this type of forage. The third category consists of 'white biomass': seeds, fruits and specialized storage organs, with large concentrations of starch-rich and protein-rich tissues and little generalized digestion inhibitors.

Let us start by looking at the case of an early stage of forest succession where the quality distribution of green and white biomasses can overlap. Examples of such quality distributions are presented by Stenseth *et al.* (1977), a somewhat schematized example is reproduced in Fig. 2. Next, let us assume that we have an array of herbivore types with different abilities to exploit low-quality forage. Items with quality (Q) lower than a specific threshold value (Q_m) are not exploitable for a given herbivore. Consequently, carrying capacity (K) is directly proportional to the amount of forage with quality higher than Q_m.

By presenting the information of Fig. 2 in the form of cumulative distribution of forage quality (Fig. 3), we see how K behaves as a function of Q_m. There are two plateau regions, where K is rather insensitive to changes in Q_m, separated by a steep slope. One plateau coincides with very low values of Q_m where there is little potential food with still lower quality. The other lies in the seam between green and white biomasses. In Fig. 3, both the low-quality plateau and the green–white plateau have negative slopes. Other types of food distributions could make the plateaux perfectly horizontal and might create a third plateau between brown and green biomass. The

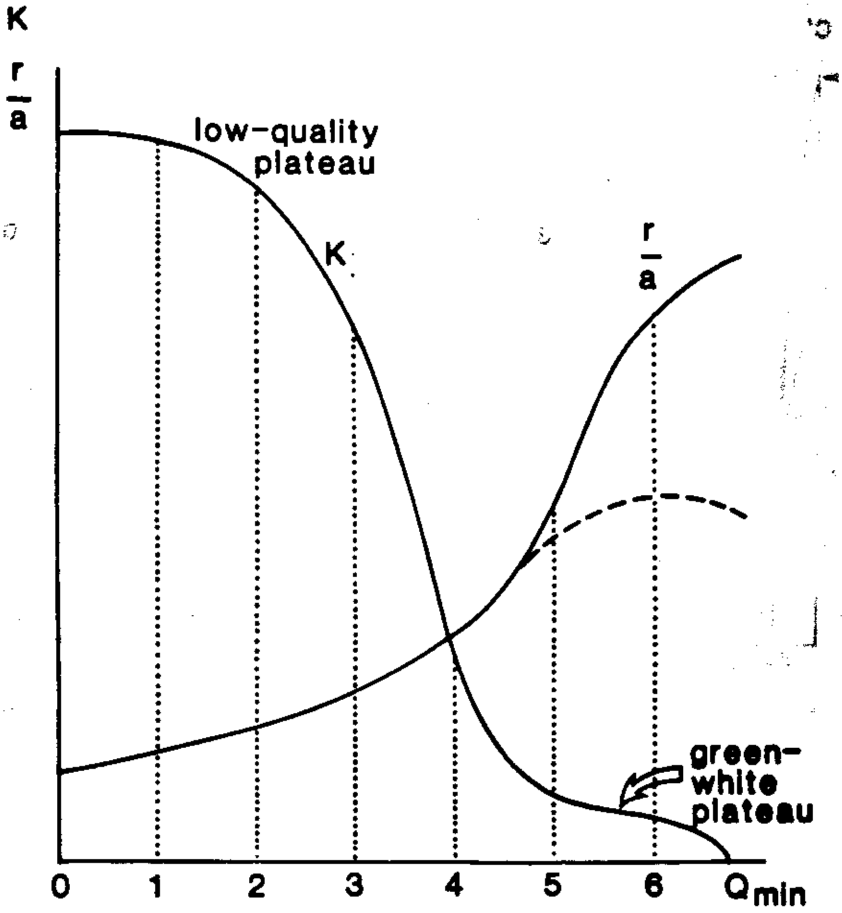

Figure 3. Carrying capacity (K) and the intrinsic reproduction rate to attack rate ratio (r/a) as functions of the minimum quality exploitable forage (Q_{min}). The dashed r/a curve stands for areas with severe winters. The relation between K and Q_{min} is based on Fig. 2.

green–white plateau might even have a positive slope, if utilization of white biomass requires special adaptations, e.g. due to the presence of shells or toxins ('From guilds to communities' page 24).

