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Author(s): Lauri Oksanen, Stephen D. Fretwell, Joseph Arruda, Pekka Niemela

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EXPLOITATION ECOSYSTEMS IN GRADIENTS OF PRIMARY PRODUCTIVITY

LAURI OKSANEN,* STEPHEN D. FRETWELL,† JOSEPH ARRUDA,† AND
PEKKA NIEMELÄ*

*Kevo Subarctic Research Institute, University of Turku, SF-20500 Turku 50, Finland; †Division of Biology, Kansas State University, Manhattan, Kansas 66506

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Formal studies on trophic exploitation can be traced back to the Lotka-Volterra predation models summarized by Gause (1934). Since Rosenzweig and MacArthur (1963) included the resource-determined carrying capacity of prey in predation models, the development of these models has been rapid. Holling's (1965) study showed how the saturation of predators can be included and Rosenzweig (1969, 1971) related the shape of the prey isocline to the productivity and other characteristics of the prey population. May (1972), Gilpin (1975), and Tanner (1975) have examined the behavior of predator-prey systems without a locally stable equilibrium point. A three-dimensional model able to deal simultaneously with exploitative herbivore-plant and carnivore-herbivore interactions outlined by Rosenzweig and MacArthur (1963) was actually developed by Rosenzweig (1973) and elaborated by Wollkind (1976).

However, the existence of definite predator and prey isoclines is a hypothesis, not a fact. The random predator implicit in exploitation models differs radically from the prudent predator of Slobodkin (1968). It is possible to relax the assumption of completely random exploitation (Rosenzweig 1977). In order to make the isoclines unambiguous the additional assumption is then needed that no significant changes occur in the proportion of the prey population that belongs to the most predation-susceptible age group. Further, it is essential to require that exploitation of victims with a positive reproductive potential occurs. If the exploiter is dependent on some product of a population and unable to affect its production rate, the prey isocline is transformed to a line perpendicular to the prey axis. Such a product could be aged or injured animals (Mech 1966), the social detritus of a population (Errington 1963), or plant organs of sufficiently high quality (Kalela 1962; Tast and Kalela 1971). Other production-regulated trophic interactions may be found in nature. The American mink studied by Errington (1963) does not seem an exceptionally inefficient carnivore. Some species that look like ordinary herbivores have turned out to be critically dependent on the quality of their resources

(Baltensweiler et al. 1977; Haukioja et al. 1978). Drawing on such observations White (1978) has presented a general theory of ecosystem structure, arguing that almost all populations are resource limited and that the significance of trophic exploitation is negligible.

Yet, there is empirical evidence that points toward the opposite direction. The *Opuntia* plague of Australia was eliminated by introducing a herbivore coevolved with cacti (see e.g., Krebs 1972, pp. 367–369). Reindeer have dramatic impact on vegetation when their densities are allowed to expand (Höglund and Eriksson 1973), and problems of overgrazing (i.e., strong impact of utilizer upon the utilized populations) are common enough to invite the application of exploitation models to range management (Noy-Meir 1975). For a proponent of White's hypothesis, the fact that depletion of prey is a common outcome of laboratory studies on trophic relationships (see references in Rosenzweig 1969, 1977) must also appear puzzling.

When stating that the quality of most plant material is too low to support herbivores, White (1978) neglected the possibility that a feeding strategy evolves which is energetically wasteful but ensures a sufficient rate of intake of limiting nutrients. Aphids are the clearest example of this, but low ecoenergetic efficiency accompanied by an ability to subsist on low-quality forage is found in diverse group of animals, e.g., sawflies (Haukioja and Niemelä 1974), lemmings (Batzli 1975) and zebras (Bell 1971).

The basis of the “prudent predator” hypothesis is not quite solid, either. Slobodkin (1974) maintained that the diversity of prey and the diversity of their antipredator strategies exceeds the diversity of predators. Thus, carnivores are exposed to conflicting selective pressures giving the prey an edge in the race to capture and to avoid being captured. Cohen's (1977) review does not support this statement. Perhaps herbivores are more troubled by conflicting selective pressures. Adaptations that make a herbivore an elusive prey (fleetness) or a submergent one (restricted and nocturnal activity period; see Maiorana [1975] for further discussion) conflict with ones required in efficient utilization of forage (large digestive tract, long activity period).

This discussion suffices to show that the importance of trophic exploitation is an open question. Arguments and counterarguments can be found, but such debate hardly leads anywhere. It appears more useful to state some set of assumptions (admitting that they may turn out to be unrealistic), to analyze their logical consequences, and to compare these with data. If the data and the predictions match, the plausibility of the assumptions is improved (Tricker 1965). If they conflict, this helps us replace them with better ones. It is indeed possible that correspondence between observations and predictions is just good luck, and the construction of meaningful null hypotheses may be impossible. This may be regarded as a reason to use the inductionistic approach, where the probability that chance alone is responsible for the results can be assessed by means of standard statistics. The merits of inductionism may be appreciable in young branches of science where new sets of data have a good chance to make all hypotheses obsolete. It appears, however, that if a branch of science is to develop beyond the initial stage it has to start using the hypothetico-deductive method. Predictions

and tests with all their problems seem to be the only way to differentiate useful general statements from useless ones (see Lakatos 1972).

TOWARD A TESTABLE HYPOTHESIS OF EXPLOITATION ECOSYSTEMS

Few predictions can be deduced solely from the assumption that there are exploitative relationships between populations. In order to obtain a theory with some predictive power, it is imperative to link the isocline shapes with environmental variables. This approach has been pioneered in Rosenzweig's (1971) Paradox of Enrichment. Rosenzweig assumes that an increase in primary productivity expands the isoclines of prey species. He thus suggests that there is a simple connection between an ecosystem-level phenomenon and properties of individual populations. However, the analysis was performed before Rosenzweig (1973) developed his three-dimensional exploitation model which allows an explicit consideration of the dual role of herbivores—as predators of vegetation and as prey of carnivores. Hence the robustness of the result (that enrichment leads to destabilization) can be questioned.

A simple connection between ecosystem-level units (trophic levels) and individual populations was also assumed to exist in the paper of Hairston et al. (1960). In a debate with Murdoch (1966) and Ehrlich and Birch (1967), Slobodkin et al. (1967) appeared able to demonstrate that the proposition qualifies as a scientific hypothesis. Yet, relatively little has been built on that basis, possibly because of another question discussed by the above cited critics: Is it meaningful to use trophic levels as ecological units?

