

Effects of Competition, Predation, and Dispersal on Species Richness at Local and Regional Scales

Jonathan B. Shurin^{1,*} and Emily G. Allen^{2,†}

1. Department of Ecology and Evolution, University of Chicago, Chicago, Illinois 60637;

2. Committee on Evolutionary Biology, University of Chicago, Chicago, Illinois 60637

Submitted January 23, 2001; Accepted June 18, 2001

ABSTRACT: This study explores the consequences of predator-mediated coexistence among competitors for patterns of incidence and diversity at local and regional scales. We develop a model that draws on elements of metapopulation models of competitors and food chains by allowing competitors to coexist locally in the presence of predators but not in their absence. The model predicts that predators promote regional coexistence by greatly expanding the range of conditions under which two competitors persist at equilibrium. Predators could have positive or negative effects on mean local diversity within the region depending on their dispersal rates, those of the prey, and their effects on prey extinction rates. The presence of predators increased the abundance of inferior competitors, thereby expanding the conditions for positive relationships between local and regional diversity. The model also predicted positive correlations between local diversity of predators and prey. These predictions were supported by patterns of phytoplankton, zooplankton, and fish species richness among lakes. The model may help to resolve the apparent contrast between linear patterns of local and regional richness and experimental evidence for strong invasion resistance and rapid dispersal in zooplankton.

Keywords: coexistence, dispersal, keystone predators, local and regional processes, metapopulation.

Hypotheses for the maintenance of species diversity typically focus on one of two distinct spatial scales: local and regional. The local scale refers to small, relatively homogeneous patches of habitat, while the regional scale consists of systems of patches within broad heterogeneous areas.

* Present address: National Center for Ecological Analysis and Synthesis, Santa Barbara, California 93101; e-mail: shurin@nceas.ucsb.edu.

† E-mail: egallen@uchicago.edu.

Local-scale hypotheses deal with aspects of the physical or biological environment that affect the persistence of populations within patches. Regional hypotheses, such as island biogeographic or metapopulation theories, focus on the role of movement of species among multiple patches (MacArthur and Wilson 1967; Hanski and Gilpin 1997). Local hypotheses often predict that communities are assembled according to relatively deterministic rules and that species composition should therefore be closely related to aspects of the local environment. In contrast, regional hypotheses predict that assemblages form by the stochastic processes of colonization and local extinction and should therefore be unpredictable based on local habitat features. In many systems, there is evidence that local and regional processes jointly regulate species diversity and composition (Burke and Grime 1996; Tilman 1997; Connolly and Roughgarden 1998; Karlson and Cornell 1998; Shurin 2000; Shurin et al. 2000). However, the question of the relative contributions of local and regional processes to generating geographic variation in community structure remains contentious and poorly understood (Ricklefs 1987; Cornell and Lawton 1992; Caswell and Cohen 1993; Cornell and Karlson 1997; Huston 1999; Lawton 1999; Srivastava 1999; Gaston 2000).

One approach to estimating the roles of local and regional processes is to examine the shape of the relationship between local and regional species richness. If local interactions limit the number of species capable of coexisting, then local diversity (the average number of species found within a patch) is expected to approach an upper asymptote with increasing regional diversity (Terborgh and Faaborg 1980; Ricklefs 1987; Cornell and Lawton 1992; Cornell and Karlson 1997; Lawton 1999). Alternatively, if the supply of colonists from the region is the most important factor limiting the number of species found within sites, then local richness is expected to increase continuously as a function of the size of the regional species pool. Recent reviews have concluded that linear or weakly curvilinear patterns of local and regional richness characterize many diverse groups of organisms and that regional processes therefore generally dominate in structuring communities

(Cornell and Karlson 1997; Lawton 1999; Srivastava 1999; Gaston 2000). However, a number of studies have raised issues with the interpretation of these patterns, suggesting that explanations other than strong dispersal limitation and weak local interactions may be invoked to account for linear relationships between local and regional diversity (Caswell and Cohen 1993; Huston 1999; Fox et al. 2000; Loreau 2000). In fact, previous work found that although freshwater zooplankton show linear patterns of local and regional richness on a global scale (Shurin et al. 2000), 11 local pond communities resisted invasion by >90% of the species from the regional pool and many potential invaders were repelled by interactions with the resident biota (Shurin 2000). In this study, we evaluate one potential explanation for linear patterns of local and regional richness in the presence of rapid dispersal and strong local interactions.

The hypothesis that local interactions set upper limits on local diversity is based on an inhibitional model of community assembly in which local processes act to exclude species. Resource competition is one form of local interaction that is expected to limit local diversity (Tilman and Pacala 1993). Models have shown that communities of competitors become increasingly resistant to invasion as they accumulate species (Case 1990; Drake 1991; Tilman 1994). However, in nature, species interact in ways that facilitate, as well as inhibit, one another's abilities to colonize patches (Amarasekare 2000). For instance, species can have positive effects on local diversity through mutualistic interactions or modification of the physical environment (Holmgren et al. 1997; Bertness et al. 1999; Goldberg et al. 1999; Levine 2000; Menge 2000). In addition, predators may indirectly facilitate invasion by species at lower trophic levels that are otherwise excluded by interactions with their prey (Paine 1966; Vance 1974; Grover 1994; Holt et al. 1994; Leibold 1996). Natural communities are likely to be structured by a mixture of positive and negative interspecific interactions (Holmgren et al. 1997; Levine 2000; Menge 2000). In this study, we examine the consequences of predator-facilitated coexistence among competitors for species richness at local and regional scales. The model we present is a hybrid of metapopulation models of competition and predation. We incorporate predator-mediated coexistence by allowing competitors to coexist locally in the presence of predators but not in their absence.

We use this model to address two questions. First, under what conditions do predators promote or reduce local versus regional richness among competing prey? Predators in nature can have highly variable effects on local diversity (Sih et al. 1985; Schoener and Spiller 1996; Gough and Grace 1998; Proulx and Mazumder 1998; Siemann 1998; Carson and Root 2000; Shurin 2001). Predators may sup-

press some prey species through direct trophic interactions and thereby indirectly facilitate other species, either by release from competitors (i.e., keystone predation) or intermediate predators (i.e., trophic cascades; Paine 1966; Vance 1974; Hunter and Price 1992; Holt et al. 1994; Leibold 1996). The net effects of predators on local diversity depend on the number of species that are excluded versus facilitated within a patch (Schoener and Spiller 1996). At the regional scale, spatial heterogeneity in predator communities often promotes regional diversity among species that cannot coexist locally. For instance, the presence of ponds with and without fish or salamander predators allows regional coexistence by distinct amphibian, insect, and zooplankton communities (Dodson 1970, 1974; Sprules 1972; Tonn and Magnuson 1982; Arnott and Vanni 1993; Werner and McPeck 1994; Schneider and Frost 1996; Wellborn et al. 1996; McPeck 1998; Zimmer et al. 2000). The effects of predators on local and regional diversity are likely to depend on the relationships among different ecologically important traits in the prey community (i.e., susceptibility to predators and competitive or dispersal abilities). Here we explore the range of conditions under which predators promote or prevent local versus regional coexistence among prey.

