



A Graphical Model of Keystone Predators in Food Webs: Trophic Regulation of Abundance, Incidence, and Diversity Patterns in Communities

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A GRAPHICAL MODEL OF KEYSTONE PREDATORS IN FOOD WEBS:
TROPIC REGULATION OF ABUNDANCE, INCIDENCE, AND
DIVERSITY PATTERNS IN COMMUNITIES

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Abstract.—I analyze a model of species interactions involving species that compete for a single resource and share a common “keystone predator” to study the “bottom-up” effects of productivity (potential carrying capacity of the resource) and the “top-down” effects of factors that affect the death rate of the predator on diversity, abundance, and distribution patterns in the resulting assemblages. The model predicts that coexistence of such species will occur at intermediate productivity (and at intermediate death rates on the top predator) and that superior resource exploiters will dominate at low productivity (and high predator death rates), whereas predator-resistant forms will dominate at high productivity (and low predator death rates). In this model, predator and resource densities are “buffered” against variation in productivity, but the densities of species at the intermediate trophic level are not. Given a large “pool” of potential such species, the model predicts a replacement series involving multiple pairs of species ranging from good resource exploiters to predator-resistant forms as productivity increases or predator death rates decrease. In such a case, coexistence is most likely among the more similar forms, but abundances of similar species are predicted to be negatively correlated. Furthermore, the overall density of organisms at all trophic levels is correlated with variation in productivity. Spatiotemporal heterogeneity modifies these predictions by allowing more than two species to coexist in the presence of a single resource and a single predator and by permitting positive covariation in the abundances of coexisting competitors as well. These models show the critical role of species compositional turnover in determining food web responses to bottom-up and top-down regulation by productivity and variation in predator death rates. The models also predict unimodal diversity versus productivity curves that depend in part on the degree of prey specificity by the top predator.

One of the most problematic aspects of community ecology is that multiple processes often interact in complex ways to produce patterns in community structure. In a search for simpler principles, ecologists have often become polarized into advocates for single factors that might explain variation in such patterns. This is illustrated by the long-running debate about the relative importance of “bottom-up” (emphasizing the role of competition for nutrients and other abiotic factors) versus “top-down” (emphasizing the role of top predators in a food web) regulation of communities and food webs (e.g., Hairston et al. 1960). Recent discussions on this issue have increasingly advocated the need to understand possible interactions between both types of effects on abundance and diversity

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patterns of coexisting species (e.g., Leibold 1989; Power 1992). One of the most important mechanisms that might cause such an interaction involves the roles of keystone predators on species that also compete for resources. In such a case, competition for resources (e.g., MacArthur 1972; Tilman 1982) can interact with "apparent" competition mediated via shared predators (Holt 1977; Holt et al. 1994).

The keystone predator concept (reviewed recently in Mills et al. 1993 and Menge et al. 1994) is generally attributed to Paine (1966) and is associated with experimental studies of the role of the starfish *Pisaster* in facilitating coexistence among an array of sessile intertidal invertebrates. The role of keystone predators has been very evident in freshwater lake ecosystems where carnivores—including fishes, salamanders, insects, crustaceans (e.g., Brooks and Dodson 1965; Lynch 1979; Zaret 1980; Morin et al. 1983; Kerfoot and Demotte 1984; Leibold 1991), and crustacean herbivores (e.g., Porter 1977; Shapiro 1979; Lynch and Shapiro 1981; Vanni 1987; Leibold 1989; Sterner 1989)—have been hypothesized to mediate competitive outcomes among organisms at lower trophic levels. However, the role of keystone predators has also been important in marine assemblages (Paine 1966; Lubchenco 1978), terrestrial folivores (McNaughton 1983; Pacala and Crawley 1992), and seed-eating assemblages (Brown et al. 1979; Inouye et al. 1980) and may be a common feature of many natural communities.

Most models involving keystone predators have looked to identify conditions that allow two species to coexist that would otherwise competitively exclude one another (e.g., Cramer and May 1972; Vance 1974). Competition has often been modeled by Lotka-Volterra competition equations and has rarely been developed in a broader context that explicitly considers resources and other organisms in a food web (but see Phillips 1974; Holt et al. 1994). Furthermore, models of keystone predation often focus on the traits of the species that allow coexistence more than on the traits of environments that influence the outcome of the species interactions.

The earliest models of keystone predation were directly inspired by Paine's (1966) hypothesis and focused on demonstrating that coexistence among species that would otherwise competitively exclude each other could be mediated by a common predator. The most comprehensive model was by Vance (1974), showing that coexistence of a species with a superior competitor was possible if it was also less vulnerable to the predator. In addition, the model showed that coexistence of competing prey was most likely at intermediate carrying capacity (i.e., productivity). At low productivity, the superior competitor would exclude the more resistant one because predator densities at equilibrium would be insufficient to reverse its competitive advantage. At high productivity, the more resistant form would exclude the better competitor by supporting a large predator population sufficient to reverse the net competitive relations between the two species (an effect largely due to "apparent competition"; sensu Holt 1977). Vance (1974) also showed that complex dynamics were possible for such interactions and were more likely at high productivity.

More recent elaborations of this model have focused on the role of spatial structure on keystone predator effects (Caswell 1978; Hastings 1978; Crowley

1979) and on the effects of productivity on the abundances of species (Armstrong 1979; Leibold 1989). Aside from showing when keystone predators can allow two mutually exclusive species to coexist, little has been done to explore how such predators might influence diversity among more than two competitors or how such an effect might interact with other processes that influence resource competition among their prey. However, Phillips (1974) used general algebraic arguments to show that the number of coexisting consumers limited by a single resource could be as high as one plus the number of keystone predators on those consumers. He further argued that the number of predators was not obligatorily limited in order to achieve local stability.

In this article, I develop a model to address ways that community structure might be influenced by keystone predators. I investigate both the bottom-up effects of variation in productivity and the top-down effects of variation in the top predators' death rate on abundance patterns, species diversity, and species' distributions. The model is developed graphically and emphasizes a qualitative analysis of results in an effort to understand major features of the results. A more quantitative analysis of specific models is presented in the appendix. I focus on a single predator that feeds on an assemblage of species that compete for a single resource. Phillips's (1974) analyses suggest that qualitatively similar results should obtain in the case of multiple resources and multiple predators.

The model is structured in a way similar to that used by MacArthur (1972) and Tilman (1982, 1988) and closely related to the work of Armstrong (1979), Grover (1994), and Holt et al. (1994), and it is subject to many of the same general assumptions. Analogies in model structure and their relation to conventional niche theory are discussed elsewhere (Leibold 1995). These assumptions include the role of flexible foraging behavior, the assumption of equilibrium, and the interpretation of spatial heterogeneity as discussed by Armstrong (1979), Tilman (1982, 1988), Abrams (1987, 1988, 1993), and Holt et al. (1994). The approach I develop differs from those of the above authors by being more closely linked to graphical models of competition (i.e., Tilman 1982) and by focusing on the consequences to species diversity and species' distributions.

THE MODEL

The model is presented in four parts. I first use the case with only one consumer-prey species (i.e., a three-level food chain) to develop the general formulation of the model. Second, I analyze the results of interactions between two competitors and their common resource and predator to develop the mechanistic aspects of the model. Third, I consider possible effects on coexistence when there are more than two species of competitors in a regional pool to show that a productivity gradient should result in a replacement series of pairs of coexisting species, with good competitors dominating at low productivity and resistant forms dominating at high productivity. This model also predicts that species with more similar responses to predators and food should be more likely to coexist than those with more different responses but that abundances among coexisting competitors should be negatively correlated. Finally, I examine how these results

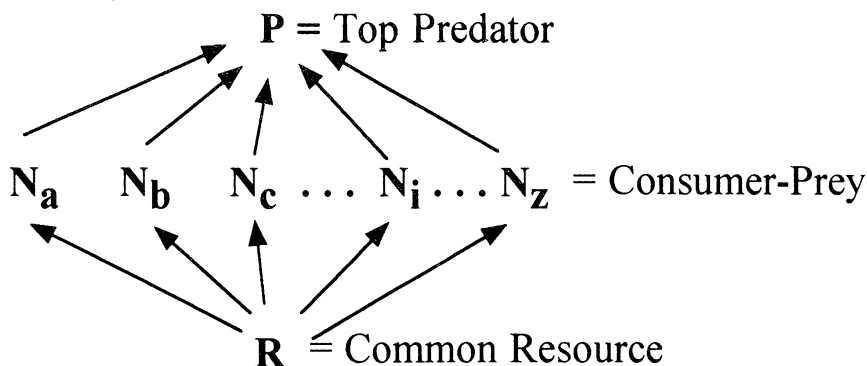


FIG. 1.—Food web diagram illustrating interactions among a number of consumer-prey species, their shared resource, and their shared predator. The P denotes a top predator, $N_a - N_z$ denote alternate species of intermediate consumer-prey, and R denotes the resource that ultimately supports all of the above populations.

might be affected by spatial heterogeneity to show that more than two consumer-prey species can coexist. Further, species pairs with more similar responses to food and predators are more likely to coexist and to have positively correlated densities than are species pairs with more different responses. All three models show that diversity of competitors should be a unimodal function of productivity.