Indeed, nature is not divided into perfectly distinct trophic levels, but it is not divided into perfectly distinct local populations, either. The appropriateness of an abstraction depends on the problem to be studied. If one wants to deduce empirical consequences from the assumption that trophic interactions are exploitative, the auxiliary assumption that trophic levels can be treated as homogenous units is inviting. Exploitation models deal with populations that make linear food chains, whereas overlapping resource utilization and branched food chains appear common in nature (see e.g., Wiegert and Odum 1969). The possibility that other populations would start to utilize the resources of a strongly predator-limited prey creates profound evolutionary problems (Van Valen 1973). If we treat trophic levels as units, then, by definition, food chains are always linear and alternate utilizers cannot exist. Such an assumption also appears realistic enough to be potentially useful. Even if all organisms must be assumed to maximize their expansive energy by using whatever resources are available (see Van Valen 1975), photosynthesis, utilization of vegetative plant organs, and carnivory require adaptations too different to allow an individual organism to be efficient in more than one of these ways of energy intake. This discontinuity also implies relative homogeneity within each trophic level. Competition within resource-limited trophic levels should make the sum of utilization curves match the distribution of resources (MacArthur 1972, pp. 59–69), so that a rather homogenous exploitation pressure should be exerted upon the populations on the level below.

In a more abstract form the core of Hairston et al. (1960) can be phrased as

follows. Trophic level B could severely decrease the density of populations on trophic level A, but the impact of trophic level C upon B prevents this from happening. However, is there any reason to interpret A, B, and C, respectively, as plants, herbivores, and carnivores? Fretwell (1977) asked this question and answered it negatively. He noted that the essential characteristic of C is that it is not exploited, but trophic level C's distance above the base of food chains cannot be fixed. Instead, Fretwell proposed that the distance depends on the rate of primary production and on the average ecological efficiency among consumers. Fretwell thus assumed that, given constant ecological efficiencies, increased primary productivity is both a necessary and a sufficient condition for the lengthening of food chains. While the first point appears clear and logical, the second one does not necessarily conform with implications of the exploitation approach. If we accept the idea that populations and trophic levels may be predation limited we must also be prepared to see situations where increased primary productivity does not pass smoothly to the top of the food chains. The more an ecological unit is limited by predation the less its standing crop can respond to an increased productivity of resources. Even the increase in its productivity is bounded by physiological constraints on turnover rate.

In order to remedy this problem, we now apply graphical predation models in the conceptual framework provided by Hairston et al. (1960) and Fretwell (1977). The densities (live mass per unit area) of plants (P), herbivores (H), and carnivores (C) are dimensions of our model (as in Rosenzweig [1973]). A fourth dimension, assumed to be the ultimate regulator of the system, is the maximum gross primary productivity allowed by the environment (G) which will be called "potential productivity" below. This formalization can be equally well regarded as a reanalysis of Rosenzweig's (1971) Paradox of Enrichment looking at a wider range of productivities, using the more powerful tool of three-dimensional exploitation models and considering the possibility that carnivores may be preyed upon by secondary carnivores.

PLANT ISOCLINE AND POTENTIAL PRODUCTIVITY

In the three-dimensional predation model of Rosenzweig (1973), plants are assumed to compete directly with each other for some resources which set an upper limit to their density. Because a similar growth curve is obtained if plants are limited by the amount of heterotrophic plant tissue that can be maintained with the maximum rate of photosynthesis allowed by the environment (which may be a more realistic assumption for terrestrial vegetation), we accept Rosenzweig's assumption as a technical shorthand. Rosenzweig (1973) further assumed that plants are not directly harmed by low density (no true Allee effect) and that herbivores are saturated at high plant densities (with a consequent technical Allee effect for plants). We include these assumptions and further assume that herbivore saturation occurs in accordance to Holling's (1965) type II functional response curve. (As we deal with trophic levels, alternate prey cannot exist; thus, type III functional response is not plausible.) Our final assumption about plants is that, in the absence of significant herbivory, their expansion conforms to the logistic

growth curve. Given this, the rate of change in plant density can be described by Tanner's (1975) equation for the growth rate of prey:

$$\frac{dP}{dt} = rP(1 - P/K) - wPH/(D + P) \quad (1)$$

where P = plant density, r = intrinsic growth rate of plants, K = maximum density of plants in the absence of herbivory, H = herbivore density, w is the maximum foraging rate of an individual herbivore, and w/D is its rate of searching when unsaturated (see Holling 1965; Tanner 1975). From equation (1) the (zero) isocline of plants can be obtained by setting $dP/dt = 0$ and solving for H as

$$H(P) = \frac{-r}{wK} P^2 + \frac{r(K - D)}{wK} P + \frac{rD}{w}. \quad (2)$$

Equations (1) and (2) are biologically meaningful only when P is positive. If there are no plants ($P = 0$), their rate of change would be determined by immigration and survival of propagules which is not included in our model. Note also that $H(P)$ can be zero only once on the positive side of the P -axis (when $P = K$). When P approaches zero, $H(P)$ approaches rD/w which is positive.

Let us examine the conditions under which the plant isocline is humped (has a local maximum when $P > 0$). By differentiating equation (2) we obtain

$$\frac{dH}{dP} = -\frac{2r}{wK} P + \frac{r(K - D)}{wK} \quad (3)$$

which is zero when $P = (K - D)/2$. Thus the necessary and sufficient condition for the hump is that $K > D$. What does an ecosystem look like which is at the limit of meeting this condition (i.e., $K = D$)? When the last term in equation (1) is divided by H , the consumption rate of an individual herbivore (R , which can be also interpreted as the rate of energy flow per unit of herbivore biomass) is obtained as

$$R(P) = \frac{wP}{D + P} \quad (4)$$

Assume further that $P = K$ (i.e., there are so few herbivores that plants are allowed to reach a density very close to resource-determined carrying capacity). Then $P = K = D$ and $R = w/2$. Since w is the maximum foraging (capturing) rate of herbivores (see above), an ecosystem where the plant isocline is at the verge of being humped should be so sparsely vegetated, because of the adversity of the physical environment, that even if herbivores entered a previously ungrazed area, they would have to spend as much time in searching for food as in feeding activities.