As discussed above, attack rate (a) can be regarded as a decreasing function of Q_m. Consequently, r/a will be an increasing function of Q_m, except maybe for the very highest values of Q_m where increasing foraging times may reverse the relation between a and Q_m. According to the arguments of experienced field mammalogists (e.g. Hansson, 1985b; Henttonen *et al.*, 1987), the appropriate form for the 'elusiveness function' ($1/a(Q_m)$) is a downward convex one. Selective folivores are somewhat more elusive than broadly folivorous species, but elusiveness increases still more sharply in the transition from folivory to granivory. A downward turn at very high Q_m values (dashed line in Fig. 3) should be relevant in northern areas for granivores using seeds that are too small for being cached in the autumn, because a thick snow cover makes it difficult to find small food particles.

Armstrong curves for a guild of herbivores/granivores with basically similar feeding ecology but with varying degrees of specialization to high-quality forage can now be constructed by

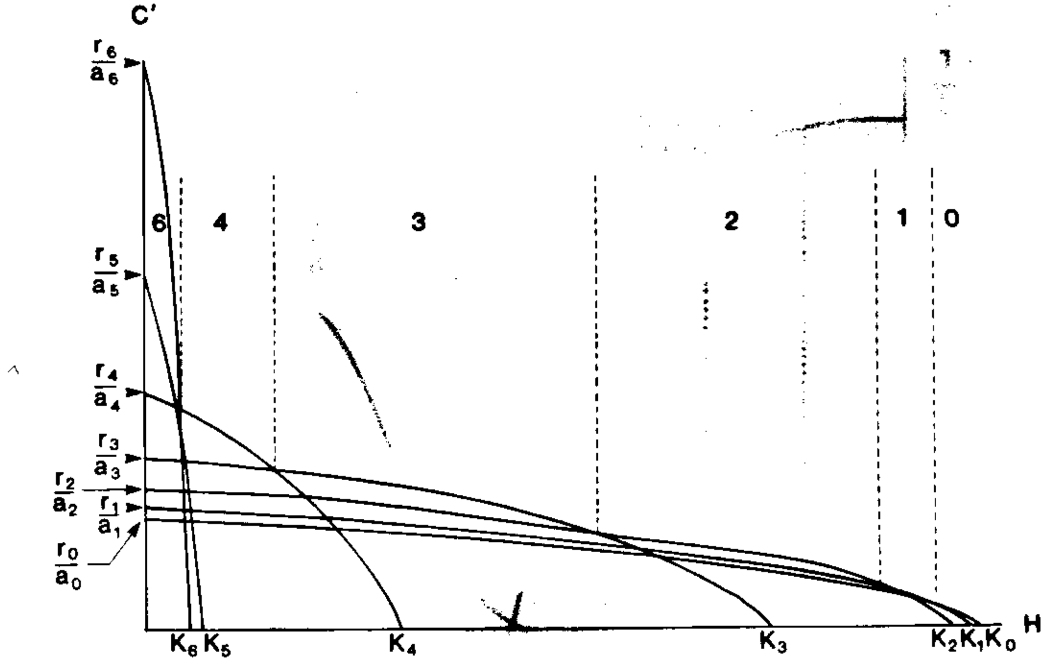

Figure 4. The Armstrong curves of seven herbivores/granivores with different degrees of specialization to high-quality forage, derived from Fig. 3. Horizontal axis: population density of herbivores/granivores (H). K_i = carrying capacity for H_i when alone. H_0 = broadly folivorous herbivore. H_1 and H_2: somewhat specialized herbivores; H_3: strongly specialized herbivore; H_4 and H_5: semi-granivores; H_6: pure granivore. The numbers above the curves refer to the prey type whose Armstrong curve is the topmost one and which consequently will prevail if predator isoclines lie within this range of population densities.

choosing different levels of specialization along the Q_m axis (levels 0–6 in Fig. 3). The accompanying K_i and a_i/r_i values can then be read from Fig. 3 as the ordinates of the intersections between the dotted vertical lines (corresponding to Q_m-values 0, 1, 2, 3, 4, 5 and 6) and the carrying capacity ($K(Q_m)$) and elusiveness ($r/a(Q_m)$) functions. We thus have the points where the Armstrong curves meet the axes. Assuming that the forms of these functions correspond to Fig. 1, graphical representation of this family of functions is now possible (Fig. 4).

