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TRADE-OFFS, FOOD WEB STRUCTURE, AND THE COEXISTENCE OF HABITAT SPECIALISTS AND GENERALISTS

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Abstract.—Species differ greatly in the breadth of their environmental distributions. Within the same collection of habitats, some species occur in many habitats, while others are only able to exist in one of a few. Trade-offs in the abilities of species to perform in various ecological interactions are important both to facilitating species coexistence within a habitat and to limiting the distributions of species among habitats. In this article I use a food web model to explore how in the same collection of habitats some species may be limited by trade-offs to occupying only one habitat, while other species may face no trade-off between habitats and therefore be able to generalize in their habitat use. Food web interactions define the available niches within a habitat. Changes in food web structure cause some niches to be lost and replaced by other niches as one moves between habitats. Species occupying these niches will have more limited habitat distributions. However, other niches may be available in the food web structures of multiple habitats, and species occupying these niches will have broad habitat distributions. Understanding the structure of trade-offs within and between communities is fundamental to predicting the types of species with broad or narrow habitat distributions.

Many organisms are confronted with a wide variety of potential habitats for occupation, with each habitat posing a different set of ecological conditions. Although no organism uses all potential habitats, species differ greatly in the range of habitats they use. Some species use only one or a few similar habitats (i.e., habitat specialists), while others use a broad range of disparate habitats (i.e., habitat generalists). A major concern of ecologists has been to understand why species differ in their degree of specialization in habitat use (e.g., MacArthur and Pianka 1966; MacArthur 1972; Strong et al. 1984). This concern addresses a fundamental question in ecology, because the degree of specialization in large part determines the pattern in the distributions of organisms in nature (Elton 1927; Andrewarthe and Birch 1954; MacArthur 1972).

Trade-offs in the abilities of species to perform in various ecological interactions have been shown to limit the habitat distributions of many species. Trade-offs arise when the ability to perform in one interaction comes at the expense of abilities to perform in other interactions (Lubchenco 1980; Tilman 1987). Zonation patterns in the rocky intertidal environment are often generated by the differential abilities of species to survive dessication versus engage in competitive and predatory interactions (e.g., Connell 1961; Paine 1966, 1974; Lubchenco 1980). Plant species segregate along nutrient gradients because of their differential abilities to

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grow and compete for various resources (e.g., light, water, minerals) and at various nutrient availabilities (Tilman 1982, 1988). In freshwater lakes the conflicting requirements of avoiding invertebrate versus vertebrate predators often cause different species assemblages to characterize water bodies with different top predators (Dodson 1970; Vanni 1986, 1988; McPeck 1990*a*, 1990*b*; Werner and McPeck 1994). Trade-offs operating at the between-community scale can therefore have profound effects on species distributions in the environment, because particular species are successful under one set of ecological conditions but are unable to maintain populations under others.

Paradoxically, trade-offs have also been implicated as possible requisites for the coexistence of species within communities (Chesson 1991). Coexistence is fostered because trade-offs force species to differentiate among niche dimensions within a community, which causes the abundances of coexisting species to be more strongly regulated by different interactions (Levin 1970; Holt 1977; Tilman 1982, 1987). For example, when the trade-off within a community involves acquiring resources versus avoiding predators, coexistence is often accomplished by some species being better at acquiring resources and other species being better at avoiding predators (e.g., Price and Brown 1983; Kotler 1984; Mittelbach 1984; Kotler and Brown 1988; Brown 1989; Kohler and McPeck 1989; Kotler et al. 1991; Leibold 1991; Longland and Price 1991).

Trade-offs therefore operate at both the within-community and between-community scales. At both scales trade-offs force species to segregate along niche dimensions. Within communities this segregation promotes species coexistence, whereas between communities this segregation also limits the distribution of species to communities in which suitable niches are available. In this article I argue that understanding why many species differ in the breadth of their habitat distributions requires us to understand how the structure of trade-offs that promote coexistence of species within communities changes as one moves between communities. Trade-offs that promote coexistence within communities are generated by the dynamics of food web interactions. As the nature of these interactions change among habitats (e.g., comparing lakes with invertebrate top predators to lakes with vertebrate top predators), so too will the trade-offs that promote coexistence in these different ecological milieus. Food web structure may make some niches available only in one ecological setting; species filling these niches will have restricted habitat distributions. Food web structures may, however, make other niches available to species in many ecological settings, and species occupying these niches will have broad habitat distributions. Predicting what types of species should have broad distributions and which should have narrow distributions therefore requires that we consider specifically how food web structure changes across environmental gradients and how these changes affect the diversity of niches available to species.