In more productive environments, the plant isocline is humped. The height of the hump is obtained by substituting $P = (K - D)/2$ into equation (2) and solving for H as

$$H_{\max} = \frac{r(K - D)^2}{4wK} + \frac{rD}{w}. \quad (5)$$

Now, we need to express K and r as functions of potential productivity (G). For K

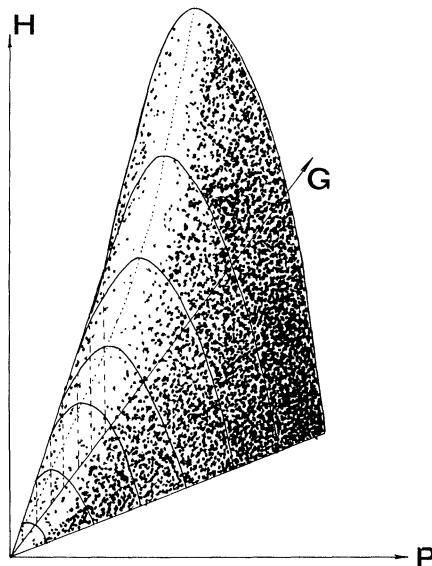


FIG. 1.—The shape of the plant isocline (horizontal axis, plant density; vertical axis, herbivore density) along a gradient of potential primary productivity (G). The ridge, formed by the humps of individual plant isoclines, is presented as a line of small dots.

this is easy: The amount of living protoplasm that can be maintained is directly proportional to the rate of photosynthesis. In plants, r is just another expression for the net productivity/biomass-ratio in early stages of secondary succession (when the plant cover is not yet closed). Hence, it appears reasonable to assume that r is directly proportional to G , too. This discussion and equation (5) yield equations (6) and (7):

$$H_{\max} = aG^2 + bG + c \quad (6)$$

where a , b , and c are positive constants and

$$K = kG \quad (7)$$

where k is a positive constant. Figure 1 presents this relation between the shape of the plant isocline and potential productivity. Note that the height of the isocline increases quadratically with increasing potential productivity, whereas the maximum density of phytomass, K , increases linearly.

In predation models, it has been customary to use the expressions biomass, amount of living protoplasm, or amount of edible material as if they were synonymous. Indeed, they are not, nor does the logic of the model require it. The model does require that density be expressed in units that are proportional both to the amount of living protoplasm and to the amount of edible material. If predation models are used in some cases of particular herbivore-plant interactions (as in Noy-Meir 1975; Caughley 1976), the ordinary interpretation of phytomass may pass this criterion. But in a general model we must define phytomass as the amount of herbage (grasses and herbs, leaves, shoot tips and phloem of woody

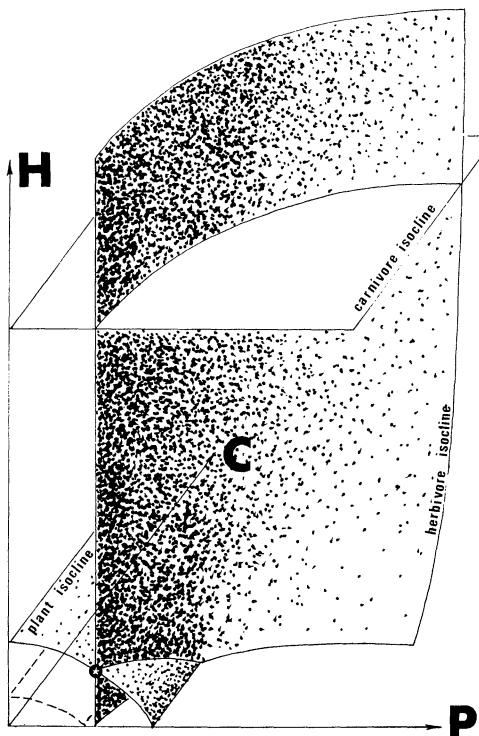


FIG. 2a.—Carnivore (C), herbivore (H), and plant (P) system at different points of the productivity (G) axis. Unstable equilibrium is a solid dot; stable equilibrium is a dot with a star. An unproductive system where the plant isocline (the rightward sloping surface) remains well below the carnivore isocline. The herbivore isocline (the surface bending backwards from the plane of the page) crosses the plant isocline on the right side of its hump and in the $C = 0$ plane, creating a stable herbivore-plant equilibrium.

plants) per unit of area. Wood is to be considered accumulated organic material, equivalent to peat in bogs, and not a constituent of phytomass at all.

CONSUMER ISOCLINES AND THE PREDICTED CHARACTERISTIC OF COMMUNITIES

Our model includes climate only indirectly, as one of the factors explaining the variation in potential productivity. The shape of consumer isoclines is made constant, because we assume that consumers are adapted to the climate in which they live and that costs of this adaptation are just a minor factor in the energy budget of consumers. We also make the implicit assumptions of Hairston et al. that territoriality does not limit the total density of any trophic level, that any effect of interference is insignificant within the trophic level as a whole and that no true Allee effect exists (see Caughley 1976). Finally, the consumption rate of herbivores and carnivores is assumed to conform to Holling's (1965) type II functional response curve and assimilation rate is assumed directly proportional to consumption rate.

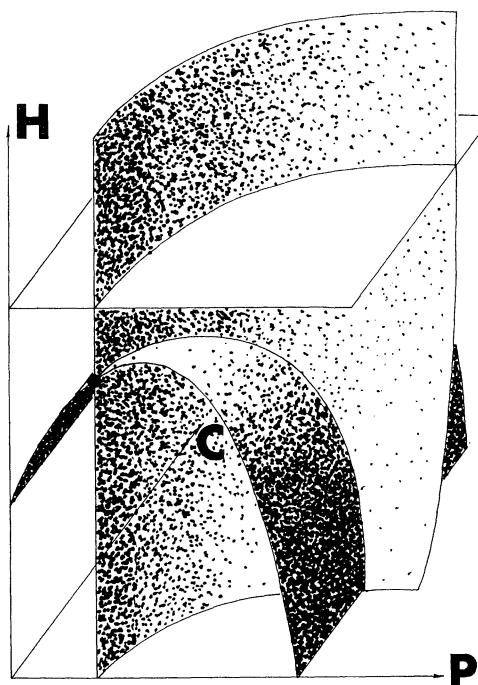


FIG. 2b.—A system where the potential primary productivity has twice the value it had in fig. 2a. The herbivore-plant equilibrium is unstable, so that sustained cyclic changes in plant and herbivore density are to be expected. Symbols as in figure 2a.