Throughout the article, I will refer to the top predator as “predator” and the lowest-level resource as “resource” but will refer to the intermediate competing prey as “consumer-prey” to highlight their intermediate position in the food web.

The basic structure of the models is illustrated by a food web graph as shown in figure 1. If all interactions are mediated only via trophic interactions (i.e., no direct interference competition within or among species) except for the negative density dependence among the resources, and populations are assumed to be uniform (no variation among individuals), each species' performance will only depend on two additional sets of variables. Each of the consumer-prey will only be affected by the predator and resource densities, whereas the predator and the resource will be affected only by the densities of the various competing consumer-prey. The model assumes that all other interactions among species are indirectly mediated by these proximate mechanisms. The graphical approach described below depends strongly on the assumptions that there is no dependence of predator feeding rates or mortality or of consumer-prey feeding rates, or conversion efficiency on consumer-prey density. However, the appendix section Type II Functional Responses and Induced Defenses suggests that the qualitative insights of the graphical approach are robust to some of these assumptions as long as the ratio of values among consumer-prey species for these parameters is not altered.

I focus on analyzing the equilibrium points of the model and generally ignore the potential for limit cycles and other forms of complex, nonequilibrium results. This is generally equivalent to assuming that the parameters are constants. Potential complications arise primarily from density-dependent parameters that could lead to “overshoots” and produce complex dynamics potentially involving limit

cycles or “chaos.” Such complications are suggested by Vance’s (1974) model and are discussed by Chesson (1986), but one might expect that long-term average values of populations subject to such complex dynamics should nevertheless correlate well with predictions based on features of the equilibrium point. The most significant exception is the possible role of such internally driven cyclic population dynamics in allowing coexistence among species mediated by their responses to the resulting variance in interspecific interactions as illustrated by models such as those of Levins (1979) and Armstrong and McGehee (1980).

A SINGLE CONSUMER-PREY SPECIES

Imagine a simple food chain model in which a single consumer-prey species interacts with a single resource and single predator. An analytic model of such a system might be described by differential equations of the form

$$\begin{aligned}dP/dt &= P(faN - d), \\dN/dt &= N(gcR - fP - m),\end{aligned}$$

and

$$dR/dt = t(s - R) - gRN,$$

where P identifies the predator density; N , the consumer-prey density; and R , the resource density. The parameters (in lowercase) represent the per capita feeding rate of the predator on the consumer-prey (f), the per capita grazing rate of the consumer-prey on the resource (g), the conversion ratio of consumer-prey consumed to predator growth (a), the conversion ratio of resource consumed to consumer-prey growth (c), the resource turnover rate (t), the intrinsic mortality rate of the consumer-prey (m), the intrinsic mortality rate of the predator (d), and the maximum resource level (s).

Figure 2 sets dN/dt equal to zero to illustrate how per capita population replacement of a consumer-prey species should be influenced by the joint densities of the resources and the predators. In this figure, three qualitatively distinct conditions are illustrated. In the lower part of the graph, resource densities are sufficiently high that the birth rate of the consumer-prey population exceeds its loss rate (including predation as well as natural “background” mortality and respiration). In the upper part of the graph, the consumer-prey population loss rate exceeds its birth rate because there is insufficient food or too much predation. The two zones are separated by a line that identifies conditions where the loss rate equals the birth rate and is a zero net growth population isocline, or ZNGI (sensu Tilman 1982). The line has a positive slope because higher food levels are required at high predator densities for birth rates to offset the higher mortality imposed by predators (Holt et al. 1994) and is described by $P = (gcR - m)/f$.

The ZNGI describes potential equilibria associated with the consumer-prey population and tends to be an attractor. If conditions are in the lower region, the consumer-prey population will increase, which should consequently lead to an increase in the predator density and a decrease in the resource. If conditions are

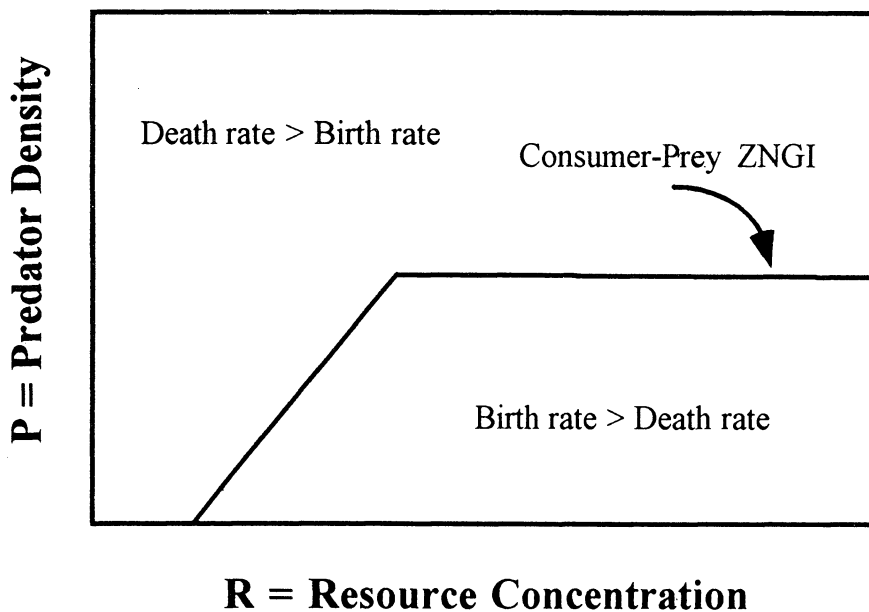


FIG. 2.—Relationships between predator density (P) and resource density (R) for an intermediate consumer-prey. In the lower region, birth rates exceed death rates, and in the upper region, death exceeds birth. The line labeled ZNGI is a zero net population growth isocline since birth rates equal death rates and satisfy conditions for an equilibrium involving the consumer-prey population.

in the upper region, the consumer-prey population will decrease with consequent opposite effects on predator and resource densities. Both effects tend to result in dynamics that change conditions back toward the ZNGI.

The ZNGI plotted in figure 2 only describes conditions for the consumer-prey population to exist at equilibrium and does not require the predator or the resource populations to be at equilibrium. Resource equilibrium further requires that the net rate of resource renewal (involving all factors other than loss due to consumption by the consumer-prey) be the same as the rate of consumption by the consumer-prey (i.e., $t[s - R] = gRN$). Similarly, the predator equilibrium requires that the predator population consume sufficient amounts of consumer-prey to offset any background mortality and metabolic requirements (i.e., $d = faN$). The role of the intermediate consumer-prey as a “middle person” can be evaluated by using vectors illustrating the balance between resource supply and predator demand and between consumer-prey feeding and ingestion by predators.

The vector in figure 3 illustrates the per capita effects of consumer-prey on resource and predator populations. I will refer to this vector as the per capita consumer-prey impact vector and denote it c_i . The vector consists of two components. The horizontal component represents the feeding rate of consumer-prey individuals on the resource population (gR ; number of resource units consumed \times time $^{-1} \times$ consumer-prey $^{-1}$) and may be a function of both resource and/or

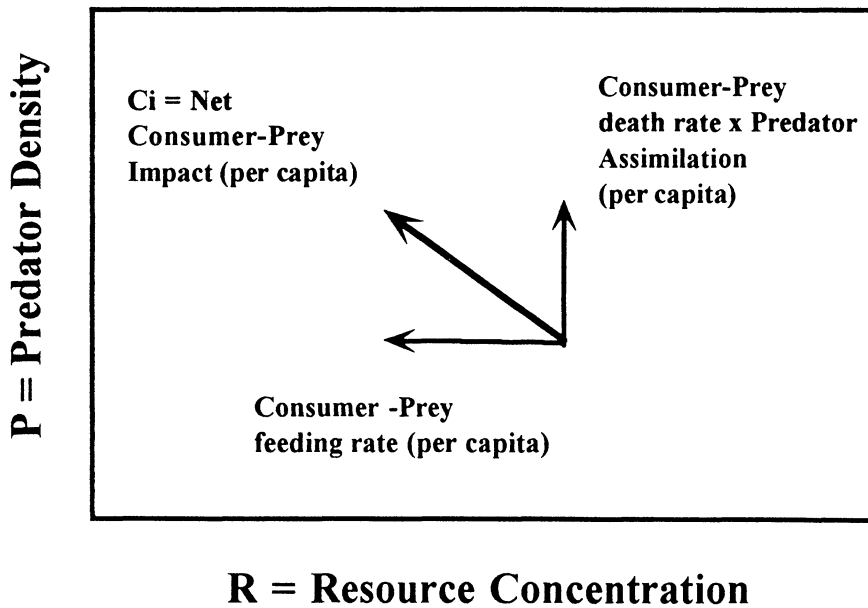
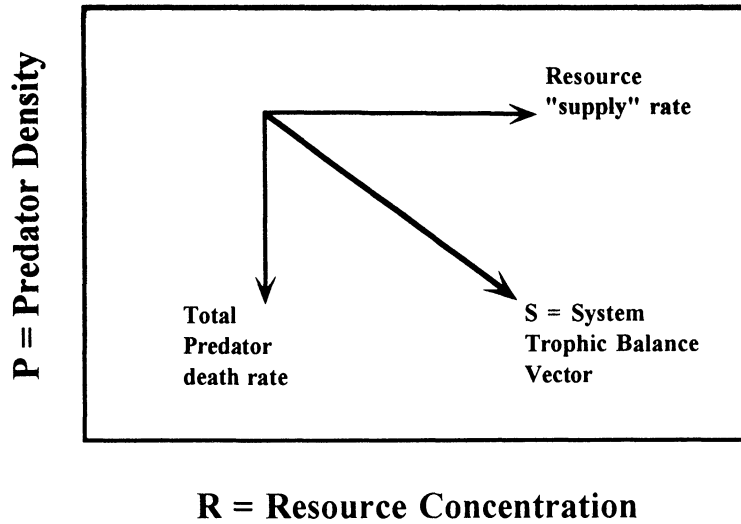