The second question asks how species richness at local and regional spatial scales are expected to co-vary when predators mediate local coexistence among prey. We begin by showing that local richness approaches an upper asymptote with increasing regional richness when species interact only through resource competition. We then contrast the relationship between local and regional species richness in metapopulation models of competitors in the presence and absence of keystone predators. The model incorporates dispersal among patches by predators and prey, competition among prey within patches that is mediated by predators, and predator effects on prey extinction rates. We ask how predators influence the regional abundances of species of different competitive ranks. If predators enhance the abundance of subordinate competitors, then they may cause otherwise saturating functions of local and regional species richness among competitors to become linear. Several authors (Cornell and Lawton 1992; Lawton 1999) have suggested that predators offer one potential explanation for the predominance of linear local/regional richness patterns. The purpose of this exercise is to explore the theoretical plausibility of predator-mediated coexistence as an explanation for linear patterns of local and regional richness in the presence of weak dispersal limitation and strong local interactions (Shurin 2000; Shurin et al. 2000).

Models

Our model incorporates elements of metapopulation models of competitors (Levins and Culver 1971; Horn and MacArthur 1972; Hastings 1980; Nee and May 1992; Tilman 1994) and food chains (Holt 1993, 1997; May 1994) as well as nonspatial models of predator-mediated coexistence among competitors (Vance 1974; Grover 1994; Holt et al. 1994; Leibold 1996). It is based on the axiom that, in the absence of mitigating factors, the maximum number of prey capable of coexisting locally at equilibrium is equal to the number of limiting resources plus the number of predators (Tilman and Pacala 1993; Grover 1994; Holt et al. 1994; Leibold 1996). The model is similar to those presented by Caswell (1978), Hastings (1978), and Crowley (1979) with several important differences. First, in our model, predators and prey may coexist indefinitely. The earlier models were motivated by communities of sessile species where each "patch" is an individual organism that is deterministically consumed by a predator in a certain time period. Our model is representative of systems where patches represent local populations, as in the lakes and ponds that motivated this work (Shurin 2000; Shurin et al. 2000). Second, we assume that prey populations go extinct at some background rate in the absence of predators. Third, propagules originate from all patch states containing a given species regardless of the presence of predators or competitors. Allowing only one patch state to produce colonists makes the model analytically tractable (Caswell 1978; Hastings 1978; Crowley 1979) but unrealistic for representing the systems in which we are interested. We contrast a metapopulation model of predator-facilitated coexistence with models of competitors and food chains in order to assess the effects of keystone predators on patterns of diversity at local and regional scales.

Metapopulation Model of Competition

Here we assume that two species are limited by a single resource and that only one can occupy a homogenous local patch at equilibrium. Models of competition between two species incorporating metapopulation dynamics have been formulated by Levins and Culver (1971), Horn and MacArthur (1972), Hastings (1980), Nee and May (1992), and Tilman (1994) and can be written as

$$\frac{dN_1}{dt} = c_1 N_1 (1 - N_1) - e N_1, \quad (1a)$$

$$\frac{dN_2}{dt} = c_2 N_2 (1 - N_1 - N_2) - c_1 N_1 N_2 - e N_2, \quad (1b)$$

where N_i represents the proportion of the total habitat

patches occupied by species i , and c_i and e_i are the colonization and extinction probabilities of species i . In the model, species 1 competitively excludes species 2 from patches. The model assumes that local interactions occur on a faster time scale than colonization-extinction dynamics. That is, species are always at their equilibrium abundance within patches so that species 2 is excluded from patches containing species 1 and species 1 immediately displaces species 2 when it invades a patch with species 2.

An interesting prediction derived from the above model is that an infinite number of competitors can potentially coexist regionally at equilibrium on a single limiting resource, provided there is a sufficiently strong interspecific trade-off between colonization or extinction rates and competitive rank (Tilman 1994). Assuming that both species have the same extinction rate ($e_1 = e_2 = e$), the equilibrium patch occupancies with both species present are

$$N_1^* = 1 - \frac{e}{c_1}, \quad (2a)$$

$$N_2^* = \frac{c_2 e - c_1^2}{c_1 c_2}. \quad (2b)$$

In this system, mean local diversity within the region (D) is equal to the fraction of patches occupied (the average number of species found within a given patch). Therefore, D is the sum of the occupancies of the two species ($D = N_1^* + N_2^*$). In order for D to increase linearly as a function of regional richness (i.e., as we go from a system with species 1 alone to species 1 and 2 together), N_2^* must equal N_1^* . That is, linear patterns of local and regional richness require that each successive addition to the regional species pool occupies, on average, as much of the habitat as the previous new species. This condition requires that

$$c_2 = \frac{c_1^2}{2e - c_1}. \quad (3)$$

If species are added in order of increasing competitive rank (i.e., if species 1 invades a region with only species 2 present), then local diversity will increase linearly only if $c_2 = 2e - c_1$. However, under some conditions, species 1 will exclude species 2. Because it is unclear how adding species in reverse order of competitive rank will affect regional diversity, we only consider cases where the regional pool is assembled in order of dominance for the models that follow.

Figure 1 shows the range of parameter values where N_1 and N_2 coexist (fig. 1A) and where $N_1^* = N_2^*$ (the condition for linear local/regional patterns, fig. 1B). Species

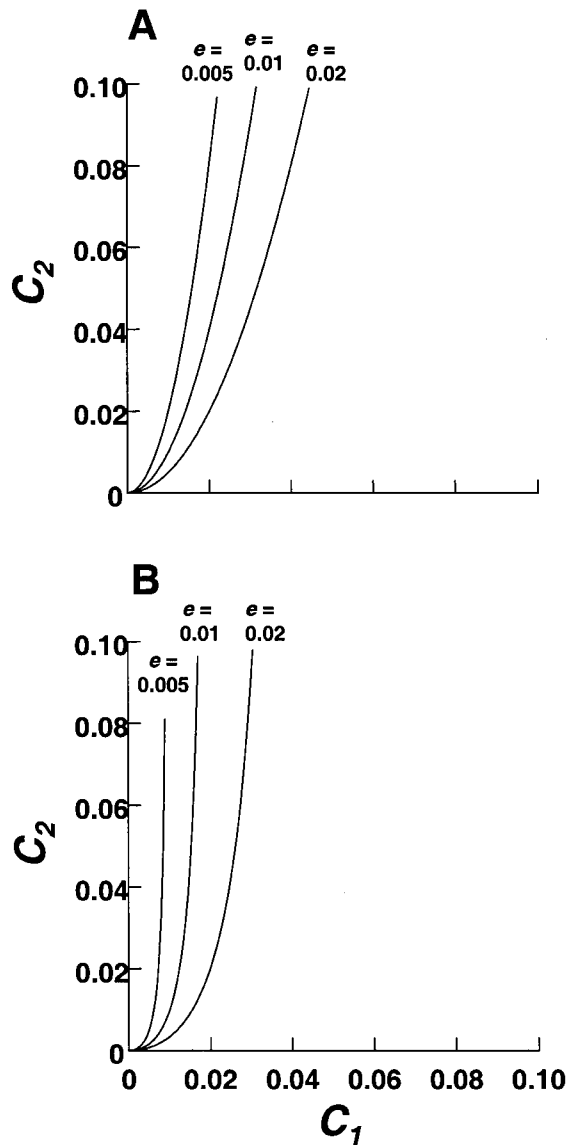


Figure 1: A, Conditions for regional coexistence of two competitors. Species 2 has positive abundance to the left of the lines shown for each extinction rate. B, Conditions where species 2 occupies the same proportion of patches as species 1 (the requirement for linear increases in local diversity when species 2 invades regionally with species 1). Species 2 has a greater occupancy than species 1 to the left of the lines shown.