The consumer isoclines thus become similar to those in the simplest version of three-dimensional predation models proposed by Rosenzweig and MacArthur (1963) except that the herbivore isocline meets the plane of zero herbivore density along a line where the C -coordinate is an asymptotically increasing function of P (fig. 2). (Bending the isocline to the $C = 0, H = 0$ line, as done by Rosenzweig and MacArthur, implies a true Allee effect.) The carnivore isocline is a plane perpendicular to the H -axis. The herbivore isocline is a surface bending from the $C = 0$ plane in the direction of the C -axis, its C -coordinate being an asymptotically increasing function of P and a monotonically increasing function of H .

Imagine that figure 1 is sliced with a vast number of planes perpendicular to the G -axis, the plant isoclines thus obtained are combined with the consumer isoclines and the resulting set of three-dimensional pictures is presented as a movie. We then see a continuous gradient of ecosystems, but no amorphous continuum. Instead there are distinct break points where one trend is suddenly replaced by another one. Some scenes of this movie are presented in figure 2, and the predicted pattern of phytomass is summarized in figure 3.

In the least productive ecosystems (fig. 2a, dotted line, and interval $G < g_0$ in fig. 3), the plant isocline does not meet the herbivore isocline, and there is no grazing chain in the ecosystem. The P/G ratio is constant. With increasing potential productivity, the plant isocline reaches the herbivore isocline, and a stable

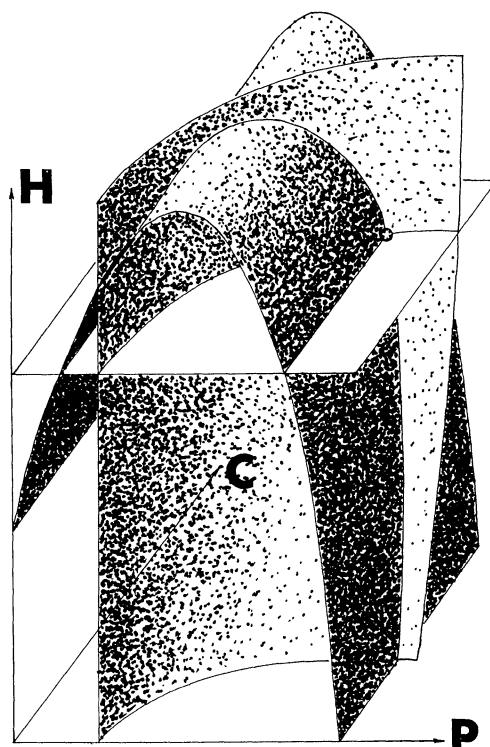


FIG. 2c.—The potential productivity is 1.25 times that of the system in fig. 2b. A locally stable carnivore-herbivore-plant equilibrium has been established. Symbols as in figure 2a.

herbivore-plant equilibrium is established. We now enter an interval (fig. 2a, interval $g_0 < G < g_1$ in fig. 3) where increased potential productivity only increases the equilibrium density of herbivores and their impact on vegetation. The phytomass remains constant. In communities with a high average ecological efficiency, the intersection of plant and herbivore isoclines can pass above the carnivore isocline before it reaches the hump of the plant isocline or even before such a hump is formed. It is also possible that the hump is reached first. Then, we would have an interval where no stable equilibrium point exists (fig 2b, interval $g_1 < G < g_2$ in fig. 3). In the less productive part of this interval, herbivores cycle with plants but may cross the carnivore isocline during phases of high density. Thus, the system may support nomad carnivores such as the snowy owl (*Nyctea scandica*) and jaegers (*Stercorarius spp.*) which move around searching for areas with high herbivore densities or survive in other kinds of ecosystems during phases of low herbivore density. As potential productivity increases further, the carnivore isocline is passed, a still unstable carnivore-herbivore-plant equilibrium is established and the role of carnivores as proximate regulators of herbivore density becomes successively more important.

Our herbivores are assumed to exhibit weak "technical mutualism" (because of

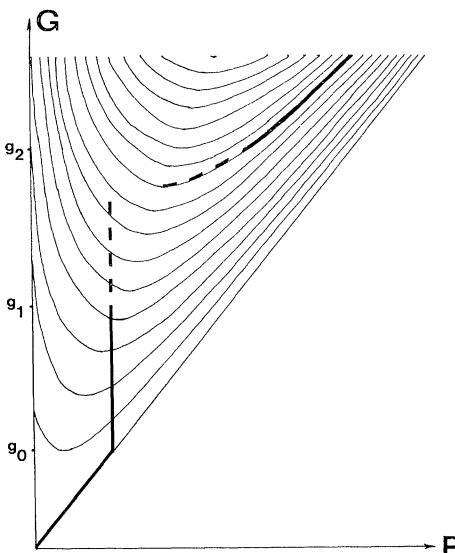


FIG. 3.—A contour map presentation of the herbivore-plant-productivity system of figure 1. The contours represent herbivore densities on the plant isocline. The path of the equilibrium point is a solid line when the equilibrium is locally stable and a dashed line when it is unstable.

carnivore saturation and lack of significant interference) at all densities. Hence the steepness of the plant isocline at the carnivore-herbivore-plant equilibrium must exceed some minimum before the triple equilibrium (fig. 2c) can be stable (Rosenzweig 1973, pp. 285–288). This occurs at $G = g_2$ (fig. 3). In more productive environments, we see stable herbivore populations, subjected to heavy carnivory but without a shortage of resources, which seems to correspond to the ideas of Hairston et al. The relation between equilibrium phytomass and potential productivity is nearly linear again and, as the potential productivity further increases, an ever decreasing fraction of primary productivity will be used by grazers (fig. 2c, interval $G > g_2$ in fig. 3). However, this scenario is conditional. If the technical mutualism among herbivores is strong enough, the three-link equilibrium point will not be stabilized and population cycles persist. Their characteristics just change from cycles in which both carnivory and depletion of vegetation are important (see Keith 1974) to relatively pure carnivore-herbivore cycles.

So far, our model has rather faithfully reiterated most conclusions of Fretwell (1977), demonstrating that the ambiguities of his approach are rather unimportant in the lower end of a productivity gradient. The main difference is that our model fails to generate the fluctuating patterns of phytomass, predicted by Fretwell. In the interval $g_0 < G < g_2$ the increasing trend in equilibrium phytomass is stopped but not reversed.