FIG. 3.—The net consumer-prey impact vector c_i . The vector has two components: a horizontal component describing the per-individual feeding rate of the consumer on the resource (gR) and a vertical one describing the per-individual contribution to the predator's birth rate via the consumer-prey's mortality rate (faP). The total per capita impact of the consumer-prey is described by the vector sum of these two components (c_i). See text for more details.

predator density. Similarly, the vertical component is the rate at which individual consumer-prey contribute to the predator population's birth rate. In effect, this is the per-consumer-prey mortality risk due to predation weighted by the conversion efficiency of the predator (faP ; number of predators born \times time $^{-1}$ \times consumer-prey eaten $^{-1}$ \times consumer-prey $^{-1}$). Another interpretation of this vector is that the slope (faP/gR) represents the consumer-prey's "progressive ecological efficiency" (sensu Lindeman 1942), and its magnitude is a general per-individual rate-scaling factor proportional to body size and metabolic rate or activity level.

For any given combination of resource and predator densities, the summed individual contributions of all the consumer-prey individuals must balance the overall resource population renewal rate and predator population food requirement. These can also be illustrated by a vector as in figure 4A. I refer to this vector as the system trophic balance (STB) vector and denote it by S . It also has a horizontal component that describes the resource renewal rate ($t[s - R]$; number of new resource units/time) that is identical to Tilman's (1982) "supply vector" in the case where there is a single resource. The vertical component is similar and describes the population death rate of the predator (dP ; number of predators dying/time). The predator population death rate should generally increase with increasing predator density, but the resource supply rate would decrease with increasing resource density.

A)



B)

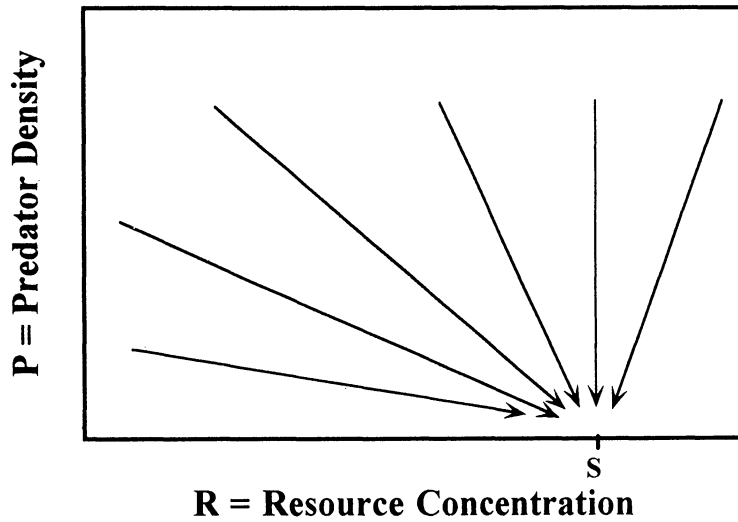


FIG. 4.—A, The system trophic balance (STB) vector S . The horizontal component describes the rate of supply of resources ($r[s - R]$), and the vertical component describes the population death rate of the predator (dP). B, A field of S vectors for an "abiotic" resource in a chemostat that renews as a linearly decreasing function of density: S is the maximum resource level (obtained when there are no higher trophic levels) and is analogous to Tilman's (1982) "supply point" for the case of a single resource.

The STB vectors should form a field that converges on the maximum equilibrium resource level (resource levels obtained in the absence of higher trophic levels). In this model, this would correspond to the resources' maximum level in the ecosystem, and the field of vectors formed would tend to be linear, as shown in figure 4*B*. If resource renewal is modeled using a more complex mechanism than that described above, the STB vectors would generally still form a field that converges on s , but these vectors may not be linear. However, the results described below do not qualitatively depend on variation in the shape of the vector field as long as the STB vectors are always directed toward the lower right of the graph (indicating that the intermediate consumer-prey are essential in converting depleted resources to predator population renewal). This essentially occurs when there are no direct mutualistic interactions (including Allee effects) in any of the populations.

At any given point (combination of predator and resource levels), the STB vector could be experimentally determined by measuring the short-term population responses by the predator and the resource to a sudden removal of the intermediate consumer-prey population. The slope of the STB vector would be determined by the relative rate at which the predator population would die of starvation (the vertical component) relative to the rate of renewal in the resource (the horizontal component). The STB vector will depend most closely on resource productivity (the STB vector at a given predator and resource density would be shallower with higher productivity) and on the loss rate experienced by the predator (the STB vector would be steeper with higher predator loss rates), respectively corresponding to bottom-up and top-down regulation of the ecosystem as a whole.

An equilibrium satisfying the conditions that both the predator and the resource populations be unchanging (regardless of whether or not the consumer-prey populations are at equilibrium) occurs when the consumer-prey impact vectors (c_i) times the consumer-prey density (N_i) is equal in magnitude but opposite in direction to the ecosystem STB vector (S). The additional requirements for an equilibrium involving all three populations (predators, resources, and consumer-prey) are satisfied by all such points that also occur along the consumer-prey ZNGI (consumer-prey at equilibrium). Multiple equilibria are possible if there are non-linear relationships among the parameters, but there is only one equilibrium when the relationships are linear.

Figure 5 shows two such equilibrium points associated with two different levels of productivity to illustrate the effects of bottom-up regulation on the outcome of interactions involving such a simple food chain. The results show that consumer-prey can invade only at productivities greater than some threshold level (labeled R_{\min}) that can satisfy their metabolic and nonpredation losses. Predators will only be able to invade at a yet higher productivity when the consumer-prey density is high enough to satisfy the predators' requirements. Further increases in productivity produce density increases along the consumer-prey ZNGI in both predator and resource density. Other analyses show that consumer-prey densities along such a gradient would not change as long as f , a , and d are constants (Oksanen et al. 1981). The effects of variation in top-down regulation of the food chain in this model are well known (see Oksanen et al. 1981; Power 1992; Abrams

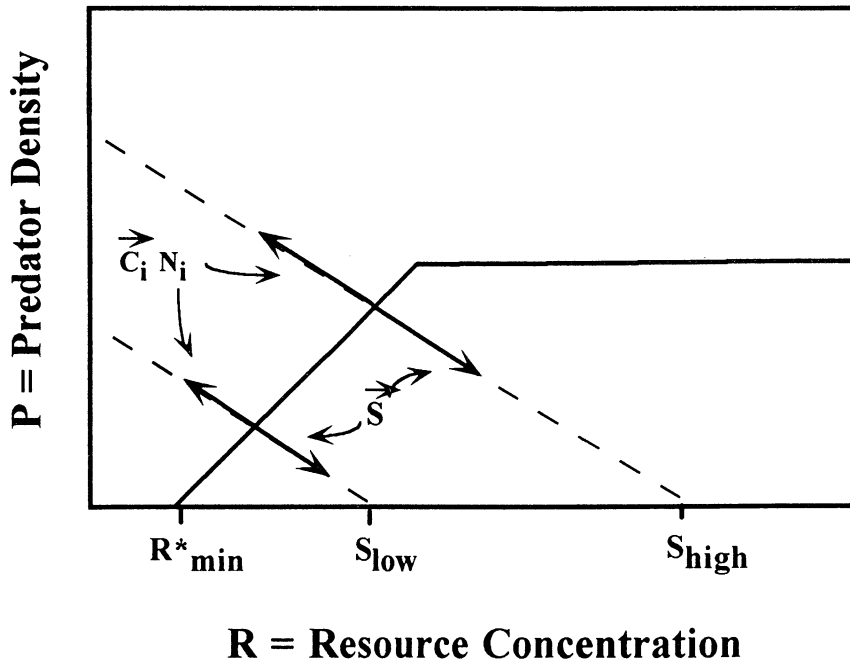


FIG. 5.—The effect of increasing productivity on a simple three-level trophic chain. Two productivity levels are illustrated with different maximum resource levels (S_{low} and S_{high}). In each case the equilibrium requires that the sum of the consumer-prey impact vectors and the STD vector be equal in magnitude but opposite in direction and that such points occur on the consumer-prey's ZNGI, as shown in fig. 2. The effect of increasing productivity is to increase the density of the predator and the resource.

1993) and indicate that equilibrium predator and resource densities will decrease and that the consumer-prey population will increase when the death rate of the top predator is increased. These results are generally only complicated by nonlinear functional responses and resource renewal rates that constrain the conditions for a stable equilibrium (e.g., Rosenzweig 1971; Oksanen et al. 1981; Schmitz 1992).