Assuming that predators lack the capacity to neutralize the anti-predator strategies of their prey, as proposed by Abrams (1986), each Armstrong curve will be associated with a predator isocline of its own. As the distances of predator isoclines from the origin increase with decreasing a (Equations 5 and 6), the predator isoclines will form a band of vertical lines. The predator isoclines for systems with only H_0 will be furthest to the left and the isocline systems with just H_6 will be the rightmost one. Such a band of predator isoclines can be depicted by placing a transparent ruler at a right angle across the H-axis of Fig. 4. The converse assumption of a dead arms race between predators and prey implies that the same predator isocline is relevant for all prey types, as the predators are then better hunters in systems dominated by more elusive prey. This assumption can be simulated by turning the ruler on its edge.

The impact of enrichment of grazer guilds

The primary productivity of the system determines the location of the Armstrong curves. In barren habitats, all Armstrong curves touch the horizontal axis close to the origin and do not meet any predator isoclines. With increasing primary productivity, the $K_i : s$ move rightwards and the band of predator isoclines starts to intersect with a successively increasing number of Armstrong curves (Armstrong, 1979). Graphically, the easiest way to analyse such a gradient is to let the scale of the H-axis change. Then, we can operate on one set of Armstrong curves and simulate increased primary productivity by moving the band of predator isoclines leftwards across Fig. 4.

This can be done easily by using the ruler techniques outlined above. A species will replace all others if its Armstrong curve is the topmost one within the whole band of predator isoclines (i.e. within the part of the figure covered by the ruler). If Armstrong curves cross between predator isoclines, stable coexistence is implied. In the arms race variant, coexistence is not possible.

When the habitat is so barren that the predator isocline (or the band of predator isoclines) does not touch any of the Armstrong curves, the equilibrium community will solely consist of H_0 (the most generalized and K-strategic herbivore). The present model predicts that its population density will persistently lie at its carrying capacity. (According to the analysis with three-dimensional models (Oksanen, unpublished analysis; see also Oksanen *et al.*, 1981), sustained, violent population fluctuations are possible.) When the habitat is barely productive enough to allow the predator isocline for H_0 to touch its Armstrong curve, an equilibrium with only H_0 and the predator will be established. However, with even slight further increase in primary productivity, H_0 becomes replaced by H_1. Soon thereafter, H_1 has to yield for H_2. This moderately selective folivore will prevail over a fairly long range of primary productivities. After a substantial increase in primary productivity, highly selective folivores and semi-granivores (H_3 and H_4) will take over. Still higher degrees of enrichment allow the pure granivore (H_6) to join the community, provided that winter conditions are favourable for the granivorous habit. Owing to its low K and a values, however, the pure granivore will hardly ever totally replace the highly selective folivore. Thus productive habitats with mild winters can be expected to harbour a mixture of granivores and highly selective folivores.

The presence or absence of predator counter-evolution is largely irrelevant to the scenario, although it does influence equilibrium biomasses and the rate at which transitions take place. Some features of the scenario depend on the details of the functions. However, with almost all reasonable function forms, one will find that four or five species will flourish over large pieces of the productivity axis. H_0 will keep the really barren regions for itself. Selective folivores (H_2 and H_3) will prevail within a wide range of moderately productive habitats. Granivores (H_6) will abound in highly productive areas with mild winters.

Extremely selective folivores (H_4) will dominate in productive areas with cold winters and be co-dominants in other productive areas, too, given the food quality distributions of Fig. 2. With more narrow quality distribution of green biomass, however, also H_4 is excluded. Then, H_3 will prevail in productive areas with severe winters, and a mixed community of H_3 and H_6 will prevail in corresponding habitats in areas with mild winters. Unless the resource distribution is much more continuous than in Fig. 2, the semi-granivorous H_5 represents a nonsense-strategy which will never make it. H_1 fares almost equally poorly for basically the same reason (because of having its Q_m within a plateau in the cumulative resource distribution; Fig. 3).