Fretwell (1977) predicted that increased primary productivity will eventually allow the formation of a fourth trophic level, with consequent relaxation of primary carnivory and intensification of herbivory. In our model this is conditional, too. The intersection of the herbivore isocline with any plane of constant

herbivore density is a line where the C -coordinate is an asymptotically increasing function of plant density (see fig. 2). The isocline of primary carnivores belongs to this set of planes, and the C -coordinate of the equilibrium point thus increases asymptotically with increased potential productivity. As a consequence, the equilibrium density of primary carnivores may eventually reach the predator isocline of secondary carnivores but may also remain below this isocline forever. The stability analysis of Rosenzweig (1973) shows that as the plant isocline becomes very steep at the three-link equilibrium, exploitation ecosystems with herbivores exhibiting technical mutualism become destabilized again. Thus noninterference exploitation ecosystems where the constellation of consumer isoclines prevents the formation of equilibria with four trophic levels seem to be subjected to the destabilization-by-enrichment effect discussed by Rosenzweig (1971).

What types of isocline constellations could occur? This depends on the ecological efficiency (production/consumption ratio) of saturated herbivores, which limits the degree to which herbivores can respond to increased abundance of resources. We expect that terrestrial food chains may belong to the latter category (three links forever), whereas aquatic ones represent the former one (lengthening to four links).

If we assume that the equilibrium density of primary carnivores in the ecosystem represented by figure 2c is at the verge of reaching the predator isocline of secondary carnivores, then how would an infinitely small increase in potential productivity influence its structure? In our model, the impact of the top trophic level is to prevent the density at the lower level from increasing. Thus, the C -coordinate of the new equilibrium point with four trophic levels must remain the same as that of the three-link equilibrium point. Further, the new equilibrium point must belong to plant and herbivore isoclines. We now insert a plane perpendicular to the C -axis through the three-link equilibrium point in figure 2c and look for a point where the lines of intersection between this plane and plant and herbivore isoclines (fig. 4) meet each other. The alternative equilibrium point appears at considerably greater herbivore density and lower plant density as compared to the three-link equilibrium point. With the slightest increase in potential productivity, the three-link equilibrium point passes behind this plane and is no longer acceptable. The four-link equilibrium point remains in this plane and, with further increase in G , climbs along the herbivore isocline, the equilibrium herbivore density keeps increasing and the plant density keeps decreasing.

Instead of secondary carnivores there may be facultative secondary carnivory. This seems probable in all food chains where herbivores and carnivores have similar sizes. Secondary carnivory can be treated as an extreme form of interference within the carnivore trophic level. Following Wollkind (1976) it seems that the rise in equilibrium density of herbivores would then be more gradual than that caused by a distinct fourth trophic level. The stability of the equilibrium would be enhanced.

THE MODEL AND REAL ECOSYSTEMS

In the previous section we saw that the model allows the existence of several alternative ecosystem states. Without some numerical assumptions we cannot

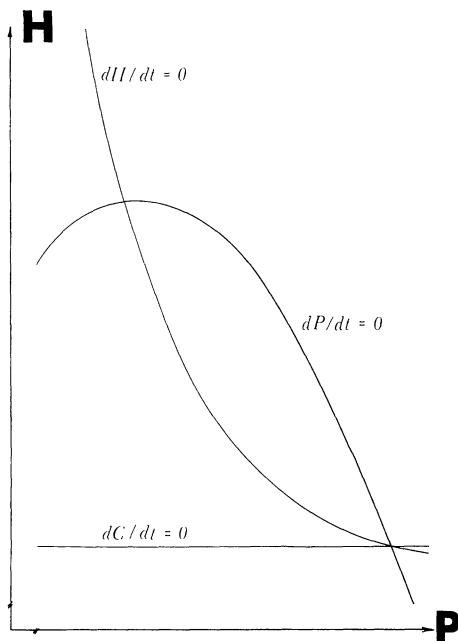


FIG. 4.—The intersections of plant, herbivore, and primary carnivore isoclines with the predator isocline of secondary carnivores (which can be imagined as a plane perpendicular to the C-axis, inserted in figure 2c through the equilibrium point of the system).

predict which one should be observed. Fortunately, also some unambiguous predictions are created. Elimination of the top trophic level or its absence because of barriers of dispersal should have a radical impact on the lower ones. In any continuous productivity gradient extending from very unproductive environments (deserts or arctic-alpine boulder fields) to relatively productive ones (e.g., broad-leaved forests), a zone characterized by intense natural grazing pressure must be found. The relationship between (equilibrium) phytomass and primary productivity along such a gradient is predicted by the model (fig. 3). We now compare these predictions to existing data.

It is a common observation of aquatic ecologists (e.g., Hrabaček 1962; Brooks and Dodson 1965; Svärdson 1976) that the presence of efficient planktivores has a dramatic impact upon the constitution of the zooplankton, as our hypothesis requires. Svärdson also notes that, besides barriers of dispersal, the composition of the planktivore community (the third trophic level) is influenced by temperature and nutrient content, the main factors determining the potential productivity of Fennoscandian lakes. He further suggests that the impact of planktivores does not stop at the second trophic level; that the decreased density of zooplankters causes increased density of phytoplankton and, consequently, increased actual primary productivity. As tentative evidence for this, he presents statistics for commercial catches showing that, at a given nutrient content, the lakes inhabited by the most efficient planktivores tend to be the most productive ones. He further notes that:

. . . the ultimate evidence, of course, is that derived from the same body of water in a normal state and

later, when its fish fauna has been eradicated. Such an experiment was recently performed in the small lake, Stocklidsvattnet, in south-western Sweden. . . . After the [eradication] treatment, alkalinity fell, visibility was doubled and the primary productivity per hour sank from 15–20 mg C/m³ in 1973 and 8–12 mg C/m³ in 1974 to only 1–3 mg C/m³ in 1975. . . . In Lake Stocklidsvattnet the fish fauna was dominated by roach, which was then ultimately responsible for a primary organic production several times higher than when the same body of water was not inhabited by any fish. (Svärdson 1976, pp. 165–166)

Lake Stocklidsvattnet may have its terrestrial counterpart on the Kaibab plateau. There, the third trophic level was also strongly decimated, the apparent result being an expansion of herbivores, decrease of phytomass, and the establishment of a new equilibrium at lower plant and herbivore densities (Rasmussen 1941). Unfortunately, the original data are rather vague (see Caughey 1970). While admitting this, we cannot see why alternate hypotheses, derived from equally vague data, should be considered more credible.