2 must have a higher dispersal rate than species 1 in order to persist and will occupy as much of the habitat as species 1 only if it has a much greater colonization rate. The conditions for regional coexistence and for linear patterns of local and regional richness become increasingly restrictive as more species are added to the regional pool (Tilman 1994). If species are added in random order with respect to their competitive rank, each new species is excluded

from local patches by an average of 0.5 more superior competitors than the previous new species. Thus, each addition to the regional pool must have a greater colonization rate in order to make an equal contribution to mean local diversity (D). In addition, the rules of competitive exclusion constrain D to be <1 (as long as $c < 1$ and $e > 0$ for all species) because only one species ever occupies a patch. The metapopulation model of competition therefore predicts that mean local diversity approaches an upper limit as the regional pool increases when species exclude one another from patches.

Metapopulation Model of a Food Chain

Models of predator and prey interaction in a metapopulation were developed by Holt (1993, 1997) and May (1994). With one species and its specialist predator, patches can be either occupied by the prey alone (N) or the prey and its predator together (P). The model assumes that the predator only becomes extinct when the prey does, that the prey's extinction probability is e when alone and e_p when it coexists with the predator, and that prey propagules originate from patches with and without the predator at a constant per capita rate c_N . The dynamics of the system can be described by

$$\frac{dN}{dt} = c_N(N + P)(1 - N - P) - c_pNP - eN, \quad (4a)$$

$$\frac{dP}{dt} = c_pNP - e_pP, \quad (4b)$$

where c_p is the colonization rate of the predator. Here, mean local diversity at the prey trophic level (D) is equal to $N^* + P^*$, where $N^* = e_p/c_p$ and P^* is given by

$$P^* = \frac{c_N - c_pN - 2c_NN \pm (c_N^2 - 2c_NNc_p + c_p^2N^2 + 4c_NN^2c_p - 4Nc_Ne)^{1/2}}{2c_N}. \quad (5)$$

In this case, if the prey's extinction rate is the same with and without the predator ($e = e_p$), then local diversity at the prey trophic level depends only on the colonization and extinction parameters of the prey.

Predator-Mediated Coexistence

In order to incorporate keystone predation in the above models, we consider that the inferior competitor (species 2) is excluded locally from patches by species 1 except in the presence of the predator. Figure 2 illustrates the al-

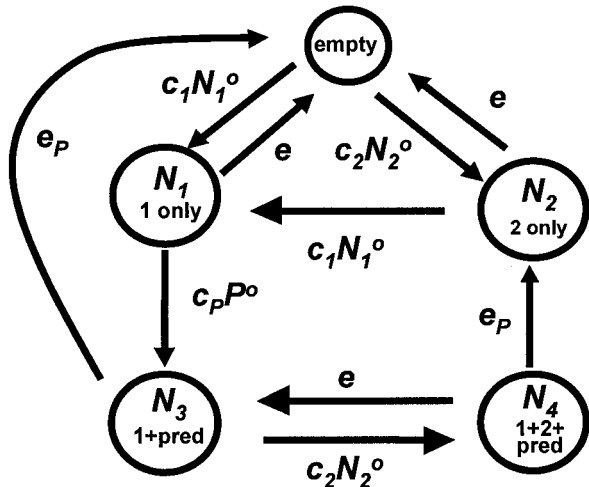


Figure 2: Schematic diagram of the metapopulation model of predator-mediated coexistence. Circles represent state variables in equations (6a)–(6d), and arrows indicate transitions among states. The labels on the arrows indicate the probability of a given transition for a patch in the state from which the arrow originates.

lowable states and transitions in the model under the rules governing local coexistence. We assume, as in the metapopulation food chain model, that the predator only goes extinct from a patch when its prey (species 1) becomes extinct and that species 1 has extinction rates of e (when alone) and e_p (when it coexists with the predator). An inferior competitor, species 2 is excluded from patches occupied by species 1 except in the presence of the predator. Species 2 goes extinct at a rate (e) that is unaffected by the presence of the predator. Occupied patches can potentially be in one of four states: N_1 = species 1 alone, N_2 = species 2 alone, N_3 = species 1 and the predator (P), and N_4 = all three species together. The dynamics of the system are described by the following equations:

$$\frac{dN_1}{dt} = c_1 N_1^o (1 - N_1^o) - e N_1 - c_p P^o N_1, \quad (6a)$$

$$\frac{dN_2}{dt} = c_2 N_2^o (1 - N_1^o - N_2) + e_p N_4 - c_1 N_1^o N_2 - e N_2, \quad (6b)$$

$$\frac{dN_3}{dt} = c_p P^o N_1 + e N_4 - c_2 N_2^o N_3 - e_p N_3, \quad (6c)$$

$$\frac{dN_4}{dt} = c_2 N_2^o N_3 - (e + e_p) N_4. \quad (6d)$$

States marked by “ o ” indicate the total proportion of states containing the species given (i.e., $N_1^o = N_1 + N_3 + N_4$, $N_2^o = N_2 + N_4$, and $P^o = N_3 + N_4$). Thus, the model assumes that colonists originate from all patches containing

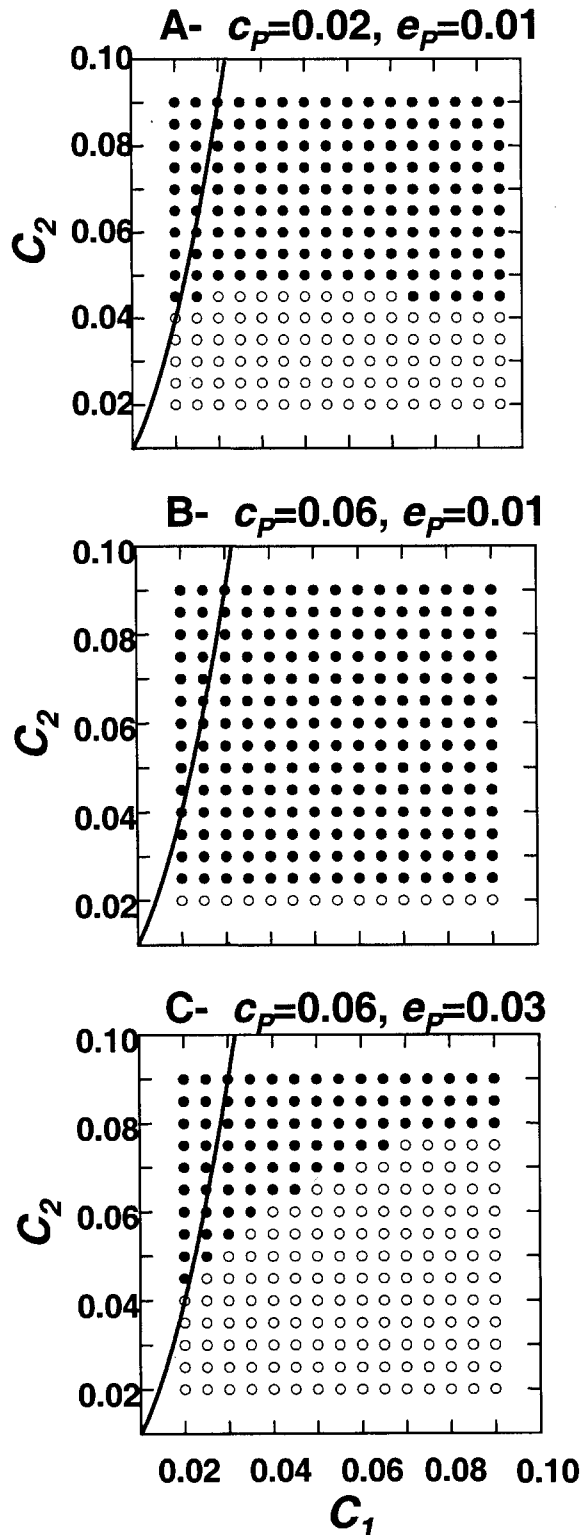
a given species at a constant rate (i.e., the presence of predators or competitors has no effect on the probability that a patch produces propagules). The proportion of empty patches (N_0) is equal to $1 - N_1 - N_2 - N_3 - N_4$, and local diversity at the prey trophic level at equilibrium is