FOOD WEB STRUCTURE AND HABITAT SPECIALISTS AND GENERALISTS

In this section I illustrate how changes in food web structure can cause some species to have narrow habitat distributions while other species have broad habi-

tat distributions. The system I want to consider is a three-trophic-level food web in which a number of midlevel consumers feed on a common resource and are themselves fed on by the same top predator.

This food web structure was first considered by Levin (1970) and has been explored in various forms by a number of authors (e.g., Phillips 1974; Vance 1978; Leibold 1989, 1996). The model I will use to illustrate relevant points was developed by Holt et al. (1994). The model assumes a top predator (its abundance is designated P) with a linear functional response for feeding on at most two midlevel consumers (whose abundances are designated N_i , where $i = 1, 2$ for the two midlevel consumers, respectively). These two consumers in turn have linear functional responses for feeding on a common resource (abundance is designated R). To maintain tractability, Holt et al. (1994) assume that the system is completely closed, the total amount of resource available to the system is fixed, and a simple mass-balance relationship holds.

With these assumptions, the dynamics of this system are given by the following equations (Holt et al. 1994):

$$\frac{dP}{dt} = P \left(\sum_{i=1}^2 a_i b_i N_i - c \right)$$

$$\frac{dN_i}{dt} = N_i (a'_i b'_i R - c'_i - a_i P) \quad \text{for } i = 1, 2 \quad (1)$$

and

$$\frac{dR}{dt} = \sum_{i=1}^2 \frac{c'_i N_i}{b'_i} + \frac{cP}{b_p} + \sum_{i=1}^2 a_i N_i P \left(\frac{1}{b'_i} - \frac{b_i}{b_p} \right) - \sum_{i=1}^2 a'_i R N_i.$$

For the top predator in this system of equations, a_i and b_i are the per capita predator attack rate and conversion efficiency on consumer species i , respectively, and c is the predator's density-independent death rate. For midlevel consumer species i , a'_i and b'_i are the per capita attack rate and conversion efficiency for the consumer eating the resource, respectively, c'_i is the density-independent mortality of consumer i , and the last term in the equation defines mortality due to predation. For the resource dynamics, the first three terms of the equation describe recycling of resource to the available pool by the density-independent mortality of the midlevel consumers, by density-independent mortality of the predator, and by the inefficiency of conversion by the predator when killing the consumers, respectively; the last summation term describes resource losses via feeding by the midlevel consumers. The parameter b_p is the number of predators produced by one unit of basal resource.

Holt et al. (1994) showed that the equilibrium outcome of interactions in this four-species system could be graphically represented in a two-dimensional space

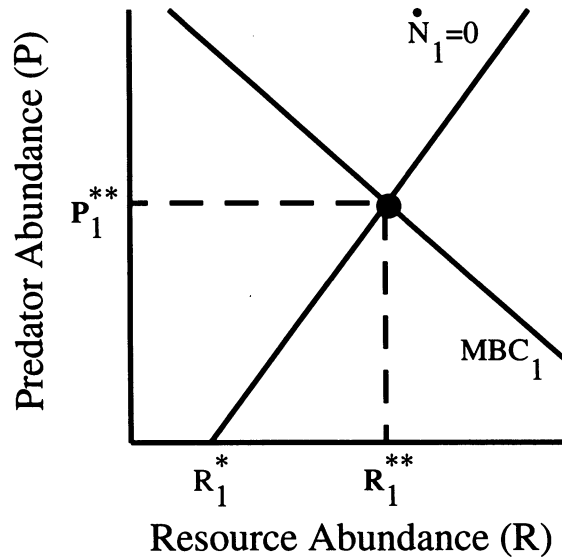


FIG. 1.—The phase plane describing the equilibrium abundances for a three-species food web, with one resource, one midlevel consumer, and one top predator. The axes of the phase plane describe the abundances of the resource (R) and the top predator (P). The line with negative slope is the mass balance constraint line for consumer species 1 (designated MBC_1), and the line with positive slope is the isocline for consumer 1 (designated $\dot{N}_1 = 0$). In the absence of the predator, consumer 1 will drive resource levels down to R_1^* , where it will come into equilibrium (the single asterisk denotes equilibrium in the absence of the predator). In the presence of the top predator, the system will equilibrate at the point where the MBC_1 line and consumer 1 isocline intersect; at this equilibrium the predator abundance (P_1^{**}) and the resource abundance (R_1^{**}) can be determined directly from the phase plane (the double asterisks denote equilibrium in the presence of the predator). (Redrawn from Holt et al. 1994.)