MODEL I: TWO CONSUMER-PREY SPECIES

We can hypothesize that different consumer-prey (additional species b–z in fig. 1) would have qualitatively similar ZNGIs as shown in figure 2 but could differ in R_{min} and/or in the slope relating R to P . For simplicity, consider cases where the ZNGIs of two species are characterized by differences in intercept and slope, which is equivalent to assuming that the ZNGIs are linear. If they are not, there is the possibility of multiple equilibria, but the solution can otherwise be quite similar. An analytic solution of the salient graphic results is shown in the appendix (under Constant Parameters) for the simple case of linear functional responses among all the organisms and where resources are modeled as abiotic and nonse-

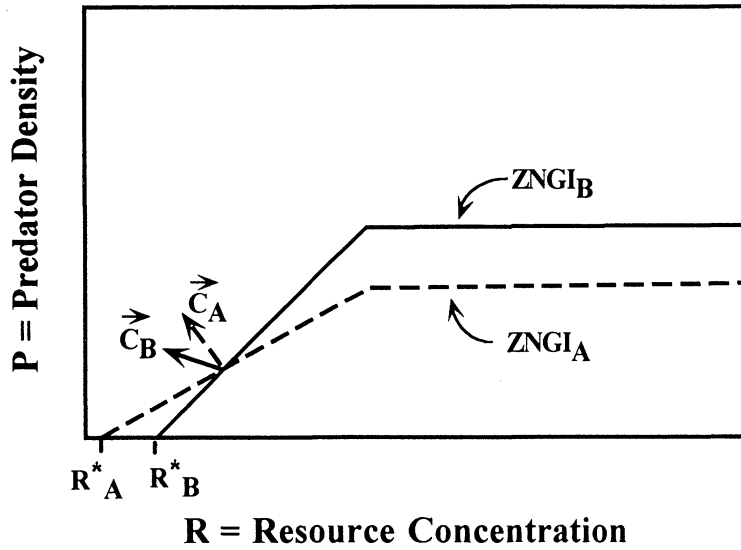
questrable. The appendix also shows that the results are qualitatively robust to two specific types of nonlinear effects: Type II functional responses by the predator in which selectivity (*sensu* Chesson 1978) does not change and consumer-prey-dependent resource availability in which relative (but not absolute) feeding rates by the consumer-prey are constant.

Coexistence of the two consumer-prey species requires that their ZNGIs cross, as shown in figure 6. This requires that the consumer-prey species express a trade-off between exploitation ability and tolerance of predation (as defined by the slope of the ZNGI, the reciprocal of the change in ambient resource levels required to offset the predation risk associated with an incremental increase in predator density). In this definition, predator tolerance can be achieved by being more difficult to catch or less preferred by the predators or by having stronger recruitment responses to incremental changes in resource levels. Another way to view this trade-off is that it implies that the species whose death rate is most affected by predation has the lowest R_{\min} (resource requirements in the absence of the predator). The point at which these lines cross is an equilibrium point required for the two consumer-prey species densities to remain at equilibrium.

The local stability of this global equilibrium point will depend on the per capita impact vectors as shown in the appendix. The conclusion is that when the species with the steeper ZNGI has the shallower per capita impact vector (species A in fig. 6A), the equilibrium is locally stable, whereas the equilibrium is locally unstable in the case where the species with the steeper ZNGI has the steeper per capita impact vector (species A in fig. 6B). In figure 6B, the equilibrium point is unstable because small deviations from the equilibrium favor the consumer-prey species that further modifies the environment in the same direction as the perturbation (i.e., positive feedback). The prediction would be that the two species would not coexist and that the "winner" would depend on initial conditions. In figure 6A, however, small deviations from the equilibrium point favor the consumer-prey species that tends to modify the environment back toward the equilibrium (i.e., negative feedback). Consequently, the condition for local stability of the equilibrium point is that there be a positive correlation between the slope of the ZNGI and the slope of the per capita impact vectors. In general, this condition seems likely since both slopes are affected by similar parameters (i.e., the ratio of predator tolerance to feeding rate of the consumer-prey), but they may differ substantially if the consumer-prey also differ substantially in digestibility to the predator or in the case where the consumer-prey differ in the extent of predator-induced defenses (see the appendix).

Given the presence of both consumer-prey species, a global equilibrium also involving unchanging predator and resource densities is mediated by changes in consumer-prey densities. Predictions concerning the densities of the consumer-prey also depend on the magnitude and slope of the per capita impact vectors of the two species. As developed in the food chain model above, equilibrium densities will occur when the sum of all the per capita impact vectors of all the individuals of both species sums to be equal in magnitude but opposite in direction to the STB vector (S) at the equilibrium point. These vectors can only satisfy this condition for positive values of both species if the STB vector is intermediate in slope

A)



B)

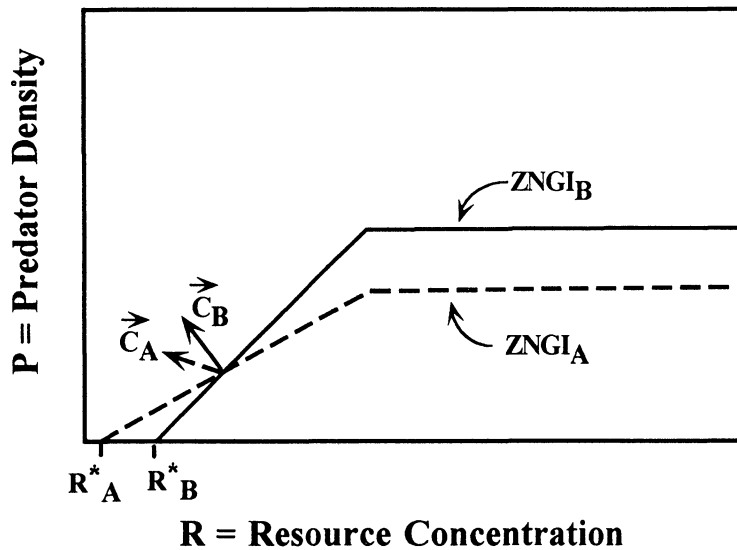


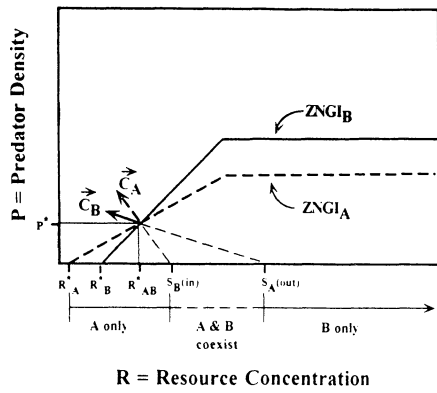
FIG. 6.—Two cases illustrating ZNGIs that intersect in the plane describing the density of the predator (P) and the resource (R). In each case, the ZNGI and the per capita consumption impact vector (c_i) are identified for each of two species of consumer-prey denoted A or B. In this case, A is a better exploiter (lower intercept of the ZNGI on the X-axis) than B, and B is more tolerant to predation than A (steeper slope of the ZNGI). A, A stable equilibrium in which each species' impact vector indicates that it has a greater relative impact on the limiting factor that most limits its relative performance (A's consumer-prey impact vector is steeper than B's). B, An unstable equilibrium in which each species' impact vector indicates that it has a greater relative impact on the limiting factor (resource or predator) that least limits its relative performance (A's consumer-prey impact vector is less steep than B's).

and therefore oriented toward maximum resource levels in the region bounded by the two consumer-prey per capita impact vectors (c_i). If the STB vector is steeper (implying low maximum resource levels or high predator loss rates) than either consumer-prey's per capita impact vector (c_i), the better exploiter will competitively exclude the more resistant consumer-prey. If the STB vector is shallower (implying high maximum resource levels or low predator loss rates) than either per capita impact vector, the more resistant consumer-prey will exclude the better exploiter. Thus, coexistence will only occur at intermediate levels of productivity.

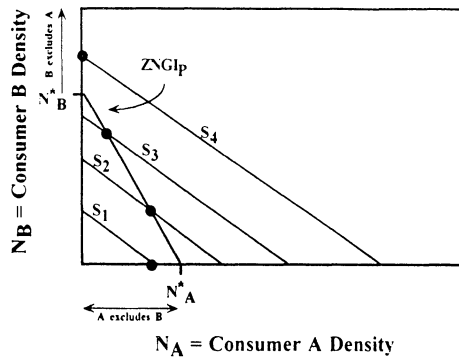
Figure 7 illustrates the effects of changes in productivity on the outcome of species interactions in this case. At the lowest productivity levels, when s of the resources is less than R_{\min} of the best exploiter (species A in fig. 7), only the resource population can exist. When s exceeds R_{\min} of the best exploiter, it can coexist with the resources, and its population size will increase with productivity. Further increases in productivity can allow the poorer exploiter to exist if s exceeds its R_{\min} but only if the better exploiter is absent. At some point, the predator can invade as discussed above, and density relations will be constrained to occur on the best exploiter's ZNGI (i.e., P and R will increase, but A will not). The enhancements of predator populations will eventually allow the poorer exploiter to invade when the corresponding STB vector (S) has a slope that is bracketed by the two per capita impact vectors (c_i). As productivity is further enhanced, the more resistant consumer-prey species can support a predator population that is large enough to completely negate any exploitation advantage of the better competitor and drives it to extinction. This result occurs when the STB