$$D = N_1^* + N_2^* + N_3^* + 2N_4^*. \quad (7)$$

Five sets of equilibria involving positive nonzero densities of any of the three species are possible from the above equations (fig. 2). Species 1 or 2 may persist alone, in which case the equilibrium occupancy of the species is $N_i^* = 1 - e_i/c_i$. If the two competitors coexist regionally but the predator is unable to persist, then the model is identical to the two-species competition model described above. When species 1 and the predator persist but species 2 is excluded, the model collapses onto the metapopulation model of a food chain. When all three species coexist, N_1^* (the equilibrium density of patches containing only species 1) is e_p/c_p , indicating that N_1 depends only on the predator’s colonization rate and the rate at which it drives the prey extinct. The steady state densities of the other three patch states are all given by the roots of fourth-order polynomials.

The model of predator-mediated coexistence contains four state variables (N_1 , N_2 , N_3 , and N_4) and five parameters (c_1 , c_2 , c_p , e , and e_p). These parameters allow us to explore the consequences of variation in dispersal ability and susceptibility to extinction in the presence of predators. Our goals are to understand how these species traits influence coexistence at local and regional scales. Metapopulation models of competition (Levins and Culver 1971; Horn and MacArthur 1972; Hastings 1980; Nee and May 1992; Tilman 1994) predict that, in order for two species to coexist regionally, the inferior competitor must be a sufficiently superior disperser (fig. 1). Nonspatial models of keystone predation predict that a species can coexist locally with a competitive dominant if it is less susceptible to the predator (Vance 1974; Holt et al. 1994; Leibold 1996). Here we explore the consequences of trade-offs in three dimensions (competitive rank, dispersal ability, and vulnerability to predator-induced extinction) for local and regional coexistence of the two prey. We only consider cases where the predator increases its prey’s extinction rate and has no impact on its rate of dispersal. Although cases may exist where predators either decrease prey extinction rates (for instance, by stabilizing population dynamics) or alter its colonization rate (perhaps by causing prey to emigrate from patches at a higher rate), we do not consider the implications of these possibilities for the predictions we derive.

In order to explore the conditions under which pred-



ators promote or prevent local versus regional coexistence, we obtained numerical solutions to equations (6a)–(6d) across a range of values for c_1 , c_2 , c_p , and e_p . The extinction rate of the prey (e) was set to a constant value of 0.01. We then systematically varied the values of the four parameters of interest from 0.02 to 0.09 in intervals of 0.005 (15 different values of each parameter) and used a computer algorithm to search for values of the four state variables where equations (6a)–(6d) were equal to 0. We therefore solved the equations with 15 values of each of four parameters (15^4 combinations = 50,625 solutions). We chose colonization rates to be greater than extinction because species that go extinct faster than they colonize patches are unable to persist. In addition, if colonization greatly exceeds extinction, then species essentially fill all of the available habitat. We therefore used values where colonization was greater than extinction but of a similar magnitude. We varied the initial occupancy of the four patch states over 20 different combinations between 0.1 and 0.9 of the habitat. Twenty starting points were used to insure that we identified all possible interior solutions to the equations (i.e., equilibria with all three species present). For all combinations of parameter values, the equations eventually converged on locally stable equilibria.

Effects of Predators on Regional Diversity

Keystone predators clearly expand the range of conditions under which two competitors coexist regionally. Figure 3 shows the combinations of c_1 and c_2 for which the two prey persist in the community for three combinations of c_p and e_p . The parameter values correspond to low predator colonization rates (c_p) and low effects on prey extinction (e_p , fig. 3A), high c_p with low e_p (fig. 3B), and high c_p with high e_p (fig. 3C). The area to the left of the curved line in each graph shows the region of the parameter space where the two competitors coexist regionally in the absence of predators (in the metapopulation model of competition, as in fig. 1A). The presence of the predator greatly increases the range of the parameter space where both competitors are present. Increasing the predator’s colonization rate enhances regional coexistence of the competitors when e_p is

Figure 3: Plots showing the conditions where two competitors coexist regionally at equilibrium. Each point indicates an equilibrium based on solutions to equations (6a)–(6d). Black symbols indicate that species 1 and 2 coexist (a two-species equilibrium), and white symbols indicate that only the dominant competitor (species 1) persists. The two species coexist regionally in the absence of predators only in the region to the left of the curved line. All black points to the right of the line indicate equilibria where the predator facilitates coexistence by the two prey when species 1 would otherwise exclude species 2.

small (e.g., cf. fig. 3A, 3B). Increasing the colonization rate of species 1 (c_1) could actually increase the likelihood that species 2 was able to persist (as in fig. 3A). This occurred because the density of patches containing the predator depends on c_1 , while the density of patches in state N_1 (that are uninhabitable by species 2) does not. Increasing the impact of the predator on prey extinction rate (e_p) makes it more difficult for species 2 to invade the system. This somewhat counterintuitive prediction results from the fact that N_1 (the density of patches occupied by species 1 alone) is equal to e_p/c_p . Increasing e_p therefore increases N_1 and also makes it more difficult for the predator to persist in the system. Since species 2 cannot invade patches in state N_1 , increasing e_p can result in species 2 being excluded from the community (cf. fig. 3B, 3C).

Another interesting prediction derived from the above model is that the inferior competitor (species 2) is no longer required to be a superior disperser in order to coexist regionally with species 1, as in the two-species model of competition (fig. 1). Prey species can coexist with dominant competitors that are also superior dispersers when the predator is sufficiently abundant (for instance, in the lower right corner of fig. 3B). Colonization-extinction dynamics have been proposed as one potential explanation for the coexistence of multiple competitors on a single limiting resource (Levins and Culver 1971; Tilman 1994). However, the conditions for such coexistence are fairly restrictive, requiring that poor competitors have substantially higher colonization rates than dominant species (fig. 1). Keystone predators relax this requirement and may therefore be important for maintaining regional diversity.

Effects of Predators on Local Diversity

Predators clearly promote regional diversity by expanding the range of conditions under which the inferior competitor invades the system (fig. 3). The effect of the predator on mean local diversity across the landscape (D ; eq. [6a]) depends on the relationships among the parameter values. Figure 4 illustrates the dependence of D on the species traits. When the dominant competitor is a weaker disperser (fig. 4A, 4B), predators often promote mean local diversity among patches (i.e., D is greater in the presence of predators than in their absence) by expanding the regional abundance of species 2. The positive effect is greatest where the c_p is large and e_p is small (the upper line in all three panels of fig. 4), the same conditions under which predators promote regional diversity (fig. 3). The presence of predators always enhances local diversity when they have no effect on the extinction rate of the prey ($e_p = e = 0.01$; fig. 4A). Local diversity can also be enhanced by predators in situations where the superior competitor is also a better disperser (fig. 4C).