On Isle Royale, the moose population irrupted before the immigration of wolves. The irruption was followed by resource depletion and decline of the moose population. After the establishment of a large wolf pack in the fifties the moose density has been relatively high, but no real irruption has occurred (Mech 1966).

The littoral communities of the Aleutians provide the most solid case to look at. In the absence of sea otters, populations of sea urchins are dense and kelp beds are almost eliminated. Recently, the sea otter has been re-established in littoral communities of some islands with consequent decrease in the density of sea urchins and dramatic increase in kelp density. The existence of treatments and controls makes the significance of predation by sea otters almost certain (Simenstad et al. 1978).

We now turn our attention to observed patterns of biomass in gradients of primary productivity. Fretwell (1977) emphasized that in relatively unproductive parts of the moisture-controlled productivity gradients of the central U.S. (from Sonoran desert to shortgrass prairies), phytomass does not appear to expand with increasing primary productivity, whereas the abundance of graminids appears to increase, suggesting intensification of grazing pressure.

The data provided by Whittaker and Niering from Sonoran deserts (1975), USA/IBP Grassland Biome data (Sims and Coupland 1979) and Hulbert's (personal communication) data from Konza Prairie confirm this impression. The aboveground phytomasses of desert communities range from 0.39 to 1.31 kg/m². On desert grassland Whittaker and Niering reported that aboveground phytomass was 0.26 kg/m² whereas the average peak aboveground biomass of the corresponding IBP site only was 0.13 kg/m². On IBP sites representing shortgrass and northern mixed prairies corresponding values ranged from 0.10 to 0.18 g/m². The average peak above ground biomasses of tallgrass prairie were again higher (0.29 g/m² on the IBP Osage site, from 0.33 to 0.50 on Konza, all values refer to sites not grazed by cattle during the study period). The range of primary productivities is about from 0.1 to 1 kg m⁻² year⁻¹.

This pattern in peak aboveground phytomass looks almost too encouraging to be true. (The decrease in aboveground phytomass from deserts to shortgrass

plains is readily understandable, because the dominance of woody plants decreases, too.) However, a look at the grazing chain reveals problems. What is left from the natural grazing chain of grasslands mainly consists of invertebrates and among them, there is no clear relationship between trophic structure and primary productivity (Dyer 1979). Carnivores are abundant even on the desert grassland site, and this appears to be the case in true deserts too (S. J. Chaplin, personal communication). If natural grazers ever were important, they must have been the big ones that are now extinct or at very low densities in most remaining grassland areas, most of their niche being taken over by cattle. As cattle had been excluded from the IBP sites discussed above, the proposed impact of grazing must have been largely evolutionary. (Plants allocating most of the production below ground had a selective advantage.) Since this interpretation depends on uncertain assumptions about the past, the case of grasslands must be regarded as inconclusive.

The IBP data are also available from the temperature-controlled arctic productivity gradient (Bliss and Wielgolaski 1973; Rosswall and Heal 1975). The information on consumer biomass is fragmentary, but predictions referring to patterns of phytomass can be tested.

In the arctic-subarctic communities represented in the material (fig. 5), potential grazers of vascular plants are present. The vascular plant data (solid figures) conform with the relationship between equilibrium phytomass and productivity predicted in figure 3. The slight discrepancies (too much phytomass in the two polar semideserts of Devon Island and in the unproductive boreal bog; the steep rise of biomass in the most productive communities) are understandable because IBP data include wood in phytomass whereas our model does not. The pattern of total phytomass (open figures) is remarkably different, the Devon Island data points showing a steep and apparently linear rise of phytomass in response to increased primary productivity. However, most of this phytomass consists of moss. A geographical barrier (a barren, partially glaciated highland) isolates the study area from the range of brown lemmings (*Lemmus*) adapted to graze moss. Hence, this discrepancy actually conforms with the predictions.

The extremely isolated antarctic islands provide excellent cases to study how the absence of parts of the grazing chain influences patterns of phytomass. As a point of reference, the expected phytomass-versus-productivity curve of fig. 5 is used. We predict that data points from relatively unproductive communities without grazers are far above the line whereas those from more productive communities with grazers but without significant carnivores should be below it. The IBP data (fig. 6) behave in accordance with this prediction. Signy Island communities without herbivorous vertebrates have much more phytomass than correspondingly unproductive arctic communities (with herbivores), whereas the productive Macquarie herbfield is far below the line. On Macquarie there are introduced rabbits, and native carnivores (skuas) are probably rather inefficient rabbit predators. The introduced feral cats appear inefficient, too (unable to enter rabbit burrows). The South Georgia data points fit the line rather well, and the situation (introduced reindeer hunted by the crew of the local whaling station) allows the establishment of a semblance of a three-link ecosystem. However, the whaling station has been closed since the early 1960's and, according to the theory

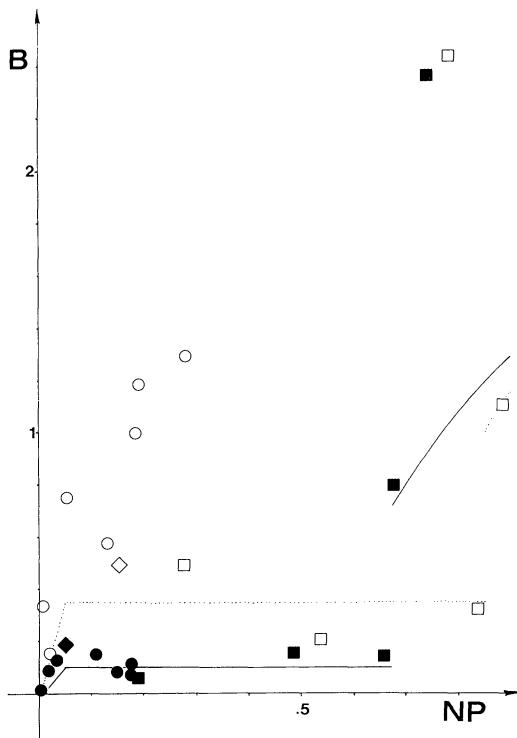


FIG. 5.—Plant communities of some arctic-subarctic IBP Tundra Project study areas, chosen on the basis of availability of data. Horizontal axis: net primary productivity (NP, kg dry wt m^{-2} year $^{-1}$), vertical axis: peak aboveground biomass (B, kg dry wt m^{-2}). Dots = Devon Island data points (a polar desert; two polar semidesert communities [cushion plant lichen, cushion plant moss]; three moist-to-wet meadows). Squares = Hardangervidda data points (lichen heath; dry meadow; wet meadow; willow thicket; birch forest). Diamond = Abisko data point (dwarf shrub; cottongrass bog). The expected pattern, derived from figure 3, is shown as a line (solid for vascular plants, dotted for the whole vegetation). Further explanation in the text.