The patterns described above can be imagined to emerge either in ecological time scale as a consequence of interspecific interactions or in evolutionary time scale as a consequence of natural selection. It seems natural to assume that the ecological scenario will apply if all potentially successful prey types are present. The evolutionary scenario has once occurred and may be repeated, e.g. on isolated islands. Evolution proceeds easily to either direction among selective folivores. Evolution from broad folivory (H_0) to selective folivory (H_2–H_4) and from selective folivory to pure granivory (H_6) is more difficult, because of the adaptive valleys represented by the two nonsense-strategies (H_1 and H_5). However, these strategies can be quite viable in the absence of more folivorous species (Fig. 4). Thus the above scenario from folivory to granivory can be regarded as a response to enrichment in ecological time, while the most plausible historical sequence is from granivory to folivory.

Whether arising through interspecific interactions or evolution, the changes in community structure tend to result in some degree of resource-limitation among herbivores even in extremely productive habitats. According to all formal analyses (e.g. Rosenzweig and MacArthur, 1963; Rosenzweig, 1973a, b; Tanner, 1975; Wollkind, 1976), this should enhance stability. Changes in community structure thus reduce or eliminate the destabilizing impacts of enrichment on herbivore–carnivore interactions (Rosenzweig, 1971), as suggested by Rosenzweig (1973b).

Another noteworthy result is that the analysis reinforces the herbivore–granivore argument of Slobodkin *et al.* (1967) without the need to introduce the granivore category in an *ad hoc* manner. Because of the discontinuity of the quality distribution of forage, granivores emerge as a distinct group, and this distinctiveness can be further strengthened by mechanical (shells) and chemical (toxins) characteristics of seeds and fruits.

From guilds to communities

The above results have been derived from assumptions maximally unfavourable for interspecific coexistence. The feeding niche of animals specialized on high-quality forage has been assumed to be entirely contained within the feeding niche of generalized grazers. If the utilization of high-quality food items requires special adaptations (see above), the granivore option will be present even in barren habitats, provided that white forage is produced in sufficient amounts to sustain specialized consumers. Moreover, presence of high-quality items of different sizes and types can lead to competitive coexistence of several granivorous taxa. This possibility seems realistic for arid ecosystems where a large part of the vegetation consists of annuals (Walter, 1968). In cold areas with almost exclusively perennial vegetation, generative plant organs can be consumed by generalized herbivores as inflorescenses and floral winter buds (Tihomirov, 1959; Ericson and Oksanen, 1987; Järvinen, 1987; Oksanen and Ericson, 1987a) and this is also the case in arid grasslands (McNaughton, 1979). Thus the assumption of contained feeding niches is reasonable in many ecosystems, though not everywhere.

Another restrictive tacit assumption is that I have ignored the fact that there are several ways plants can be low-quality forage. Two or more strictly resource-limited grazers can coexist, e.g. if one is able to handle the phenol-based defences of dicots, whereas the other can deal with the silica-based defences of graminoids. Moreover, herbivores need several types of resources (energy, amino acids, minerals; see Belovsky, 1981) which opens the possibility for competitive coexistence in accordance to Tilman's (1982) resource ratio model. Notice, however, that forage is actually handled by the gut/rumen microflora which can vary intraspecifically and even individually in space and time. Because a single species can thus occupy a broad feeding niche, competitive coexistence is not guaranteed and should, at its best, involve a few species only. Notice also that, in contrast to granivores, food size is not a legitimate niche dimension for herbivores. All seedlings and vegetative sprouts are small as juveniles. Thus heavy grazing of small plants implies that there will never be any big ones.

Adding a little predation to the system may or may not enhance the likelihood for interspecific coexistence (Noy-Meir, 1981). The cases where coexistence is enhanced in Noy-Meir's model are due to a similar mechanism as in Armstrong's model: the competitively superior species is more sensitive to predation. Coexistence of strongly predation-regulated herbivores, in turn, is trivial if they are so different in body size that they cannot be preyed upon by the same predator. As there is a large span of feasible body sizes available for herbivores, predation-regulated herbivore communities should be relatively diverse along the size axis. Similar-sized, nocturnal prey sharing the same habitat are easily perceived as identical. Then, the prey with the highest *r*/*a* ratio will exclude the others, even if feeding niches were totally different (Holt, 1977; Noy-Meir, 1981). Differences in habitat use may permit coexistence of similar-sized prey, but even this cannot be taken for granted (Holt, 1984, 1987).