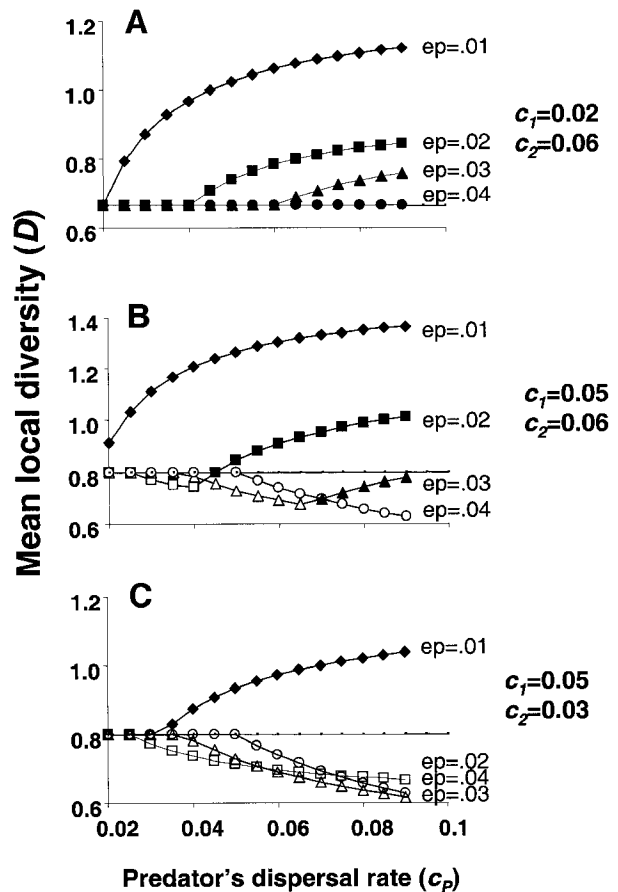


Figure 4: The effects of predators on mean local diversity (D). Each symbol represents a stable equilibrium for a given set of parameter values. Black symbols indicate that both prey coexist, and white symbols indicate that only species 1's density is >0 . The straight horizontal line indicates the value of D in the absence of the predator.

Predators also reduce mean local diversity for some combinations of parameter values, including some where the predator promotes regional coexistence by two prey that would not otherwise coexist (fig. 4B, 4C). Increasing the colonization rate of the predator decreases D when e_p is large (fig. 4B, 4C). When e_p is greater than e , increasing c_p often decreases D until the predator reduces the density of patches in state N_1 to a sufficient level to permit invasion by species 2 (fig. 4B). Once the predator facilitates regional invasion by species 2, further increases in c_p have positive effects on D by allowing species 2 to occupy a greater proportion of the landscape. The nonlinear effects of c_p on D depend on the ability of the predator to promote regional coexistence by the two competitors. The model therefore predicts that specialist predators can promote regional diversity and either reduce or enhance mean local diversity (D), depending on the parameters. For some

combinations of parameter values, the predator both promotes regional coexistence and depresses D (fig. 4B), leading to contrasting effects on species diversity at different spatial scales.

Covariance between Local and Regional Richness

The hypothesis that strong dispersal limitation and weak local interactions lead to linear patterns of local and regional richness requires that each successive addition to the regional species pool occupies, on average, the same proportion of the habitat. One way to achieve this result is if species are noninteractive locally, then each species i displays one-species metapopulation behavior and occupies a proportion $N_i = 1 - e_i/c_i$ of the patches. In this case, local richness increases as a linear function of regional richness with a slope equal to the average occupancy of all the species in the region (Hugueny and Cornell 2000). When species exclude inferior competitors locally, the conditions for linear local/regional patterns become increasingly restrictive as more species are added to the region. The metapopulation model of two-species competition allows for the possibility of linear patterns of local and regional richness. However, this relationship requires a strong trade-off between competitive rank and dispersal rate (fig. 1). As more species are added to the regional pool, the average species's occupancy is expected to decline for reasons discussed under the metapopulation model of two-species competition. Here we examine the conditions for linear patterns of local and regional diversity in the spatial model of keystone predation.

Predator-mediated coexistence expands the range of conditions where we expect to find linear patterns of local versus regional species richness by relaxing, but not removing, the requirement for a trade-off between competitive rank and dispersal rate. Figure 5 shows the conditions where species 2, the inferior competitor, occupies as much of the habitat as species 1 for the model of two-species competition and for different parameter values in the model of predator-mediated coexistence. The conditions for linear local/regional richness patterns are only met in the competition model when species 2's colonization rate greatly exceeds species 1's (in the upper left corner of fig. 5). Increasing the predator's colonization rate (c_p) expands the region of the parameter space where these conditions are met by increasing the steady state occupancy of species 2. However, this prediction only applies when the predator's colonization rate exceeds the rate at which it drives its prey extinct ($c_p > e_p$). When e_p is large, the predator's abundance is reduced or else it is unable to persist in the system. In this case, the predator will have minimal effects on the abundance of species 2. In addition, linear local/regional richness patterns require

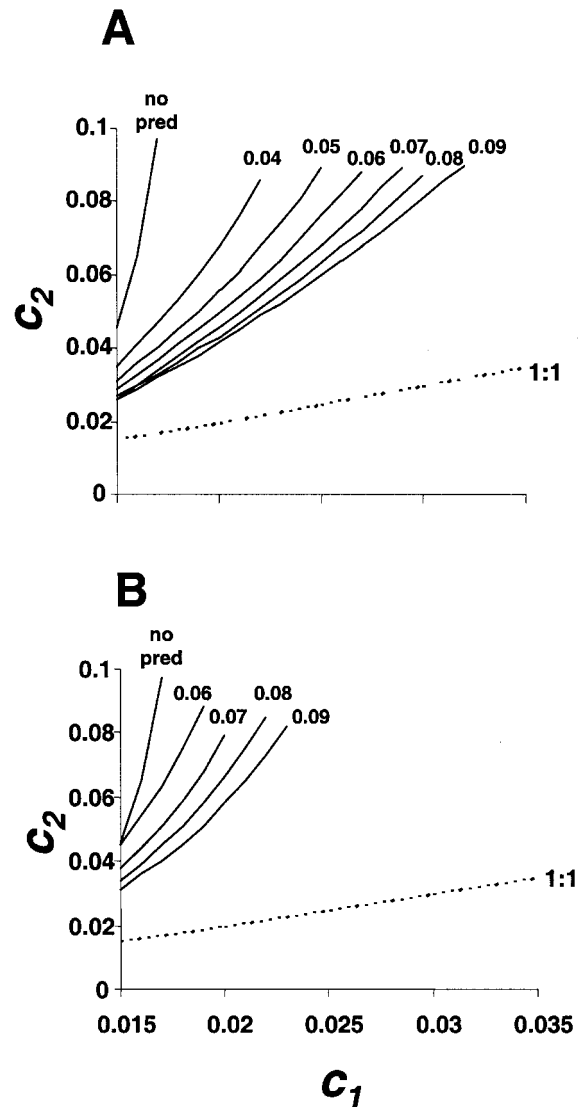


Figure 5: The conditions where the two competing prey occupy the same proportion of the habitat (the requirement for linear patterns of local and regional richness). The lines indicate combinations of parameter values where the steady state occupancy of species 1 and 2 are equal ($N_1^o = N_2^o$). Species 2's abundance is greater than species 1's to the left of the line. The number over each line indicates the dispersal rate of the predator (c_p). A, $e_p = 0.01$. B, $e_p = 0.02$.

that species 2's colonization rate exceeds that of species 1 (fig. 5). However, the trade-off required to produce such patterns in the model of predator-mediated coexistence is less stringent than in the model of two-species competition. Thus, keystone predators remove the requirement that competitive subordinates be superior dispersers in order to coexist regionally with dominant species. However, a trade-off between competitive and dispersal abilities

is required in order to produce linear patterns of local and regional richness.