defined by the abundances of the top predator (P) and the resource (R) (fig. 1). When only one midlevel consumer is present, two lines in this space define the equilibrium for the system (Holt et al. 1994). The first is a line defining the mass balance constraint for consumer i (denoted the “MBC line” for consumer i , or MBC_i) when the top predator and basal resource are both at equilibrium (designated P^{**} and R^{**} , respectively) (fig. 1). The MBC line of each consumer is given by

$$P^{**} = b_p \left(S - \frac{c}{a_i b_i b_i'} \right) - b_p R^{**}. \quad (2)$$

Additional parameters in this equation are S , the total amount of resource in the system, and b_p , the number of predators produced by one unit of basal resource. Note that the MBC lines for both midlevel consumers have the same slope, but they can differ in intercepts according to differences in the predator's attack rate (a_i) and conversion efficiency (b_i) on each consumer and the consumers' own

conversion efficiencies of basal resources (b'_i). The second line is the isocline for consumer i , which is given by

$$P^{**} = \frac{a'_i b'_i}{a_i} R^{**} - \frac{c'_i}{a_i}. \quad (3)$$

The isocline has positive slope. At predator/resource combinations above the isocline, the consumer population will decline in numbers because of the high number of predators relative to resource availability, and the system will move toward the isocline (Holt et al. 1994). At predator/resource combinations below the isocline, the consumer population will increase because of the greater resource availability relative to predator abundance, and the system will again move toward the isocline (Holt et al. 1994). As with standard competition models, in the absence of the predator, the consumer whose isocline intersects the resource axis at the lower resource abundance will competitively exclude all others. This point of intersection is given by the quotient ($a'_i b'_i / c'_i$), which implies that the best competitor is the species that has the greatest ratio of converting resource into consumer individuals to loss due to its own density-dependent mortality (Tilman 1982; Holt et al. 1994). With only one consumer species, the equilibrium for the system is defined by the point where the MBC line and isocline intersect (fig. 1; Holt et al. 1994).

I use this graphic framework to explore how changes in food web structure caused by differences in the top predators between two communities can promote the coexistence of a "habitat generalist," which does not face a fitness trade-off between communities, and a "habitat specialist" in each community.

Specialists in Two Food Webs

For habitats that have different top predators, ecologists have focused their attention primarily on the species that segregate between communities. I will call these species the "habitat specialists." Aquatic communities provide many examples of such changes in species composition of ponds and lakes with different top predators. Differences in top predators usually result from direct interactions among the top predators. For example, in the littoral zones of lakes, invertebrate predators such as large dragonflies are often the top predators in lakes where fish cannot colonize or are excluded by physical factors (e.g., pH), whereas these large dragonflies are themselves excluded from lakes supporting fish populations because of fish predation (Hall et al. 1970; Crowder and Cooper 1982; McPeck 1990a). Analogous processes also generate differences in the top predators in the pelagic zone of lakes. Each top predator has some prey that are only able to coexist with it. These species replacements are generally found to result primarily from the differential susceptibilities of the prey species to the various predators; competition usually plays little or no role in these species replacements (e.g., Dodson 1970, 1974; Sprules 1972; Vanni 1986, 1988; McPeck 1990a; Arnott and Vanni 1993; but see Werner and McPeck 1994). These prey have antipredator defenses that are particularly effective against one of the predators but not against the other (e.g., McPeck 1990b; Werner and McPeck 1994).