FIG. 7.—The effects of productivity on predator and resource densities and on the occurrence of two consumer-prey species. *A*, The ZNGIs of two competitors that differ in both tolerance of the predator and exploitation ability are shown to intersect, which can allow coexistence. Their c_i vectors are illustrated such that they allow coexistence to be stable. *B*, The ZNGIs of the predator and the resource populations are shown in a graph whose axes are the densities of the two consumer-prey species A and B. A single ZNGI is shown for the predator, illustrating its use of the consumer-prey as substitutable resources and this relation's lack of dependence on productivity. Four different ZNGIs are shown for the resource population, illustrating its dependence on productivity from low (labeled S_1) to high (labeled S_4). *C*, The predicted pattern of abundance of species across such a gradient in productivity for predators and resources (*upper part of graph*) and consumer-prey species (*lower part of graph*). If the carrying capacity of the resource is less than the best competitor's minimum resource requirement (R_A^* in fig. 7A), equilibrium populations of none of the higher trophic levels can be supported. If the carrying capacity is higher but less than that required to support a minimum required population density of species A (N_A^* in fig. 7B), only the best competitor can exist. Above this level both the best competitor and its predator can exist. Species B is competitively excluded (by mechanisms including both resource and "apparent" competition) by A until the productivity reaches some level that allows B to invade (at S_B in fig. 7A). Both species can coexist via a "keystone effect," and resource and predator densities will be constant (shown as R_{AB}^* and P^* in fig. 7A) until productivity is so high (S_A in fig. 7A) that the net effect of B is to exclude A, largely by supporting higher predator populations such that A is not the best overall competitor (including both the effects of resource and "apparent" competition).

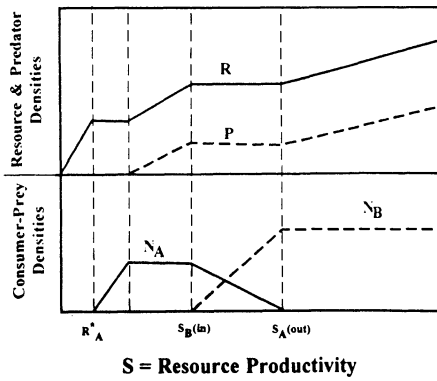
A)



B)



C)



vector becomes shallower than the poorer exploiter's per capita impact vector.

Another way to examine the effect of increasing productivity is to plot the ZNGIs for the predator and the resource populations (rather than those of the consumer-prey species as shown above) as functions of the densities of each of the two consumer-prey species, as shown in figure 7B. Because predator and resource densities are fixed by the intersection of the consumer-prey isoclines (fig. 7A), the predator's ZNGI is determined by the way the two consumer-prey combine to affect the predator's growth rate. In this simple, linear model, the two consumer-prey represent substitutable resources (*sensu* Tilman 1982) and should show a negative linear relation. The resource ZNGI is determined by the set of densities of the two consumer-prey that result in a loss rate that matches its renewal rate. Since both consumer-prey feed on the resource, the resource ZNGI will have a negative slope, with conditions toward the origin resulting in net resource density increases and conditions away from the origin resulting in net resource density decreases due to overgrazing. This ZNGI should be a function of productivity as illustrated by the lines labeled S_1 , S_2 , S_3 , and S_4 showing the effects of increasing productivity. At S_1 , the productivity of the resource is insufficient to support a consumer-prey population that is sufficient to support the predator and the resource, and the predator cannot coexist (though it may be possible for the resource to coexist with either of the consumer-prey species alone). At S_2 , the resource and predator can coexist with the two consumer-prey species, and the equilibrium densities of the consumer-prey are shown by the equilibrium point where the two isoclines cross. Further increases in productivity, shown by S_3 , illustrate that the equilibrium densities of the two consumer-prey are modified and that the less resistant species declines in abundance while the more resistant species increases. Finally, at very high productivity, S_4 , the predator would drive the less resistant consumer-prey extinct and would be entirely supported by the more resistant consumer-prey population.

The consequent relation between the equilibrium species abundances and ecosystem productivity (as indexed by the density of resources in the absence of higher trophic levels, S) are illustrated in figure 7C. The predictions are, first, that changes in the density of predators and resources will alternate between showing joint increases with productivity and no change. This "stepwise" pattern of density changes across a productivity gradient is similar to that obtained for linear food chains as described by Oksanen et al. (1981) and Mittelbach et al. (1988). When the densities of the consumer-prey are not functions of productivity, the resources and predator populations are; when the densities of the consumer-prey are functions of productivity, the resource and predator populations are not. Second, predator and resource densities should be positively correlated with productivity, whereas consumer-prey populations will replace each other with negative correlations in their densities over the productivity range where they coexist. In general, we might expect that the total density of consumer-prey individuals (the sum of their individual densities) would increase, as shown in figure 7C, because the predator's per capita feeding rate (f_i) will go down but its requirements will not ($f_i a_i N_i = d$); thus, its resources (*i.e.*, the consumer-prey densities) should increase unless this is offset by a much higher conversion effi-

ciency (a_i) on the more resistant consumer-prey (Abrams 1993). We might further expect that this assumption would most clearly be violated when the more resistant consumer-prey is larger in body size, in which case the variable could be expressed in terms of biomass density to conclude that biomass at the consumer-prey trophic level should generally increase (unless this trend is compensated by a much higher assimilation efficiency by the predator on the more resistant consumer-prey). Third, diversity of consumer-prey is unimodal with a maximum of two at some intermediate level of productivity. Finally, because the effect of increasing the predator death rate (d) is to make the STB vector steeper, the predictions are the reverse of those described above for the effects of increasing productivity (see the appendix for a formal analysis).

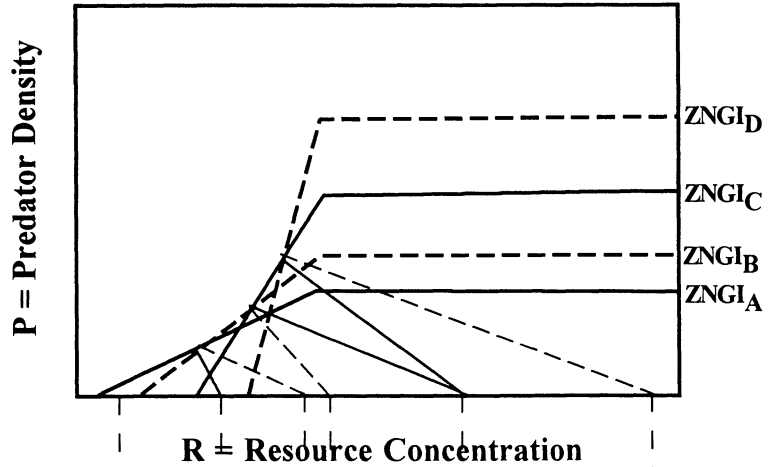
The above results all apply to the food web shown in figure 1. However, susceptibility to predators can extend to the point where organisms at a given trophic level are completely invulnerable to the top predator. For the case in which there are two consumers, the effect is to modify the predictions of the models described above as follows (see Phillips 1974; Grover 1994). If productivity is high enough to support such a population in the presence of a better resource exploiter, any further effects of productivity on equilibrium densities of organisms only affect this invulnerable species. Under these conditions, the predator, resource, and more vulnerable consumer-prey species are not further affected at equilibrium by variation in productivity, although they do respond to variation in predator loss rates, as does the model described above (i.e., reducing the predator death rate enhances the better resource exploiter and reduces the densities of the resource and less vulnerable consumer-prey). Further, in such a case there are two species coexisting at the highest production levels, and diversity does not decline with increased productivity.

MODEL 2: MANY CONSUMER-PREY SPECIES

The features of the model for the two-species case described above can be used to evaluate predictions for a scenario that involves more than two consumer-prey species, as shown in figure 8. In figure 8, only species that have ZNGIs that show an overall trade-off between resource exploitation ability and tolerance of the predator (as defined above) are illustrated. Other potential species that are inferior in both traits are predicted to be driven extinct by the illustrated ones, and potential species that are superior in both traits are conversely predicted to drive the illustrated array extinct.