Covariance between Local Predator and Prey Richness

The predator's potential to promote local prey richness is greatest when its own abundance is high (fig. 4). This aspect of the model predicts positive associations in local occupancy of predators and species 2, the weaker competitor. In addition, the maximum number of competing prey that can coexist locally is equal to (or one greater) than the number of specialist predators. A potentially infinite number of competitors may therefore be added to the regional pool, provided each supports one specialist-predator population (Tilman and Pacala 1993; Grover 1994). Although models of specialist predators may best represent parasitoids or pathogens, generalist predators often differ in their prey preference and degree of specificity. The presence of multiple generalist predators with different prey preferences may therefore decrease the potential for competitive exclusion by any particular prey species. Mutually facilitated invasion between predators and prey is therefore expected to produce positive correlations between diversity among consumer and resource species. The metapopulation model of keystone predators offers one potential mechanistic explanation for such patterns.

Empirical Evaluation of Model Predictions

We present the model of predator-mediated coexistence in a "metacommunity" as a potential explanation for linear patterns of local and regional diversity in the presence of strong local interactions and weak dispersal limitation (Shurin 2000; Shurin et al. 2000). In order to evaluate the plausibility of this explanation, we tested the prediction that local predator and prey diversity will be positively correlated among local sites. Several studies have documented positive correlations in diversity between trophic levels, especially between plants and insects (Murdoch et al. 1972; Southwood et al. 1979; Prendergast et al. 1993; Siemann et al. 1998). However, predator and prey diversity may be linked because of mutually facilitated invasion, as in the model, or because both respond positively but independently to the same aspects of the local environment. For instance, species richness may increase with productivity across trophic levels (Siemann 1998).

In order to test for associations in diversity among trophic levels, we analyzed data from a published survey of fish, zooplankton, phytoplankton, and limnological features in 50 lakes in the Adirondack Mountains (Siegfried et al. 1989). We consider phytoplankton, zooplankton, and fish to represent trophic levels even though there is considerable omnivory and trophic complexity within these

groups. For instance, although some of the fish species are piscivorous as adults, most or all are planktivorous as juveniles or larvae. We used multiple regression to determine whether diversity at a trophic level was related to that at the next higher level after accounting for the variation that could be explained by measured abiotic factors. That is, we performed stepwise regressions of phytoplankton and zooplankton taxonomic richness on 10 limnological variables using a forward selection procedure (see table 1). Once we selected the final abiotic model with all significant variables included, we added species richness at the next higher trophic level to the predictor variables. A positive correlation among diversity at adjacent trophic levels that was independent of abiotic factors would support the predictions of the model. Zooplankton richness was a significant predictor of phytoplankton richness after accounting for the variation explained by limnological features (table 1). Similarly, fish and zooplankton richness were positively correlated after removing the influence of the habitat variables (table 1). Therefore, the model prediction of positive associations of diversity across trophic levels was supported by the data. Sprules (1975) reached a similar conclusion based on surveys of central Ontario lakes; there were significant correlations in fish and crustacean zooplankton diversity that could not be explained by measured aspects of the abiotic environment. These patterns suggest that invasion of new species may be facilitated by species at either lower or higher trophic levels.

Although the model's prediction of positive correlations between predator and prey diversity was supported by the survey of Adirondack lakes, these patterns could be driven by unmeasured abiotic features of the lakes. In order to mechanistically test the assumptions and predictions of the model, Shurin (2001) describes an experimental test of predator-facilitated invasion and the effects of dispersal on the control of local zooplankton diversity and trophic structure. The results of the experiment supported several model predictions. Introduction of fish and insect predators (notonectids) precipitated extinctions by a number of large-bodied zooplankton species and thereby indirectly facilitated invasion by species from the regional pool. When local communities were isolated from the regional species pool, both fish and notonectids reduced local zooplankton diversity. In the presence of dispersal by a large number of species, fish increased zooplankton diversity while notonectids had no effect. The experiment supported the model prediction that the effects of predators on local diversity depend on the level of dispersal of prey among habitats (fig. 4). The model may therefore be appropriate for describing the control of zooplankton community structure at local and regional scales.

The experiment also suggested two features of planktonic communities that contrast with the model and that

Table 1: Stepwise regressions (forward selection procedure) of zooplankton species richness (crustaceans and rotifers) on limnological features and fish richness and of phytoplankton taxonomic richness on limnological features and zooplankton richness for 50 lakes in the Adirondacks

Source	Coefficient	<i>t</i>	df	<i>P</i>
Phytoplankton species richness: ^a				
Constant	23.12	26.77	1	<.001
pH	3.34	2.84	1	.007
Area (ha)	1.86	1.98	1	.054
Zooplankton richness	2.14	1.80	1	.039
Zooplankton species richness: ^b				
Constant	15.92	26.65	1	<.001
pH	2.40	3.21	1	.003
Secchi depth (m)	-1.97	-3.28	1	.002
Fish richness	2.22	3.00	1	.002

Source: Data from Siegfried et al. 1989.

Note: All predictor variables were standardized to the same scale by subtracting the mean and dividing by the standard deviation. All variables with $P < 0.1$ are shown. The P values for limnological variables are from two-tailed tests. For predator (zooplankton or fish) richness, P values are from one-tailed tests since the model predicts positive slopes.

^a Effects of zooplankton species richness and environmental variables on phytoplankton richness in Adirondack lakes. Not in model: conductivity, Secchi depth, maximum depth, chlorophyll *a*, dissolved organic carbon, total phosphorous, NO_3 , and NH_4 .

^b Effects of fish species richness and environmental variables on zooplankton richness in Adirondack lakes. Not in model: area, conductivity, maximum depth, chlorophyll *a*, dissolved organic carbon, total phosphorous, NO_3 , NH_4 .

may influence the effects of predators on patterns of local and regional richness. First, fish reduced local zooplankton richness in the absence of dispersal from the region by extirpating an average of 1.7 species locally. However, when local communities were connected to the regional pool, fish indirectly facilitated invasion by an average of 3.2 new species. Fish therefore facilitated invasion by more species from the region than they excluded locally. The metapopulation model of keystone predators assumes that one species is susceptible to the predator and its competitor is facilitated. If more species are indirectly facilitated than excluded, then invasion by predators may be more likely to enhance local prey diversity as shown by the experiment.