The change from a narrow guild perspective to broader community perspective thus changes predictions on interspecific coexistence. Predation-structured communities of productive ecosystems should harbour granivores and large numbers of coexisting selective grazers, with different body sizes but similar feeding niches. Possibilities for interspecific coexistence are much more limited in habitats with strictly resource-limited grazers. Notice also that there does not seem to be any unquestionable predation equivalent for the famous intermediate disturbance hypothesis (Grime, 1973; Connell, 1978), stating that maximum diversity is obtained at moderate levels of disturbance. Apparently, the Grime–Connell mechanism requires non-equilibrium conditions where disturbance starts local successions which are out of phase with each other.

Does it work? Relation to changes in the structure of the herbivore community from tundras to temperate forests

Productivity clines due to changes in temperature are ideal for testing the predictions, because changes in the abundance of annual plants do not confound the picture. Starting from high-arctic areas, we find grazer communities obviously structured by competition for winter resources. In the winter, graminoids are eaten by muskoxen (*Ovibos moschatus*) or by the high-arctic reindeer/caribou (*Rangifer tarandus*). Their winter niches are slightly different: muskoxen eat even arctic willows, while high-arctic reindeer utilize mosses at least as emergency winter food (Tener, 1965; Hubert, 1977; Thomas and Edmonds, 1984; Tyler, 1987). Coexistence between reindeer/caribou and muskoxen is nevertheless precarious. Northeastern Devon Island, Ellesmere Island and northernmost Greenland have muskoxen but not caribou (Tener, 1965; Hubert, 1977), while the converse situation prevails in the eastern parts of the Canadian arctic archipelago (Thomas and Edmonds, 1984) and in Svalbard (Tyler, 1987). Muskoxen were introduced to Svalbard in 1932 and thrived until the early 1970s. Then, as the local reindeer population recovered, muskoxen went extinct, apparently because of competition for winter food (Klein and Ståland, 1984).

Other herbivores have subordinate roles. Collared lemmings (*Dicrostonyx* species) are locally abundant in snowy habitats unsuitable for the digging ungulates (Fuller *et al.*, 1977). Ptarmigans (*Lagopus mutus, L. hyperboreus*) feed on the heavily defended dicots of windblown ridges (Lövenskiöld, 1964; Cramp and Simmons, 1980). Arctic hares (*Lepus arcticus*) seem to be largely confined to nunataks and to small, isolated 'oases' in polar deserts which the ungulates cannot exploit (Smith and Wang, 1977).

In the middle arctic zone, the somewhat higher winter precipitation (Walter *et al.*, 1975) favours burrowing grazers, but the general idea of grazer communities structured by resource competition (MacArthur, 1972) applies to middle arctic tundras, too. Lowland areas only harbour two overwintering grazers: brown lemmings (*Lemmus* species) exploiting mosses and graminoids; and collared lemmings (*Dicrostonyx* species) utilizing dicots (Batzli *et al.*, 1980; Černjavskij and Tkačev, 1982). In upland areas, lichens are consumed by reindeer (Batzli *et al.*, 1980), and dicots of windblown ridges by rock ptarmigans.

In the low-arctic zone, the diversity of the grazer community is higher. Some differences between middle and low arctic biota can be regarded as directly dependent on physical conditions. For instance, the appearance of parka squirrels (*Spermophilus undulatus*) and singing voles (*Microtus gregarius, M. miurus*) (Ognev, 1928–56; Bee and Hall, 1956; Batzli *et al.*, 1980; Batzli and Henttonen, 1990) can be attributed to the direct impact of higher summer temperatures. (Soils thaw deeper, thus allowing the construction of ground squirrel burrows. Warm days also favour the haying habit of singing voles.) Other differences between middle and low arctic grazer communities indicate genuinely different assembly rules. The most luxuriant low-arctic habitats are dominated by strictly nocturnal root voles (*Microtus oeconomus*), specialized to high-quality subterranean plant organs (Tast, 1966, 1974; Viitala, 1977; Oksanen and Oksanen, 1981; Batzli and Henttonen, 1990), and by agile, semi-granivorous red voles (*Clethrionomys rutilus*; Henttonen *et al.*, 1977; Oksanen and Oksanen, 1981; Henttonen and Peiponen, 1982; Viitala, 1984). In areas where voles occur, lemmings are normally confined to the less productive parts of the habitat complex, apparently due to high predation pressure in luxuriant willow thickets (T. Oksanen, 1991). The dominating gallinaceous birds are now willow grouses (*Lagopus lagopus*), utilizing browse of relatively high quality, although ptarmigans occur on barren ridges down to the timberline (von Haartmann *et al.*, 1963–72).