the departure of the carnivore should lead to a strong increase in herbivore density and to consequent changes in the vegetation of the most productive biotopes. The report of the IBP team (in Rosswall and Heal 1975) conforms with this: Reindeer density is said to be increasing; local replacement of the giant tussock grass, *Poa flabellata*, and the shrub, *Acaena magellanica*, by light swards of *Poa annua* has occurred. Also these data suggest that mammalian grazers are the ones that make a difference.

In continuous polar productivity gradients, biomass patterns appear to conform to figure 3 and the isolated areas deviate from this pattern in the predicted way. Indeed, the data points are so few that the observed fit can be coincidence. Thus, we suggest two further observations that one should be able to make if the fit is a real one.

1. Since most mammals have difficulty crossing water barriers, we should find

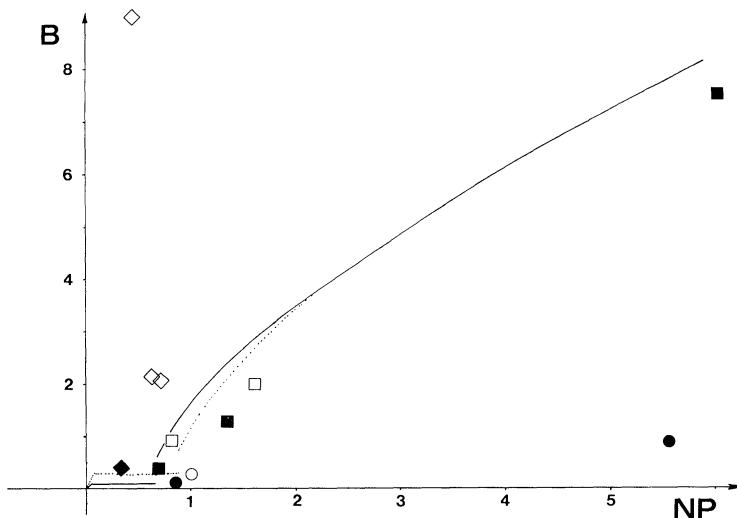


FIG. 6.—Plant communities of antarctic-subantarctic IBP study areas chosen and plotted as in figure 5. Diamonds = Signy Island data points (three moss banks [without vascular plants]; *Deschampsia antarctica*, meadow [vascular plant data only]). Dots = South Georgia data points (*Festuca contracta*, meadow; *Acaena magellanica*, shrub; stand of *Poa flabellata*). Squares = Macquarie data points (herbfield; *Poa foliosa*, grassland). In the two most productive communities, the share of cryptogams is negligible, so that total and vascular plant data could not be plotted separately.

situations resembling those of antarctic and subantarctic islands from arctic and boreal islands isolated by smaller stretches of sea. Because carnivores have much lower population densities than herbivores the risk of local extinction can also be expected to be much higher for carnivores (see MacArthur 1972). Thus, moderately isolated islands can be expected to be largely devoid of carnivores, but have the herbivore trophic level intact. Strongly isolated islands should not have mammalian grazers, either. Cases of the former type are predicted to resemble Macquarie (even relatively productive communities being subjected to heavy herbivory); those of latter type are predicted to resemble Signy (massive plant cover even on relatively unproductive sites). The outer islands of the Baltic Sea are moderately isolated. Corresponding to predictions, extremely high hare densities and depletion of vegetation has been observed (Häkkinen and Jokinen [1974] and references therein). The islands of Spitsbergen are high arctic and strongly isolated. Lemmings are absent whereas wild reindeer are present. Consequently, we predict that the islands should have massive moss banks whereas the lichen grounds of the main island should be strongly depleted and that the reindeer has, at least to some extent, started to utilize the more abundant moss resources.

2. A comparison between figure 9 and figure 6 suggests further observations referring to population cycles. In areas where the annual net aboveground productivity ranges from 50 to 150 g/m², all grazers, even rodents, should be noncyclic. The strongest population cycles should occur when the grazed community (or

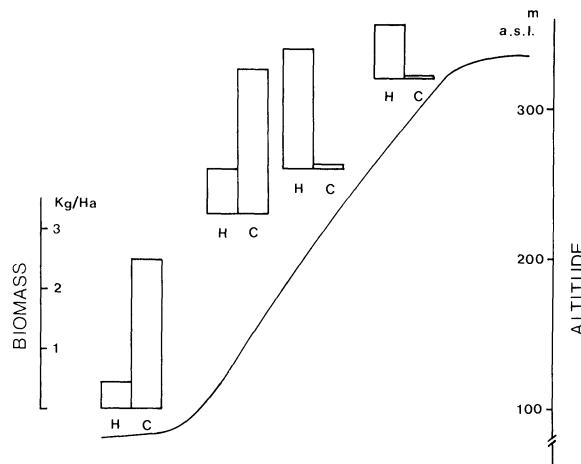


FIG. 7.—The trophic structure of invertebrates (aphids excluded because of their mutualism with ants) living in the foliage of mountain birch (*Betula pubescens* ssp. *tortuosa*) at the southern slope of Mount Jesnalvaara, Finnish Lapland (H = herbivores, C = carnivores).

stratum) produces annually 300–600 g/m². If strong population cycles are found in more productive communities, our model predicts that carnivory is the main proximate cause of decline in herbivore densities, because resource shortage has progressively less importance with increased primary productivity. The few studies of microtine populations in extremely unproductive environments (Fuller et al. 1975; Birney et al., 1976) appear to confirm prediction 2. Birney et al.'s study is especially interesting, because they showed that increased productivity in the environment (reflected in increased rodent populations) leads to population fluctuations. Further, the phytomass (interpreted as cover by the authors) also fluctuated in all but the lushest study area. In this area, a particularly dense stoat population was reported to exist.