Second, both fish and insect predators reduced populations of several large-bodied zooplankton and also consumed a number of benthic prey. Generalist predators are likely to be more common than specialists (Polis 1991) and may be less susceptible to the extinction of any particular prey species. An analogous model with generalist predators was developed in which the predator could coexist with either of the two prey species (J. B. Shurin, unpublished data). The model with generalist predators had one more patch state than the specialist (i.e., species 2 and the predator could coexist) and one more parameter (the extinction rate of species 2 with the predator). Generalist predators maintained higher regional abundance than specialists by being able to invade more patches. The

greater occupancy of the predator led to greater facilitation of the weaker competitor. The conclusions from the generalist model were, however, in good qualitative agreement with those of the specialist; the predator enhanced regional diversity, had variable effects on local diversity, and expanded the conditions for linear local/regional patterns. The ability to consume multiple prey is likely to be important for determining the impact of predators on local and regional community structure. However, the violation of the assumption of specialist predation did not influence the main qualitative predictions derived here.

Conclusions

Considering the joint effects of predation, competition, and dispersal on community structure at local and regional scales generates a number of insights into the causes of geographic patterns of species composition and diversity. First, colonization-extinction dynamics produce heterogeneity in predator distributions among sites. The regional presence of sites with and without predators creates the opportunity for spatial refugia due to indirect effects transmitted by predators through their prey. Such refugia greatly enhance regional coexistence among competitors that interact so strongly that they cannot coexist locally (fig. 3). Predators tend to promote regional coexistence when they have high dispersal rates (and are therefore

regionally abundant) and small effects on prey extinction rates (fig. 3). A number of empirical examples suggest that the positive effects of predators on regional coexistence may be common. For instance, the presence of ponds with and without fish or salamander predators allows regional coexistence by distinct insect, zooplankton, and amphibian faunas (Dodson 1970, 1974; Sprules 1972; Giguère 1979; Tonn and Magnuson 1982; Arnott and Vanni 1993; Werner and McPeck 1994; Schneider and Frost 1996; Wellborn et al. 1996; McPeck 1998; Zimmer et al. 2000). The positive effect of predators on regional diversity at lower trophic levels may therefore be a relatively general phenomenon.

Dispersal among sites within a region may help to explain the variable impacts of predators on local species diversity at lower trophic levels found in many empirical studies. Predators enhanced mean local diversity across the landscape when they had no effect on prey extinction rates (fig. 4A). Local diversity was reduced by predators that increased their prey's extinction rate when the subordinate competitor (species 2) was unable to persist in the community (fig. 4B, 4C). Increasing the predator's colonization rate generated more vacant patches, which eventually permitted invasion by species 2. Once species 2 was able to coexist, further increases in the predator's colonization rate increased mean local diversity (fig. 4B). Field experiments have found that predators can have positive (Paine 1966; Sih et al. 1985; Proulx and Mazumder 1998; Carson and Root 2000) or negative (Paine and Vadas 1969; Sih et al. 1985; Schoener and Spiller 1996; Spiller and Schoener 1998) effects on prey diversity. An experiment motivated by this model (Shurin 2001) found that the effects of fish and insect predators on local zooplankton diversity depended on connection to the regional species pool. This finding was in good agreement with the model predictions. The experiment and the model suggest one way in which local processes such as predation can interact with colonization-extinction dynamics to shape community structure.

Finally, the model may help to resolve the apparent contrast suggested by linear patterns of local and regional diversity in crustacean zooplankton (Shurin et al. 2000) and experimental evidence for strong invasion resistance (Shurin 2000). Comparing models of two-species competition in the presence or absence of predator-mediated coexistence showed that predators relax the conditions for linear patterns of local and regional species richness. If regions of low prey richness also have relatively few predators, then local habitats may support fewer prey species as competitive exclusion is more likely to occur. Other forms of interspecific facilitation, such as modification of the physical environment, could also produce similar patterns. Predator-mediated coexistence may therefore be one

of several types of local interactions giving rise to linear relationships between local and regional species richness. Understanding the relationship between local and regional diversity requires that we consider the effects of different types of local interactions on coexistence at local and regional scales.

Acknowledgments

This work benefited greatly from discussions with H. Cornell, D. DeAngelis, P. de Valpine, G. Dwyer, M. Leibold, C. Pfister, S. Richards, A. Tessier, and T. Wootton. C. Siegfried provided the raw data from the survey of Adirondack lakes. J.B.S. was supported by the National Science Foundation (NSF) dissertation improvement grant DEB-9972656 and a postdoctoral fellowship from the National Center for Ecological Analysis and Synthesis (funded by the NSF [DEB-0072909], the University of California, and the Santa Barbara campus).

Literature Cited

- Amarasekare, P. 2000. The geometry of coexistence. *Biological Journal of the Linnean Society* 71:1–31.
- Arnott, S. E., and M. J. Vanni. 1993. Zooplankton assemblages in fishless bog lakes—influence of biotic and abiotic factors. *Ecology* 74:2361–2380.
- Bertness, M. D., G. H. Leonard, J. M. Levine, P. R. Schmidt, and A. O. Ingraham. 1999. Testing the relative contribution of positive and negative interactions in rocky intertidal communities. *Ecology* 80:2711–2726.
- Burke, M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. *Ecology* 77:776–790.
- Carson, W. P., and R. B. Root. 2000. Herbivory and plant species coexistence: community regulation by an outbreaking phytophagous insect. *Ecological Monographs* 70:73–99.
- Case, T. J. 1990. Invasion resistance arises in strongly interacting species-rich model competition communities. *Proceedings of the National Academy of Sciences of the USA* 87:9610–9614.
- Caswell, H. 1978. Predator-mediated coexistence: a non-equilibrium model. *American Naturalist* 112:127–154.
- Caswell, H., and J. E. Cohen. 1993. Local and regional regulation of species-area relations: a patch-occupancy model. Pages 99–107 in R. E. Ricklefs and D. Schluter, eds. *Species diversity in ecological communities: his-*