Figure 8 illustrates that the outcome of these interactions will depend on productivity and on top-down regulation of predator loss rates in a way that is generally an extrapolation of the results for the two-species case. For any given productivity (i.e., resource density in the absence of higher trophic levels), there are multiple possible equilibria involving at most two consumer-prey species. The possible equilibria include all of the ones that have per capita consumer-prey impact vectors that bracket the supply vectors associated with that level of productivity. These represent alternate stable states for the community that depend on initial conditions and/or productivity levels. In general, the identity of coexist-

A)



B)

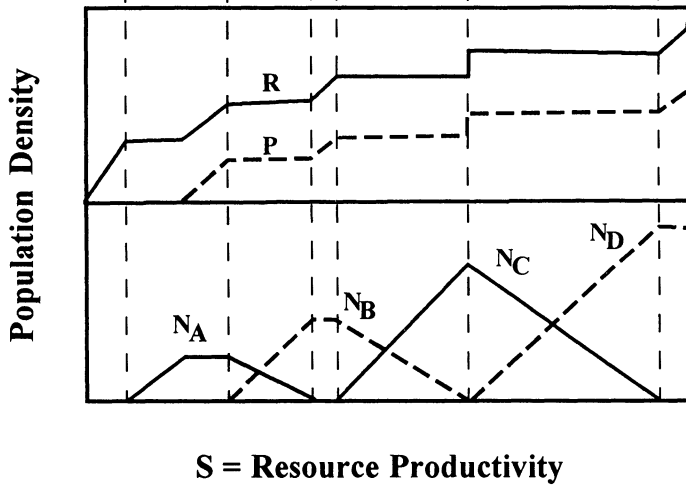


FIG. 8.—A, ZNGIs (*thick lines*) for the case in which there is a large array of consumer-prey species available to colonize that exhibit an overall trade-off between resource exploitation ability (minimum resource requirements in the absence of the predator) and susceptibility to the predator (slope of the ZNGI). Thin lines illustrate the range of STB vectors for each possible uninvadable equilibrium point that are associated with resource carrying capacities that would allow coexistence of each pair of species. The per capita impact vectors are assumed to allow stable coexistence as in fig. 7A. B, The predicted pattern of abundance of species across such a gradient in productivity for predators and resources (*upper part of graph*) and consumer-prey species (*lower part of graph*). Notation is as in fig. 7.

ing consumer-prey species will show a consistent pattern across the productivity gradient. At low productivity, pairs of coexisting species will tend to consist of good exploiters that are not tolerant of predation, whereas at high productivity, coexisting pairs of species will be tolerant of predation even though they will be poor resource exploiters. Intermediate species will tend to coexist at intermediate productivity. Thus, the prediction is that the distributions will show a replacement series of coexisting species ranging from good resource exploiters to resistant forms. Consumer-prey diversity is predicted to go from one to two to one across this gradient, assuming that the most resistant consumer-prey is still vulnerable to predation.

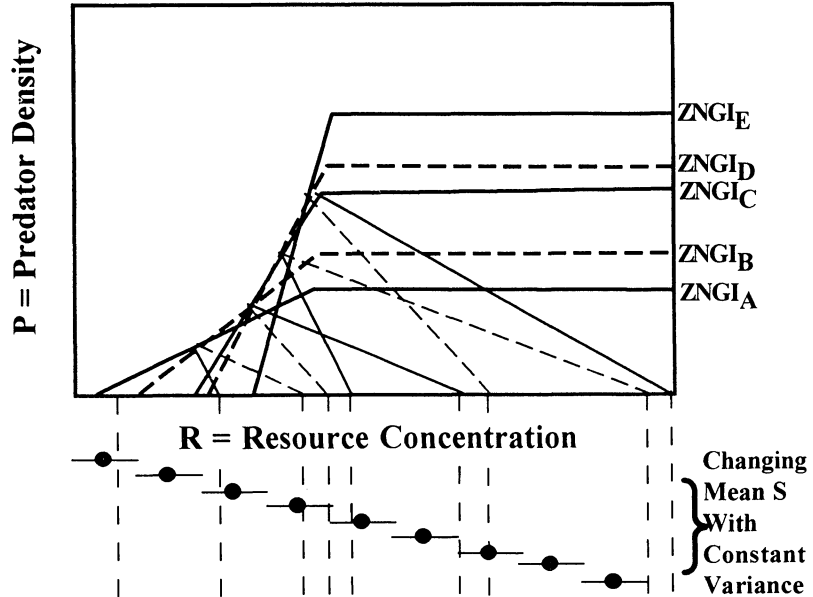
Associated patterns in the abundances of each of the populations are illustrated in figure 8B. The predictions are, first, that diversity will increase at low productivity and might decrease at high productivity. Second, pairs of coexisting consumer-prey species will replace each other along a productivity gradient, with the most similar species pairs (species at adjacent points along the susceptibility/exploitation ability axis described by their ZNGIs) coexisting and dissimilar species pairs having more exclusive distributions. Third, abundances will generally increase for both predators and resources across a productivity gradient but will be strongly associated with species turnover of the consumer-prey assemblage. When there is no such turnover, the predator and resource densities are predicted to be constant (at least in the linear case considered here, where there is no intraspecific interference behavior). Fourth, abundances of consumer-prey species will be negatively correlated for those conditions where they coexist. Finally, the predictions for top-down regulation by variation in the predator loss rates are the reverse of these predictions.

MODEL 3: MANY CONSUMER-PREY SPECIES AND ENVIRONMENTAL HETEROGENEITY

Some of these predictions are potentially modified by the role of environmental heterogeneity in productivity. This effect can be illustrated by characterizing the productivity of a given site by a range of points (rather than a single point), as in figure 9, showing the effects of sites with a given mean (indicated by a dot in fig. 9) and a given range (illustrated by flanking horizontal lines to the mean). The effects of such local site heterogeneity can be examined by assuming that the outcome will be a weighted sum of the expected outcomes of each of the possible single point results spanned by the range of local heterogeneity.

This way of examining the role of heterogeneity involves a number of implicit assumptions similar to those used by Tilman (1982) and Brown and Rosenzweig (1986) and discussed by Abrams (1988). The assumptions imply that philopatry and/or adaptive cost-free habitat selection are operating to minimize the occurrence of organisms in microsites where they would be competitively inhibited (see Brown and Rosenzweig 1986 for some potential implications of violating these assumptions). This approach essentially ignores source-sink (Pulliam 1988) relations among populations at different microsites (where populations at inappropriate microsites can be supported by colonization from more favorable microsites) and the role of the "storage effect" (Chesson 1986) on species interactions.

A)



B)

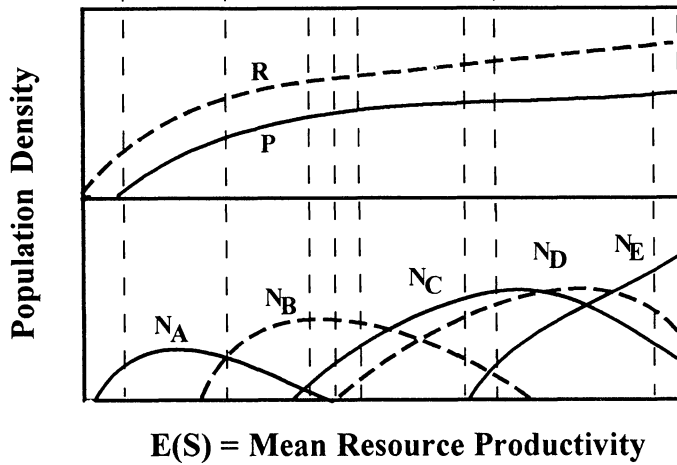


FIG. 9.—As in fig. 8 except as modified to include the effects of spatial patchiness in the resource productivity. A, ZNGIs (thick lines) and extrapolations of impact vectors back to the resource axis (thin lines) of five competing consumer-prey species. The horizontal line with a marked midpoint between the two panels indicate that sites with a given average productivity (identified by the central point) contain patches that span a range of conditions (illustrated by the horizontal line). The prediction is that the outcome will consist of a weighted sum of the outcomes expected without such patchiness (as shown in fig. 8). B, The predicted pattern of abundance of species across such a gradient in productivity for predators and resources (upper part of graph) and consumer-prey species (lower part of graph). See text for additional details.

In addition, the approach implies that the predator and consumer-prey benefit additively from the multiple effects of heterogeneity at different sites. Although this approach seems a somewhat simplistic view of the role of heterogeneity and ignores many of the known effects that occur in spatially explicit models (e.g., Chesson 1986; Kareiva 1986; Pacala 1986; Abrams 1988), it may serve as a heuristic method to determine how robust the predictions derived above may be to potential effects of spatial and temporal heterogeneity in productivity.

The results illustrated in figure 9 show that many of the abrupt changes in the behavior of the model derived above are "smoothed out" by such heterogeneity. Average predator and resource densities are predicted to increase with productivity as above, but the effect is more likely to be gradual as the effects of small-scale heterogeneity are averaged out via changes in the frequency of patches with different productivities. Similarly, the abundance patterns of the consumer-prey species are also predicted to become more continuous over such a productivity gradient, as shown in figure 9.

However, a few new results might be expected. First, there might be more than two consumer-prey coexisting at a time because of the effects of heterogeneity, and thus the shape of the diversity versus productivity curve might peak at a diversity greater than two and have a more continuous appearance than in the absence of such heterogeneity (contrasting fig. 8*B* with fig. 9*B*). Second, owing to this effect, diversity would be predicted to decline at very high productivity even if there were a completely invulnerable consumer-prey species, since it would be predicted to drop to two species from an intermediate peak with more than two consumer-prey species. Finally, correlations in the densities of coexisting species might not necessarily be negative (as was described above) because the within-patch tendency for this to occur would be counteracted by the increased probability that co-occurrence would be facilitated across patches for similar species. This can be seen by comparing the association of densities for similar species in figure 9*B* (i.e., species C and D) and by noting that increases in one species are not necessarily correlated with decreases in a competitor. The tendency for positive correlations to occur (given coexistence among pairs of species) is highest for the species pairs with the most similar ZNGIs along the trade-off axis of exploitation versus predator susceptibility.