We can model these species replacements between two communities in the

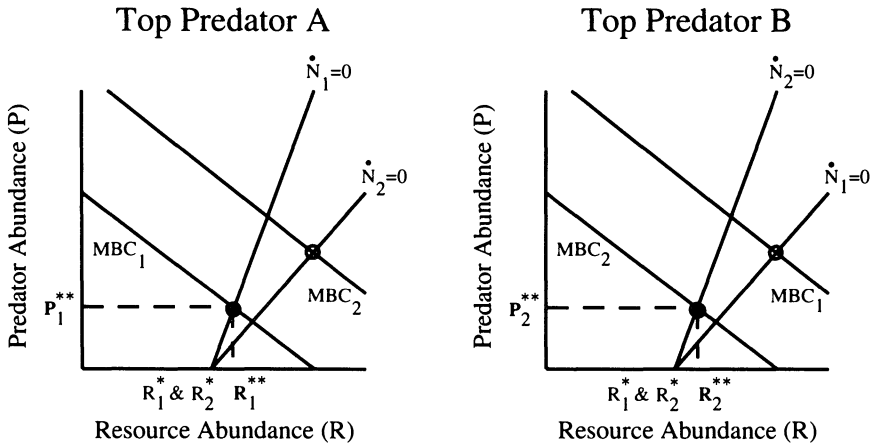


FIG. 2.—Graphic representation of the situation described in the *Specialists in Two Food Webs* section. Each panel depicts the isoclines and mass balance constraint (MBC) lines for two midlevel consumers that both feed on the same resource and are both fed on by the same top predator. The two panels represent communities with different top predators. Both consumers have the same abilities to acquire and convert the resource into their own biomass in both communities and the same density-independent mortality rates, and each top predator has equal conversion efficiencies for the two consumers (see text for details). Species 1 is less vulnerable to top predator A, and species 2 is less vulnerable to top predator B. The equilibrium with each consumer present alone is given by the point where the species' isocline and MBC line intersect (circled). The open circle identifies the equilibrium for the consumer that will be replaced if the other consumer invades. The filled circle identifies the stable equilibrium; this consumer can invade and completely replace the other. This combination of parameters for these two consumers results in their segregation between the two food webs.

framework described earlier. Each habitat is defined by a top predator (A or B), and only one of these predators exists in each habitat. Two midlevel consumers are differentially vulnerable to these two top predators. Consumer 1 is less vulnerable to predator A than consumer 2 (i.e., $a_2 > a_1$ against predator A), but consumer 2 is less vulnerable to predator B than consumer 1 (i.e., $a_1 > a_2$ against predator B). For simplicity, I assume that the qualitative nature of the resources does not differ between the communities with different top predators, which appears to be true in nature for comparable systems (e.g., Vanni 1986, 1988; McPeck 1990a; Werner and McPeck 1994), and that these two consumers are identical except for their vulnerabilities to the two predators (i.e., $b_1 = b_2$, $a'_1 = a'_2$, $b'_1 = b'_2$, and $c'_1 = c'_2$). These differential vulnerabilities to the predators define a trade-off between these two habitats for these species.

For the community in each habitat defined by a top predator, the equilibrium for each midlevel consumer when the other is initially absent can be mapped and evaluated for whether the other consumer can invade this equilibrium when rare (fig. 2). Holt et al. (1994) use this invasibility criterion to evaluate what the final community composition will be. The assumptions of equal resource uptake rates, resource conversion efficiencies, and density-independent mortality rates for the

two consumers imply that their isoclines intersect the resource axis at the same point in each community (fig. 2). For the community with predator A, the assumption of $a_2 > a_1$ causes the MBC line for consumer 2 to be above the MBC line for consumer 1, and the isocline for consumer 2 to have a shallower slope than the isocline for consumer 1 (fig. 2). Consequently, consumer 1 can always invade and completely replace consumer 2 in the community with predator A (fig. 2). These relationships between the MBC lines and isoclines will be reversed in the community with predator B because $a_1 > a_2$, and so consumer 2 can always invade and completely replace consumer 1 in the community with predator B (fig. 2). Ultimately, consumer 1 should only coexist with predator A, and consumer 2 should only coexist with predator B.

Interestingly, fewer predators and less resource will exist at equilibrium with the ultimate winning consumer for each community than with the other consumer at equilibrium by itself. For example, in the community with predator A, fewer predators and less resource will exist at the equilibrium with consumer 1 than when consumer 2 is at equilibrium and consumer 1 is prevented from invading (fig. 2). This result occurs because predator A has a lower attack rate on consumer 1; consumer 1 will therefore have a larger population size at equilibrium, and consequently consumer 1 will drive resources to a lower level.