In the boreal taiga, the assembly patterns change even further. An example of the composition of the small mammal subcommunity in the Swedish central taiga, based on a twice-a-year trapping record during 1971–88 by Hörnfeldt (1991) (in total: 11 527 specimens) is shown in Table 1; a basically similar pattern can be seen in other long-term records from the northern and central subzones of the taiga (Henttonen *et al.*, 1977, 1987; Mihok and Fuller, 1981; Hörnfeldt *et al.*, 1990). Selective folivores prevail, while wood lemmings are rare and, consequently, mosses remain largely unutilized.

Table 1. The composition of the central boreal small mammal community at Umeå, Sweden, according to Hörnfeldt *et al.*, (1990).

Species	Habit	Percentage of captures
Myopus schisticolor	Broadly folivorous	1.33
Clethrionomys rufocanus	Folivorous	17.44
Microtus agrestis	Folivorous	12.62
Arvicola terrestris	Folivorous, selective	0.02
Clethrionomys glareolus	Folivorous, selective	68.46
Apodemus flavicollis	Granivorous	0.14

The ungulate–lagomorph subcommunity of the taiga is dominated by browsers with largely identical food preferences but widely different body sizes: the moose (*Alces alces*), the roe deer (*Capreolus capreolus*) or some equivalent small cervid (which may be absent in areas with deep snow) and a lagomorph (*Lepus timidus* in Eurasia, *L. americanus* in North America), all preferring aspen, rowan and hanging birch as their winter food (Ognev, 1928–56; Burt and Grossenheider, 1968; Siivonen, 1975). Juveniles of the same trees and shrubs are gnawed by microtine rodents, and buds of adults are consumed by gallinaceous birds. Thus the degree of convergence in winter resource use is high, and many boreal herbivores depend on a resource basis which could be undercut by other consumers. Evidence for predation-controlled population dynamics exists for ungulates (Messier and Crête, 1985) and hares (Sinclair *et al.*, 1988). As in the case of small mammals, ungulates adapted exploit cryptogams as their main winter resource (woodland reindeer/caribou) occur at low densities only, apparently due to the abundance of predators, supported by more predation-resistant alternative prey (Bergerud, 1988).

Besides the two major subcommunities, the boreal zone harbours 'odd grazers' which lack counterparts in the arctic and are characterized by novel ways of dealing with predation. Porcupines (*Erethizon dorsatum*) defend themselves by spines, whereas beavers (*Castor* species) use aquatic habitats as shelter. Their winter food, however, is practically identical with the preferred diet of browsing ungulates and bark-gnawing rodents (Burt and Grossenheider, 1968;

Siivonen, 1975). Pure granivores are represented by common or red squirrels (*Sciurus vulgaris*, *Tamiasciurus hudsonicus*), using conifer seeds that are big enough to make hoarding of winter resources feasible (Smith, 1981).