Studies performed at Kevo Research Institute, northeastern Lapland, give some information about the trophic structure among invertebrates in a subarctic timberline area. In these timberline forests, the only abundant tree species (mountain birch, *Betula pubescens* ssp. *tortuosa*) is repeatedly devastated by outbreaks of the geometrid moth *Oporinia autumnata* (Tenow 1972). Normally severe outbreaks occur in highland areas which may subsequently change into tundras, whereas lower slopes and river valleys tend to remain undamaged (Kallio and Lehtonen 1973). There is also a clear gradient in the trophic structure of invertebrates associated with birch foliage (fig. 7). In valley forests, both herbivores (mainly aphids and beetles) and carnivores (mainly ants) are present. (Ants apparently get most of their energy from sugars excreted by aphids.) Along the slope, there is a transition from a three-level trophic structure into a two-level one, and on a hilltop with just scattered, shrublike birches the density of carnivores is negligibly small (more detailed data will be published by P. Niemelä and K. Laine).

Given the data presented above that seemed to stress the importance of mammals, the situation appears enigmatic. We suggest that both mammals and invertebrates are important but invertebrates, often able to complete their life cycle during the most favorable season, are much less sensitive to variations in annual primary productivity. On the other hand, ectothermal carnivores are likely to be immobilized by low temperatures. If this is the case, then the terrestrial grazing chain consists of two fundamentally different branches: one homeothermic and vertebrate; the other ectothermic and arthropod. The present version of our hypothesis is then applicable to the vertebrate branch. When dealing with arthropods it may be more useful to keep the plant isocline unchanged along a cline of declining annual productivity, as long as productivity during the most favorable month is reasonably constant. The carnivore isocline would vary in response to temperature, yielding patterns similar to those found for homeothermic food chains.

The transition from three-link to four-link trophic structure, which we expect to find at least in aquatic ecosystems, offers perhaps the most interesting and counterintuitive prediction: An increase in primary productivity should lead to decreased phytomass, increased herbivore density, and unchanged density of primary carnivores. The predation pressure of primary carnivores upon herbivores should decrease, with consequent changes in life history characteristics of herbivores (from r - to K -strategy).

Svärdson (1976) reported that in the eutrophic lake, Hjälmaren, the bulk of commercial catches consists of the sander, a secondary carnivore, whereas planktivores (primary carnivores) prevail in the more oligotrophic big Swedish lakes. Increased productivity thus appears to lead to a transition from a three-link to a four-link ecosystem, as predicted by our theory. Unfortunately, Svärdson did not report whether this difference in trophic structure is reflected in the constitution of lower trophic levels.

A similar transition from three-link to four-link ecosystems in some Kansas farm ponds was studied by Arruda (1979). The trophic structure primarily associated with the macrophyte-periphyte complex, consisting of producers, herbivorous benthic invertebrates, benthic carnivores, and *Centrarchidae* fishes (top carnivores, TC) is plotted against total primary productivity in fig. 8. The Centrarchids are quite opportunistic and have no dislike of herbivorous prey, so their biomass has been added to the biomass of benthic carnivores to yield the sum of all carnivores biomass (C).

The small number of ponds and the necessity to use a part (the macrophyte-periphyte complex) as representative of the whole (the pond) may limit the generality of the results. Nevertheless, the predictions are tentatively corroborated and the data support the counterintuitive prediction that increased primary productivity results in decreased phytomass. Variation in life-history characteristics of benthic invertebrates corresponds to the idea that more productive ponds have less intense primary carnivory (Arruda 1979).

The correspondence between observations and predictions appears encouraging. Even in the case of Isle Royale which served as a counterexample against the

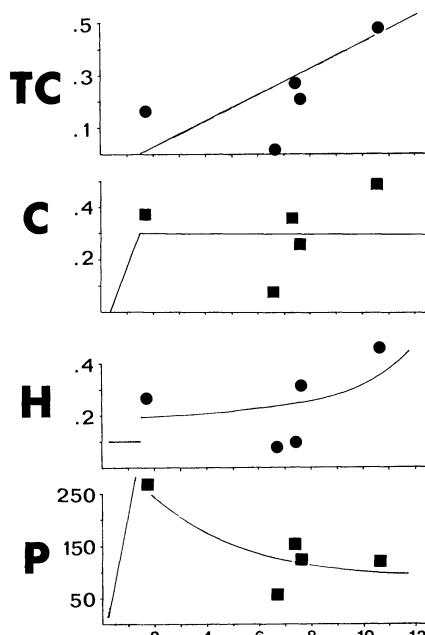


FIG. 8.—Structural trends in the farm pond ecosystems. Data source: Arruda 1979. Horizontal axis: actual gross primary productivity ($\text{g oxygen m}^{-2} \text{ day}^{-1}$), vertical axis: biomass (g dry mass m^{-2} , P = plants, H = herbivores, C = all carnivores, TC = top carnivores alone). The expected pattern is shown as a solid line. The expected relationships are derived from figure 4 (by letting the plant isocline expand) and from accompanying discussion.

random predator approach, exploitation appears to be a major controlling force. Yet the fragmentary nature of our test material is a severe weakness. The situation calls for a detailed analysis of biomass patterns, population dynamics and life-history traits along some gradients of primary productivity and also for further theoretical work.

We are presently investigating the dichotomy between mammalian and arthropod branches of terrestrial grazing chains which require changes in the model as applied to terrestrial ecosystems. The fact that our exploitation models also ignore seasonality weakens the plausibility of our statements about stable and cyclic populations, inviting further theoretical work in this area as well.

SUMMARY

Based on the assumption that each trophic level acts as a single exploitative population, a model relating the trophic structure of ecosystems to their potential primary productivity is developed. According to the model, herbivory pressure should be most severe in relatively unproductive environments. With increased potential productivity, the role of predation in herbivore regulation should become more important and the impact of herbivory upon plant communities should

decrease. In very productive environments, increase in herbivory pressure is again probable, at least in aquatic ecosystems. The predicted pattern of phytoplasm and predicted results of manipulations are compared with available data. A reasonable fit between predictions and observations is found, although the sparsity of data and methodological uncertainties weaken the corroboration in several cases. In terrestrial ecosystems, the present version of the model seems best applicable to the vertebrate branch of the grazing chain, whereas the arthropod branch may be more sensitive to temperature than to average annual productivity.

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