A Generalist in Two Food Webs

In nature we often see habitat generalist species that exist in more than one community and consequently coexist with habitat specialists in a number of communities. In New England intertidal communities, crusting algae occur across bathymetric zones defined by segregating algae and crustaceans (Lubchenco 1980). In the high-altitude pond system in the Rocky Mountains, *Diaptomus col-oradensis* is abundant in ponds with different top predators, while other zooplankton are forced to segregate between the different top predators (Dodson 1970, 1974; Sprules 1972). In lake littoral zones, *Enallagma* damselfly species segregate between lakes with fish and dragonflies as top predators, while species in the sister genus *Ischnura* are abundant in both lake types (McPeck 1990a). Given this conceptual framework, we can now ask whether one species can be identified that could invade, come to a stable equilibrium, and coexist with the habitat specialists in both communities in figure 2 and, if so, what abilities such a species should possess.

First consider the criteria for the stable coexistence of two midlevel consumers in one food web. Holt et al. (1994) showed that fulfilling the following three criteria results in the stable coexistence of two midlevel consumers. First, one consumer must be able to drive resources to a lower level than the other in the absence of the predator (i.e., R^* for one consumer must be lower than that for the other) (mathematically, $c'_j/c'_i < [a'_j b'_j]/[a'_i b'_i]$). In other words, one consumer must be better than the other at exploiting the resource. Second, the consumer with the lower R^* must have a shallower slope to its isocline than the other consumer so that the isoclines cross ($[a'_j b'_j]/[a'_i b'_i] < a_j/a_i$). In other words, the competitive advantage enjoyed by one consumer must be more than counter-vailed by the predator attack rates: the better resource exploiter must suffer a

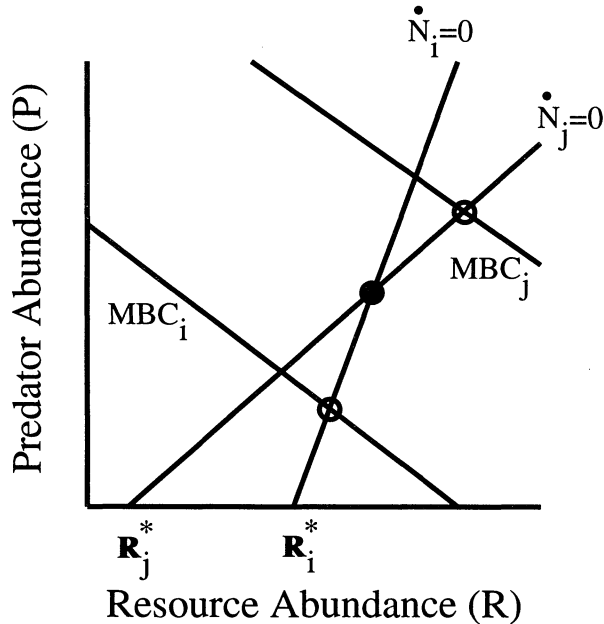


FIG. 3.—Requirements for the stable coexistence of two midlevel consumers in one food web. Two midlevel consumers, i and j , differ in both resource acquisition rates and predator susceptibilities. Consumer j has a lower R^* , which means that consumer i is better than consumer j at acquiring and converting the resource into its own biomass. However, consumer j also has a disproportionately higher attack rate by the top predator, which causes consumer j 's isocline to have a shallower slope than consumer i 's and its MBC line to be above that of consumer i . The open circles identify the equilibria for each consumer when present alone, and the filled circle identifies the stable two-consumer equilibrium point. These conditions imply that for stable coexistence, the two consumers must trade off abilities differently: one consumer must be better at acquiring resources, while the other consumer must be better at avoiding predation (Holt et al. 1994).

disproportionate share of predation. Third, the MBC line for the consumer with the lower R^* must be above the MBC line for the other consumer ($a_i b_i b'_i < a_j b_j b'_j$). This criterion requires that the predator acquire more basal resource through the better competitor than through the poorer competitor (note that if the resource transfer efficiencies at both steps are similar for the two consumers [i.e., $b_i \approx b_j$ and $b'_i \approx b'_j$], this criterion will always be true if criteria 1 and 2 are true). Satisfying these three criteria results in a phase plane diagram qualitatively the same as that shown in figure 3, and the equilibrium is globally stable (see app. B in Holt et al. 1994). Coexistence therefore requires that the two midlevel consumers settle the within-community trade-off of acquiring resources and avoiding predators differently, with one settling the trade-off in favor of superior resource acquisition and the other settling the trade-off in favor of superior predator avoidance (see also Levin 1970; Phillips 1974; Vance 1978; Leibold 1989, 1996).