The transition from the boreal zone to the temperate one in the small mammal subcommunity of Sweden has been thoroughly studied by Hansson (1985a, b, 1987, 1988; Hansson and Henttonen, 1985; Hansson and Jaarola, 1989). The study has taken advantage of the amplifying effect of altitude on latitude in central Sweden, where a relatively sharp limit, called Limes Norrlandicus, thus exists between truly boreal taiga and mixed hemiboreal forests. The purely granivorous wood mouse (*Apodemus sylvaticus*) is rare throughout the true taiga, but immediately south of Limes Norrlandicus, it emerges as a co-dominant of the small mammal subcommunity (Hansson, 1987; Fig. 4). In the same area, a more folivorous race of the bank vole gives way to a more granivorous one (Hansson, 1985b) and also in the field vole, the degree of specialization to high-quality forage increases (Hansson and Jaarola, 1989). In more continental areas, the *Clethrionomys*-dominated taiga community stretches to lower latitudes (Zablodskaja, 1971; Koškina and Korotkov, 1975), as do cold and snowy winters. In temperate areas with mild winters, the small mammal subcommunity of forests is characterized by roughly equal abundance of semi-granivorous bank voles and purely granivorous wood mice (Southern, 1979; Secher Jensen, 1982). In open fields, field voles prevail (Schindler, 1972) and seem to be regulated by predation (Erlinge *et al.*, 1983; Erlinge, 1987), while granivorous mice occur at somewhat lower numbers.

A glimpse of a relatively undisturbed grazer community of temperate forests is provided by the big preserves (formerly hunting parks of noblemen) in Poland. In addition to the above-discussed rodents, the browser-grazer guild of Polish deciduous forests consists of six species – the European bison (*Bison bonasus*), the red deer (*Cervus elaphus*), the fallow deer (*C. dama*), the roe deer (*Capreolus capreolus*), the field hare (*Lepus europaeus*) and the rabbit (*Oryctolagus cuniculus*). Owing to profound sexual dimorphism in temperate ungulates, there are actually 10 distinct size categories of medium-sized to large browsers (rabbit, 2 kg; field hare, 5 kg; roe deer, ♀ 15 kg, ♂ 25 kg; fallow deer, ♀ 40 kg, ♂ 80 kg; red deer, ♀ 100 kg, ♂ 200 kg; and bison, ♀ 500 kg, ♂ 900 kg (Pucek, 1964; Bjärvall and Ullström, 1985)). Differences in feeding ecology are minor; all species can be regarded as browsers with well-developed taste for high-quality food, although the degree of specialization to high-quality food varies, being maximal in the roe deer (see Dzieciolowski, 1970; Borowski and Kossak, 1972; Kossak, 1981; Perzanowski *et al.*, 1986; Krasinska *et al.*, 1987). In addition to browsers, Polish forests harbour large numbers of wild boars (*Sus scrofa*; see Jezierski, 1977), feeding on acorns, tubers, rhizomes and many types of animal food (earthworms, larvae, rodents and carrion; see Genov, 1981).

Corresponding North American communities seem to be essentially similar except that the New World equivalents of wild boars (peccaries, *Pecari angulatus*) have considerably more southern distribution and are absent from temperate, deciduous forests (Burt and Grossenheider, 1968). However, due to the impact of the Rockies, the North American climate is essentially more continental than the European one. In comparable parts of the Eurasian continent, wild boars are also restricted to low latitudes.

Along gradients from temperate lowland forests to higher elevations, the patterns discussed above are reversed. On north–south oriented mountain chains, like the Rockies and the Appalachians, subalpine grazer communities are practically identical with boreal ones, except for especially rugged areas which offer the possibility to escape predators by climbing. This option is exercised, e.g. by the European chamois, *Rupricapra rupricapra*, (Lomnicki, 1961; Wierzema, 1984) and by the American bighorn sheep (Geist, 1971). On isolated mountains, boreal species are often lacking and their niches are occupied by their closest temperate counterparts.

The wintering grazer community of the alpine tundra typically consists of three or four mammals and a ptarmigan. One mammal is a climbing ovid, adapted to graze on windblown ridges. In Europe, this niche is occupied by the ibex (*Ibex ibex*, Hofmann and Nievergeldt, 1972) which has been shown to exclude the chamois by means of exploitation competition (Schröder and Koffler, 1984). In North America, the mountain goat (*Oreamnos americanus*) seems to have a similar niche. Rocky habitats with deep snow are occupied by a small mammal; usually some pika (*Ochotona* species; Ognev, 1928–56; Broadbrooks, 1965; Orr, 1977). However, pikas have been poor in recolonizing glaciated areas (Broadbrooks, 1965), leaving the small mammal niche vacant in some areas, where it has been invaded by some microtine rodent (e.g. the European snow vole, *Microtus nivalis*; see Bjärvall and Ullström, 1985). The third regular inhabitant of the alpine tundra is a marmot (in Europe, *Marmota marmota*; in North America, *M. flaviventeris* or *M. caligata*) which utilizes habitats where summer forage production is sufficiently plentiful to allow the build-up of fat reserves sufficient for hibernation. Mountains where alpine meadows have deep soils usually also harbour an alpine 'gopher' (in Eurasia, *Spalax* species, see Bjärvall and Ullström, 1985; Ognev, 1928–56; in North America, *Thomomys* species, see Burt and Grossenheider, 1968), foraging on the roots and rhizomes of alpine plants.