DISCUSSION

Predictions concerning the bottom-up and top-down responses of the community to variation in productivity and to predator death rates can be summarized for each of the models as shown in table 1, where they are also contrasted to their effects on food chain models. The results show that in the absence of variation in the number of trophic levels, interesting contrasts appear among the models. The most striking contrast is between the food chain model and the simplest model with two competing consumer-prey species (model 1). The food chain model shows that resource and predator densities respond strongly but that the intermediate consumer-prey is strongly buffered against variation in either productivity or predator loss rates. The reverse is true for the model of two consumer-prey species

TABLE 1

CONTRASTING PREDICTION OF THE EFFECTS OF PRODUCTIVITY AND OF DEATH RATE OF THE TOP PREDATOR ON THE OUTCOME OF FOOD WEB INTERACTIONS

MODEL	RESPONSE VARIABLE							
	BOTTOM-UP EFFECT				TOP-DOWN EFFECT			
	<i>R</i>	<i>P</i>	<i>N_i</i>	<i>S</i>	<i>R</i>	<i>P</i>	<i>N_i</i>	<i>S</i>
With fixed number of trophic levels:								
Food chain (1 consumer-prey species)	i	i	0	NA	d	d	i	NA
Model 1 (2 consumer-prey species)	0	0	h*	i**	d	d	h*	0
Model 2 (<i>N</i> consumer-prey species)	i	i	h*	i**	d	d	h*	d**
Model 3 (<i>N</i> species with local patchiness)	i	i	h*	h	d	d	h*	h
With variation in number of trophic levels:								
Food chain	i	i	i	NA	d	d	i	NA
Model 1	i	i	h*	i**	d	d	h*	d**
Model 2	i	i	h*	i**	d	d	h*	d**
Model 3	i	i	h*	h	d	d	h*	h

NOTE.—Letters designate increases (i), decreases (d), or hump-shaped (h) responses to either the effects of increasing productivity (bottom-up) or increasing predator death rate (top-down). The table shows responses in resource densities (*R*), predator densities (*P*), individual consumer-prey species densities (*N_i*), and species diversity (*S*). A single asterisk denotes that humped responses are expected to all but the least vulnerable species that will increase (potentially asymptotically) in response to the bottom-up and decrease in response to the top-down effects. Double asterisks indicate that the predictions shown correspond to the effect when there is a completely invulnerable resource consumer potentially present. The predictions are for a hump-shaped effect in the absence of such an invulnerable species (see text).

where the predator and resource densities are buffered against such variation in productivity or in predator loss rates but the intermediate consumer-prey species are not. This contrast is not as striking when compositional species turnover in the consumer-prey is possible (models 2 and 3). In this case, the densities of organisms at all trophic levels are affected, with predators and resources being enhanced at higher productivities and with consumer-prey species showing individually humped density responses with a cumulative density (under the simplifying assumption that conversion efficiencies are the same for all organisms) that shows an increase. These models can thus explain positive biomass correlations with productivity for all trophic levels but predict that it will be associated with compositional turnover of species across the gradient. Differences between the models with and without spatial heterogeneity are more subtle and primarily involve the predicted effects of productivity on diversity when there is a completely invulnerable consumer. In the presence of spatial heterogeneity, a hump-shaped diversity/productivity curve is expected, whereas the model without such heterogeneity predicts an overall increasing effect. This model can thus provide an additional explanation for observations of unimodal diversity versus productivity relations, which have been increasingly documented (e.g., Rosenzweig and Abramsky 1993; Tilman and Pacala 1993).

When more than two species are at the intermediate trophic level (i.e., models 2 and 3), there are also contrasting predictions about the expected associations

of species in either a productivity or predator death rate gradient. In the absence of such heterogeneity, the abundances of coexisting competitors are expected to be negatively correlated, whereas in the presence of heterogeneity, correlations might become positive. In both cases, species with adjacent ranks on the susceptibility-exploitation trade-off axis are expected to be more likely to coexist than are species that are less similar. However, in the presence of heterogeneity, there is also the likelihood of a positive association between similarity and the correlations in the abundances of species pairs. These associational patterns are expected only because of the role of species turnover along a strong environmental gradient and would be absent if variation among communities was not strongly associated with environmental change.

This model can provide a basis for synthesizing our understanding of the interaction between two modes of community regulation by showing how interactions mediated by shared resources (e.g., MacArthur 1972; Tilman 1982) and those mediated by the action of predators (e.g., Holt 1977; Oksanen et al. 1981) interact. Previous evaluations of the roles of bottom-up and top-down regulation on community structure have too often dichotomized rather than synthesized these two classes of species interactions. Although previous models have investigated such interactions between predation and competition (i.e., Vance 1974; Walters et al. 1987; Leibold 1989; Abrams 1993; Grover 1994; Holt et al. 1994), these have not investigated the role of species compositional turnover. The model described here is most striking by showing that such compositional turnover of species can qualitatively alter predictions about the responses of communities to either top-down or bottom-up regulation (table 1).

In general, observations of natural communities (especially freshwater lentic communities) support the predictions of the models described above. They generally show positive correlations among biomass relations at all trophic levels, in response to variation (natural or experimentally imposed) in productivity, and alternating responses among adjacent trophic levels, in response to variation in top predators (usually experimentally imposed) as documented in numerous experimental studies (reviewed in Leibold 1989) and natural surveys (e.g., Mills and Shiavone 1982; McQueen et al. 1986; McCauley et al. 1988; Agusti et al. 1991). Furthermore, they are supported by observations indicating compositional change of species with different ecological traits thought to affect predator susceptibility and exploitation ability (e.g., Watson and McCauley 1988; Agusti et al. 1991).

Armstrong (1979), Grover (1994), and Holt et al. (1994) develop a slightly different approach to modeling the effect of a keystone predator on two competing consumer-prey species than that developed above and in modeling "assembly rules" for food webs with prey-specific predators: Their model uses a mass-balance equation to derive an additional set of equilibrium constraints on the isoclines of the two consumer-prey species in the space defined by predator and resource density. The results are congruent with those obtained above for model 1, using vectors to examine the roles of the consumer-prey in mediating interactions between predator and resource density, and they confirm the results of Phillips's (1974) and Abrams's (1993) algebraic analyses of food web structure.

However, the vector notation is not dependent on a mass-balance constraint, as their model is. It would therefore apply to food webs that might ultimately depend on energetic constraints (e.g., light limitation) and "sink" resource populations, as well as to nutrient-limited food webs and to portions of food webs competing for "biotic" resources (i.e., "source webs" sensu Cohen et al. 1990) where a mass-balance equation may not be appropriate. The graphical approach developed here suggests that their predictions for models with more specific constraints and assumptions are qualitatively robust to many of these assumptions. The graphical approach developed here using impact vectors is also more convenient for future models exploring interactions involving multiple resources and predators since they can be linked directly to current models of resource competition (e.g., MacArthur 1972; Tilman 1982) and because the model can be conveniently extended to investigate the role of species turnover along environmental gradients (as described above in models 2 and 3).

The contrast between the models described here and those involving specialist predators (Grover 1994) suggests that specialist predators are less likely to enhance regional species diversity but more likely to be associated with high local diversity than are generalist predators. A unique feature of the effect of specialist predators is that when productivity is high enough to allow such a species to invade, further increases in productivity will affect the densities only of the invulnerable consumer, and resource and predator densities will remain constant, as suggested by Phillips (1974). This type of situation will also prevent productivity from having any further effects on the number of coexisting species unless some other form of population regulation (e.g., intraspecific interference competition) also occurs. Thus, on a local level, specialist predators who feed on only one consumer-prey (in this model, on good resource exploiters) consistently enhance local diversity by allowing coexistence with an invulnerable consumer (see Cornell and Lawton 1993). In contrast, generalist predators will tend to have less consistent effects in allowing coexistence between any particular pair of species because they will enhance coexistence only at particular productivity levels because of the additional effects of "apparent competition." However, on a larger regional scale involving ecosystems with a broad range of productivities, each generalist predator will enhance diversity by allowing coexistence among large numbers of pairs of species (in a model without local heterogeneity) and by allowing more than two species to coexist locally (in models with local heterogeneity). Neither of these effects will occur with specialist predators, and consequently specialist keystone predators are not as likely to produce "humped" diversity curves (relating local diversity to productivity) as are generalist predators. Such a distinction between communities dominated by specialist versus generalist predators might also explain some important suggested differences in community-level responses to productivity among different types of ecosystems (see Strong 1992; Hairston and Hairston 1993).

Finally, this model also provides an additional explanation for unimodal relations between diversity and productivity to those listed by Rosenzweig (1992). Several recent studies have increasingly documented such unimodal diversity-productivity relations and often cite Tilman's hypothesis (Tilman 1982; but see

Tilman and Pacala 1993) as a possible explanation. Although there are a number of other possibilities (reviewed in Rosenzweig 1992; Rosenzweig and Abramsky 1993; Tilman and Pacala 1993), none of these studies have mentioned the possibility that interactions involving keystone predators might be important. Given the complexity of trophic webs documented in recent compilations (e.g., Pimm 1982; Cohen et al. 1990) and the frequent observation of more "intermediate" species than either "basal" or "top" species, the model presented here seems like a particularly plausible one in cases where there is strong reciprocal feedback among populations of organisms at different trophic levels.