From this, a species expressing only one phenotype that could invade and coexist with the specialists in both communities would have two key properties:

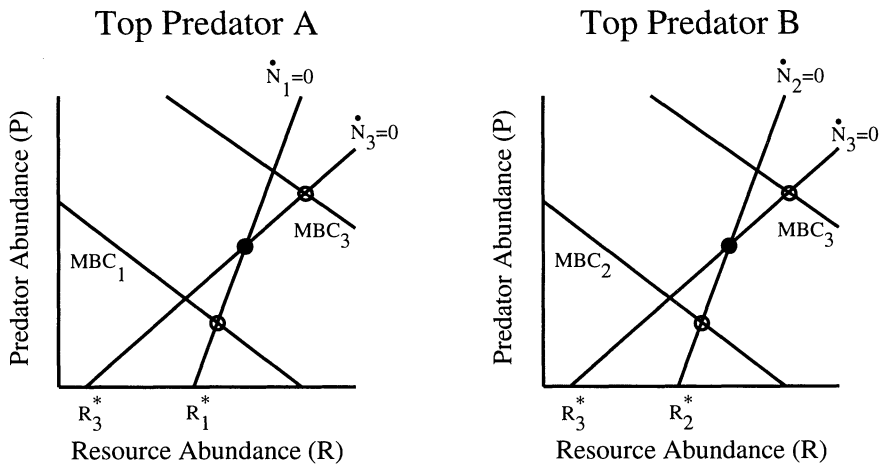


FIG. 4.—A case of a generalist coexisting with two specialists. For the two food webs, consumer 3 can invade both and coexist at a stable equilibrium with each specialist under the different predation regimes. Consumer 3 exhibits the properties of being better than either specialist at acquiring resources but suffers greater mortality because of predation in each food web. In each panel the open circles identify the equilibria for each consumer when present alone, and the filled circle identifies the stable two-consumer equilibrium point.

it must be better than either specialist at exploiting the resource, but it must suffer greater predation rates than each coexisting specialist from each top predator. This means that such a species would have a lower R^* , a shallower isocline, and a higher MBC line than the specialist in each community (fig. 4). The phenotype of such a species should therefore make it a superior resource exploiter but relatively ineffective at avoiding any particular predator; it can coexist with the specialist in each community because it settles the trade-off posed by the food web structure differently from each specialist. However, unlike the specialists, this species does *not* face a trade-off between the communities; the “better resource exploiter but poorer predator avoider” niche is available in both communities. This species is a generalist based on its habitat distribution, because it (e.g., consumer 3 in fig. 4) can thrive in multiple ecological conditions that force other species (e.g., consumers 1 and 2 in fig. 4) to segregate.

Another type of species expressing only one phenotype that could invade and coexist with the specialists in both communities would be one that is better than both specialists at avoiding both top predators but poorer than both at exploiting the resource. However, such a species is biologically improbable because it requires that one antipredator defense be most successful against multiple predator types, while less effective antipredator defenses be effective against only one type of predator. Given the nature of trade-offs, it is probably more likely that the specificity and effectiveness of antipredator defenses are positively related.

DISCUSSION

The generalist and the specialists discussed in the previous sections experience the environment very differently. What to an ecologist would appear to be a

major change in the environment (i.e., change in the top predator of a food web) is also experienced by specialists as a major discontinuity in the environment that causes some habitats to be hospitable and others to be inhospitable. The generalist, on the other hand, would perceive the same environmental discontinuity that forces specialists to segregate as a relatively minor alteration that would not affect its persistence in either habitat.