- torical and geographical perspectives. University of Chicago Press, Chicago.
- Cornolly, S. R., and J. Roughgarden. 1998. A latitudinal gradient in northeast Pacific intertidal community structure: evidence for an oceanographically based synthesis of marine community theory. *American Naturalist* 151:311–326.
- Cornell, H. V., and R. Karlson. 1997. Local and regional processes as controls of species richness. Pages 250–268 in D. Tilman and P. Kareiva, eds. *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton, N.J.
- Cornell, H. V., and J. H. Lawton. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology* 61:1–12.
- Crowley, P. H. 1979. Predator-mediated coexistence: an equilibrium interpretation. *Journal of Theoretical Biology* 80:129–144.
- Dodson, S. I. 1970. Complementary feeding niches sustained by size-selective predation. *Limnology and Oceanography* 15:131–137.
- . 1974. Zooplankton competition and predation: an experimental test of the size-efficiency hypothesis. *Ecology* 55:605–613.
- Drake, J. A. 1991. Community-assembly mechanics and the structure of an experimental species ensemble. *American Naturalist* 137:1–26.
- Fox, J. W., J. McGrady-Steed, and O. L. Petchey. 2000. Testing for local species saturation with nonindependent regional species pools. *Ecology Letters* 3:198–206.
- Gaston, K. 2000. Global patterns in biodiversity. *Nature* 405:220–227.
- Giguère, L. 1979. An experimental test of Dodson's hypothesis that *Ambystoma* (a salamander) and *Chaoborus* (a phantom midge) have complementary feeding niches. *Canadian Journal of Zoology* 57:1091–1097.
- Goldberg, D. E., T. Rajaniemi, J. Gurevitch, and A. Stewart-Oaten. 1999. Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. *Ecology* 80:1118–1131.
- Gough, L., and J. B. Grace. 1998. Herbivore effects on plant species density at varying productivity levels. *Ecology* 79:1586–1594.
- Grover, J. P. 1994. Assembly rules for communities of nutrient-limited plants and specialist herbivores. *American Naturalist* 143:258–282.
- Hanski, I., and M. E. Gilpin, eds. 1993. *Metapopulation biology: ecology, genetics and evolution*. Academic Press, San Diego, Calif.
- Hastings, A. 1978. Spatial heterogeneity and the stability of predator-prey systems: predator-mediated coexistence. *Theoretical Population Biology* 14:380–395.
- . 1980. Disturbance, coexistence, history, and competition for space. *Theoretical Population Biology* 18:363–373.
- Holmgren, M., M. Scheffer, and M. A. Huston. 1997. The interplay of facilitation and competition in plant communities. *Ecology* 78:1966–1975.
- Holt, R. D. 1993. Ecology at the mesoscale: the influence of regional processes on local communities. Pages 77–88 in R. E. Ricklefs and D. Schluter, eds. *Species diversity in ecological communities*. University of Chicago Press, Chicago.
- . 1997. From metapopulation dynamics to community structure: some consequences of spatial heterogeneity. Pages 149–164 in I. Hanski and M. E. Gilpin, eds. *Metapopulation biology: ecology, genetics and evolution*. Academic Press, San Diego, Calif.
- Holt, R. D., J. Grover, and D. Tilman. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. *American Naturalist* 144:741–771.
- Horn, H. S., and R. H. MacArthur. 1972. Competition among fugitive species in a harlequin environment. *Ecology* 53:749–752.
- Hugueny, B., and H. V. Cornell. 2000. Predicting the relationship between local and regional species richness from a patch occupancy dynamics model. *Journal of Animal Ecology* 69:194–200.
- Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73:724–732.
- Huston, M. A. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos* 86:393–401.
- Karlson, R. H., and H. V. Cornell. 1998. Scale-dependent variation in local vs. regional effects on coral species richness. *Ecological Monographs* 68:259–274.
- Lawton, J. H. 1999. Are there general laws in ecology? *Oikos* 84:177–192.
- Leibold, M. A. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. *American Naturalist* 147:784–812.
- Levine, J. M. 2000. Complex interactions in a streamside plant community. *Ecology* 81:3431–3444.
- Levins, R., and D. Culver. 1971. Regional coexistence of species and competition between rare species. *Proceedings of the National Academy of Sciences of the USA* 68:1246–1248.
- Loreau, M. 2000. Are communities saturated? on the relationship between alpha, beta, and gamma diversity. *Ecology Letters* 3:73–76.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of*

- island biogeography. Princeton University Press, Princeton, N.J.
- May, R. M. 1994. The effects of spatial scale on ecological questions and answers. Pages 1–17 in P. J. Edwards, R. M. May, and N. R. Webb, eds. *Large scale ecology and conservation biology*. Blackwell Scientific, Oxford.
- McPeck, M. A. 1998. The consequences of changing the top predator in a food web: a comparative experimental approach. *Ecological Monographs* 68:1–23.
- Menge, B. A. 2000. Testing the relative importance of positive and negative effects on community structure. *Trends in Ecology & Evolution* 15:46–47.
- Murdoch, W. W., F. C. Evans, and C. H. Peterson. 1972. Diversity and pattern in plants and insects. *Ecology* 53: 819–829.
- Nee, S., and R. M. May. 1992. Dynamics of metapopulations: habitat destruction and competitive coexistence. *Journal of Animal Ecology* 61:37–40.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100:65–75.
- Paine, R. T., and R. L. Vadas. 1969. The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. *Limnology and Oceanography* 14:710–719.
- Polis, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. *American Naturalist* 138:123–155.
- Prendergast, J. R., R. M. Quinn, J. H. Lawton, B. C. Eversham, and D. W. Gibbons. 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* 365:335–337.
- Proulx, M., and A. Mazumder. 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology* 79:2581–2592.
- Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. *Science (Washington, D.C.)* 235:167–171.
- Schneider, D. W., and T. M. Frost. 1996. Habitat duration and community structure in temporary ponds. *Journal of the North American Benthological Society* 15:64–86.
- Schoener, T. W., and D. A. Spiller. 1996. Devastation of prey diversity by experimentally introduced predators in the field. *Nature* 381:691–694.
- Shurin, J. B. 2000. Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. *Ecology* 81:3074–3086.
- . 2001. Interactive effects of predation and dispersal on zooplankton communities. *Ecology* (in press).
- Shurin, J. B., J. E. Havel, M. A. Leibold, and B. Pinel-Alloul. 2000. Local and regional zooplankton species richness: a scale-independent test for saturation. *Ecology* 81:3062–3073.
- Siegfried, C. A., J. A. Bloomfield, and J. W. Sutherland. 1989. Acidity status and phytoplankton species richness, standing crop, and community composition in Adirondack, New York, USA lakes. *Hydrobiologia* 175:13–32.
- Siemann, E. 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology* 79:2057–2070.
- Siemann, E., D. Tilman, J. Haarstad, and M. Ritchie. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. *American Naturalist* 152: 738–750.
- Sih, A., P. Crowley, M. McPeck, J. Petranka, and K. Strohmeier. 1985. Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics* 16:269–311.
- Southwood, T. R. E., V. K. Brown, and P. M. Reader. 1979. The relationships of plant and insect diversities in succession. *Biological Journal of the Linnean Society* 12: 327–348.
- Spiller, D. A., and T. W. Schoener. 1998. Lizards reduce spider species richness by excluding rare species. *Ecology* 79:503–516.
- Sprules, W. G. 1972. Effects of size-selective predation and food competition on high altitude zooplankton communities. *Ecology* 53:375–386.
- . 1975. Factors affecting the structure of limnetic crustacean zooplankton communities in central Ontario lakes. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 19:635–643.
- Srivastava, D. S. 1999. Using local-regional richness plots to test for species saturation: pitfalls and potentials. *Journal of Animal Ecology* 68:1–16.
- Terborgh, J. W., and J. Faaborg. 1980. Saturation of bird communities in the West Indies. *American Naturalist* 116:178–195.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75:2–16.
- . 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78:81–92.
- Tilman, D., and S. Pacala. 1993. The maintenance of species richness in plant communities. Pages 13–25 in R. Ricklefs and D. Schluter, eds. *Species diversity in ecological communities*. University of Chicago Press, Chicago.
- Tonn, W. M., and J. J. Magnuson. 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. *Ecology* 63:1149–1166.
- Vance, R. R. 1974. Predation and resource partitioning in one predator–two prey model communities. *American Naturalist* 112:797–813.
- Wellborn, G. A., D. K. Skelly, and E. E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics* 27:337–363.

Werner, E. E., and M. A. McPeck. 1994. The roles of direct and indirect effects on the distributions of two frog species along an environmental gradient. *Ecology* 75: 1368–1382.

Zimmer, K. D., M. A. Hanson, and M. G. Butler. 2000.

Factors influencing invertebrate communities in prairie wetlands: a multivariate approach. *Canadian Journal of Fisheries and Aquatic Sciences* 57:76–85.

Associate Editor: Donald L. DeAngelis