In a very broad sense, this model can be a useful way to explore how species interactions involving multiple trophic levels interact with species interactions at a single trophic level. It thus provides a link between models that focus on food chains (e.g., Oksanen et al. 1981) and those that focus on competition within a trophic level (e.g., MacArthur 1972; Tilman 1982; Abrams 1988). Further, since the model is developed using very similar graphical methods and a similar framework of assumptions (Leibold 1995), it can provide a useful context for developing diagnostic predictions for alternate possible explanations for empirical work. Elaborations of this basic model should thus provide additional insights about how species interactions can structure entire communities of organisms and not just limited subsets of putative competitors or predator-prey pairs (e.g., Abrams 1992).

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APPENDIX

ANALYTICAL SOLUTIONS TO GRAPHICAL RESULTS

CONSTANT PARAMETERS

The quantitative analysis of feedback loops (Levins 1975; Puccia and Levins 1985) can be used to analyze a model of two consumer-prey species that share a single "abiotic" and "nonsequestered" limiting resource and a single predator, as shown in the loop diagram illustrated in figure 1. Using the same notation as in the food chain model, and using subscripts to denote parameters associated with the two alternate consumer-prey species, the population dynamic equations describing such a system are

$$\begin{aligned} dP/dt &= P(a_1 f_1 N_1 + a_2 f_2 N_2 - d), \\ dR/dt &= R[t(s/R - 1) - g_1 N_1 - g_2 N_2], \\ dN_1/dt &= N_1(g_1 c_1 R - f_1 P - m_1), \end{aligned}$$

and

$$dN_2/dt = N_2(g_2 c_2 R - f_2 P - m_2).$$

The Jacobean matrix describing the system dynamics at equilibrium is

$$\begin{array}{cccc} 0 & 0 & a_1 f_1 P^* & a_2 f_2 P^* \\ 0 & -ts/R^* & -g_1 R^* & -g_2 R^* \\ -f_1 N_1^* & g_1 c_1 N_1^* & 0 & 0 \\ -f_2 N_2^* & g_2 c_2 N_2^* & 0 & 0. \end{array}$$

In the linear case where all the parameters are constants, the equilibrium densities of the four populations are

$$\begin{aligned} P^* &= (g_2 c_2 m_1 - g_1 c_1 m_2) / (f_2 g_1 c_1 - f_1 g_2 c_2), \\ R^* &= (m_1 f_2 - m_2 f_1) / (f_2 g_1 c_1 - f_1 g_2 c_2), \\ N_1^* &= [a_2 f_2 (s/R^* - 1) - dg_2] / (a_2 f_2 g_1 - a_1 f_1 g_2), \end{aligned}$$

and

$$N_2^* = [dg_1 - a_1 f_1 (s/R^* - 1)] / (a_2 f_2 g_1 - a_1 f_1 g_2).$$

These results show that P^* and R^* do not change with s (the bottom-up effect of productivity) or d (the top-down effect of predator control) but that N_1^* and N_2^* do so linearly and in opposite directions for each of these variables. Furthermore, they show that the response of N_1^* is opposite in sign to that of N_2^* .

The stability of the system can be analyzed by defining feedback at the various levels of the system as outlined by Puccia and Levins (1975) as follows:

$$\begin{aligned} F1 &= -ts/R^*, \\ F2 &= -(g_1^2 R^* c_1 N_1^* + g_2^2 R^* c_2 N_2^* + a_1 f_1^2 P^* N_1^* + a_2 f_2^2 P^* N_2^*), \\ F3 &= -(tsP^*/R^*)(a_1 f_1^2 N_1^* + a_2 f_2^2 N_2^*), \end{aligned}$$

and

$$F4 = (g_1 c_1 a_1 f_1 f_2 g_2 + g_2 c_2 a_2 f_1 f_2 g_1 - g_1^2 c_1 a_2 f_2^2 - g_2^2 c_2 a_1 f_1^2) P^* N_1^* N_2^* R^*.$$

The conditions for local stability are that all these values be less than zero and that

$$F1F2 + F3 = ts(g_1^2 c_1 N_1^* + g_2^2 c_2 N_2^*) > 0.$$

Given positive values for each of the parameters in the model (i.e., by definition given the conventional meanings of predation), the local stability of the equilibrium is completely dependent on $F4$. If we assume without loss of generality that $g_1 c_1 / f_1 < g_2 c_2 / f_2$, it can be shown that $F4$ is negative only if $a_1 f_1 / g_1 < a_2 f_2 / g_2$. Since $g_i c_i / f_i$ is the slope of the ZNGI in the graphical model and $a_i f_i / g_i$ is the slope of the impact vector, these results show that the species that is more vulnerable to predation must be the better resource exploiter and must also have the greatest "progressive ecological efficiency." Using the equations for the equilibrium densities, this result also shows that the better resource exploiter is replaced by the less vulnerable competitor as productivity increases. If the resource is modeled as a "biotic" resource and the function $r(1 - R/K)$ is used instead of $t(s/R - 1)$, then $F1 = -r/K$ and $F3 = -r(a_1 f_1^2 N_1^* + a_2 f_2^2 N_2^*)/K$. Stability still depends on $F4$ as defined above since $F1F2 + F3$ is still positive.

TYPE II FUNCTIONAL RESPONSES AND INDUCED DEFENSES

It is not necessarily clear how such a model would be influenced by having density-dependent parameters. Obviously if the density dependence is strong enough to change the sign of the interaction coefficients, the results would differ wildly. Also, nonlinear effects can change the stability properties of the model and in some cases change the

patterns of feedback in the system. One particular problem that might severely limit the utility of the model is that the top predator may not have a linear functional response (Holling 1959). Clearly, functional responses involving substantial switching of preferences would dramatically alter the results shown above by making the impact vectors strongly dependent on consumer-prey density. Such responses are beyond the scope of the current graphical approach. However, the robustness of the results described above can be evaluated for the simple case where predator satiation can be described by an effect of the weighted sum of the consumer-prey on the feeding rate, assuming that relative preferences do not change. To do this, we substitute f_i by $f_i/(w_1N_1 + w_2N_2 + w_3)$ in the dynamic equations of the model. The impact of bottom-up and top-down effects of productivity and predator death rates on equilibrium densities can be made using feedback analysis (Puccia and Levins 1985) to show that

$$\partial P^*/\partial s = 0$$

$$\partial R^*/\partial s = 0$$

$$\partial N_1^*/\partial s = a_2 f_2 N_1^* N_2^* P^* (g_2 c_2 f_1 - g_1 c_1 f_2) / [F4(w_1 N_1^* + w_2 N_2^* + w_3)^2]$$

$$\partial N_2^*/\partial s = -a_1 f_1 N_1^* N_2^* P^* (g_2 c_2 f_1 - g_1 c_1 f_2) / [F4(w_1 N_1^* + w_2 N_2^* + w_3)^2]$$

and

$$\partial P^*/\partial d = 0$$

$$\partial R^*/\partial d = 0$$

$$\partial N_1^*/\partial d = -g_2 N_1^* N_2^* P^* R^* (g_2 c_2 f_1 - g_1 c_1 f_2) / [F4(w_1 N_1^* + w_2 N_2^* + w_3)]$$

$$\partial N_2^*/\partial d = g_1 N_1^* N_2^* P^* R^* (g_2 c_2 f_1 - g_1 c_1 f_2) / [F4(w_1 N_1^* + w_2 N_2^* + w_3)],$$

where

$$F4 = (g_1 c_1 a_1 f_1 f_2 g_2 + g_2 c_2 a_2 f_1 f_2 g_1 - g_1^2 c_1 a_2 f_2^2 - g_2^2 c_2 a_1 f_1^2) P^* N_1^* N_2^* R^* / (w_1 N_1^* + w_2 N_2^* + w_3)^2.$$

Thus, the rate of change of the equilibrium densities with respect to s will be the same as in the linear model since $F4$ of the linear model is equal to $F4$ of this model times $(w_1 N_1^* + w_2 N_2^* + w_3)^2$, and the equations describing the effect of productivity change on changing the equilibrium densities are identical. Assuming only positive values for weighing function, the response of the community to changes in the predator death rate are also qualitatively identical, although they will be quantitatively different since the denominator of the relation differs somewhat. These results would not hold when the relative per capita feeding rates of the predator on the two consumer-prey species are density dependent (i.e., when there is some degree of change in the predator's selectivity and f_1/f_2 is not a constant). The stability conditions involving feedback at different levels show that feedback in this model is negative for $F1$, $F2$, and $F3$; that $F3$ is larger than $F1$ times $F2$; and that the conditions allowing $F4$ to be negative are the same as the linear model. In sum, the only difference in the two models is that actual equilibrium values will differ from the linear model by some constant (with respect to productivity) that is a complex function of the functional response parameters.

A similar analysis can be made to show that the model might be robust to a number of other nonlinearities that do not affect the relative (though not absolute) values of the $a_i c_i f_i$ and g_i parameters. For example, consider the effect of consumer-prey density on the resource (g_i) that can be described as the weighted sum of the consumer-prey densities (i.e., substituting g_i with $g_i/(w_1 N_1 + w_2 N_2 + w_3)$). Such effects could arise if there are consumer-prey density-dependent inducible responses by the resource to grazing that do not change the relative vulnerabilities of the resource to the two consumer-prey. The effects of parameter changes in productivity and in predator death rates will again be

qualitatively similar to the linear model. In sum, this analysis shows that the results of the graphical approach have some degree of robustness to nonlinear effects when these nonlinearities do not alter the symmetry that implies that the better resource exploiter is less vulnerable to predators and has a greater progressive ecological efficiency.

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