The grazer community of the alpine tundra is thus structurally similar to its arctic counterpart. All grazers are broadly folivorous and their regional coexistence is allowed by specialization to entirely different types of food, usually accompanied by habitat segregation. As in the case of the arctic (see Batzli *et al.*, 1980), strong impact of natural herbivores on the vegetation seems to be the rule, if native herbivores have not been reduced to remnant populations by human actions (Thorn, 1982; Huntly, 1987; Oksanen and Oksanen, 1989). The differences as compared with the arctic tundra can be interpreted as due to differences in the physical habitat. The fossorial habit and hibernation are possible in alpine areas, whereas the frozen arctic soils preclude the former option and severely limit the latter one. As in some continental low-arctic areas, high summer temperatures favour haying small mammals over lemming-type winter grazers.

The data discussed above suggest that the big change in the assembly rules of the herbivore community takes place somewhere in the low-arctic (low-alpine) or subarctic (subalpine) zone. In the middle and high arctic zones and in their altitudinal counterparts, all major components of plant biomass have their consumers and regional coexistence of two herbivores utilizing similar forage seems only possible via habitat segregation (usually between a small mammal, utilizing snowy habitats and an ungulate utilizing less snowy ones). Within the boreal (subalpine) zone, grazers adapted to low-quality food disappear, while several species can coexist as selective folivores/browsers, provided that their body sizes are sufficiently different or that they have some novel ways of eluding predation (spines, climbing, hiding in ponds) which make attack rates frequency dependent. The next major change, emergence of genuine granivores and omnivores as co-dominants of the herbivore–granivore community, seems to be related to snow-free winter conditions. Apparently, the productivity level required for the shift is reached already in the taiga, but difficulties with finding seeds under the snow limit the advantages of the granivore option.

Exploitation ecosystems revisited

The view of the relation between primary production and the composition and dynamics of the herbivore–granivore community outlined above shows both convergences with and divergences from the purely population dynamical model of Oksanen *et al.* (1981). The two converge in the broad view of how folivore population dynamics are related to primary productivity, but differ in details. Oksanen *et al.* (1981) predicts that herbivores of productive habitats are strictly predator limited and do not respond to enrichment of the habitat or to experimental provision of food. The present model, in turn, predicts that some degree of resource-limitation of herbivores exists even in the most productive habitats and that the equilibrium biomass of herbivores may increase with increased primary productivity and provision of supplemental food.

The magnitude of the response of herbivore biomass to enrichment in three-link ecosystems depends on factors that are difficult to evaluate at the present level of knowledge. If the arms-race view is correct and carnivore interference is insignificant, there will be no response whatsoever. In the absence of predator counter-evolution, the response will depend on the trade-off between the ability to utilize low-quality forage (K) and predator resistance ($1/a$). Assuming no predator counter-evolution, an about four-fold increase in biomass from habitats with strictly resource-limited folivores to areas dominated by selective folivores and granivores would be consistent with Fig. 3. A response of about this magnitude has also been experimentally generated by providing large quantities of high-quality food in a piece of north boreal taiga (Henttonen *et al.*, 1987).

According to Oksanen *et al.* (1981), removal of predators from productive habitats immediately leads to a massive grazer outbreak, accompanied by profound devastation of the vegetation and replacement of competitive plants by grazing-tolerant ones. According to the present model, however, the impact of such a manipulation could be two-staged. In the first stage, the most folivorous community members increase while the most granivorous ones go extinct. Depending on the degree of folivorousness of the most K-strategic species, the vegetation will be influenced to some extent. However, total devastation of the vegetation may require introduction of broad-scale folivores or their dispersal from barren areas.

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