This type of generalist species contrasts sharply with the usual notions about how species are able to generalize in their use of different habitats. Generalists are usually thought to experience the same types of trade-offs between communities that force specialists to segregate. Three prevalent types of generalists have been described and considered in both theoretical and empirical studies. All three of these generalist types require the existence of fitness trade-offs between ecological conditions, and each embodies a different way to accommodate such fitness trade-offs. The three types are a polymorphic species in which specialist genotypes for the various ecological conditions are maintained in the species (Levene 1953; Dempster 1955; Hedrick 1986), a phenotypically plastic species in which genotypes are capable of expressing the correct phenotype for the ecological conditions in which they develop (Levins 1968; Smith-Gill 1983; Lively 1986; Sultan 1987; Van Tienderen 1991; Moran 1992; Scheiner 1993), and a "jack-of-all-trades" species in which the phenotypic distribution maintained in the species is intermediate to the optimal phenotypes for the ecological conditions experienced (Levins 1968; MacArthur 1972; Felsenstein 1979). Various genetic, developmental, and ecological potentialities influence which of these three types of generalists will evolve in a given system (see the previously cited references), but all are based on the premise that different phenotypes (or genotypes) give maximum fitness in different environments.

In contrast, the habitat generalist type described in the previous section can exist because the position in the food webs occupied by such a species presents no fitness trade-off between the two communities, or, stated another way, the same niche exists in both communities. Environmental heterogeneity should therefore affect specialists and these various generalist types very differently. For the three generalist types (polymorphic, phenotypically plastic, and jack-of-all-trades) requiring fitness trade-offs to evolve and maintain an advantage over specialists, either individuals must be dispersed to spatially variable ecological conditions at random each generation, or populations must experience temporal variation in ecological conditions through time (see previous references); heterogeneity in ecological conditions favors the evolution and persistence of these generalist types. With temporal ecological constancy or no random apportionment of individuals among spatially variable conditions, polymorphisms and intermediate phenotypes will not be maintained by natural selection (Levene 1953; Dempster 1955; Felsenstein 1979; Hedrick 1986), and phenotypically plastic species will also be at a disadvantage relative to specialists if any cost of plasticity exists (Lively 1986; Moran 1992). Consequently, either specialists or one of these three generalist types should be found in any particular system, but they should not coexist.

Persistence of the generalist type discussed in this article should be insensitive to the regime of environmental heterogeneity. Given that trade-offs within each

community provide more than one niche to permit coexistence (e.g., fig. 4), this generalist should be able to coexist either with specialists or with any of the three other generalist types. The derivation given earlier assumes relative temporal constancy of general ecological conditions (i.e., one top predator will be predictably found at any geographical location for long periods). Habitat specialists are expected to occupy the "superior predator avoider but poor resource exploiter" niche position in each community. If, however, the top predator found at any particular geographical location varies over time, one of the generalist types favored by between-community trade-offs should occupy these niches if they can evolve. But because these two ecological conditions are essentially the same to the generalist occupying the "superior resource exploiter but poor predator avoider" niche, it should be able to coexist either with specialists (in a temporally constant environment) or one of the other generalist types (in a temporally variable environment) in the other niches. Note also that this generalist type will experience relatively little or no temporal variability regardless of the "true" variability in the environment (i.e., the variability affecting species in the other niches).

The difficulty in empirically demonstrating the existence of trade-offs between what should be disparate ecological conditions for many species suggests that the differential availability of niches across ecological conditions may be a common feature of nature. The existence of fitness trade-offs across ecological conditions has been notoriously difficult to demonstrate. For example, herbivorous insects often display no correlation in performance when raised on different host plants (see reviews in Futuyma and Moreno 1988; Jaenike 1990; Via 1990). This observation has led many to stress the importance of ecological agents such as predators and parasitoids over plant secondary chemistry in determining insect diet breadth (e.g., Jeffries and Lawton 1984; Strong et al. 1984; Bernays and Graham 1988; Holt and Lawton 1993). The framework outlined in this article highlights the possibility that some species do experience trade-offs across multiple host plants and others do not. Many ecological processes may regulate insect abundances on a particular plant species. Some processes may operate on many plant species (e.g., natural enemies), while other processes may be restricted to just a few plant species (e.g., plant secondary compounds that are unique to specific plant groups). If interactions on any particular plant host cause species to differentiate according to these interactions into different niches, then species occupying niches that are not dependent on plant host (e.g., superior enemy avoidance) will not experience trade-offs across multiple hosts, while species occupying niches that are specialized to a particular host plant (e.g., superior detoxification of plant specific compounds) will experience trade-offs across host plants. Some of the confusion and debate in the literature may be caused by not recognizing that species have differential abilities to engage in various interactions, and these differences in abilities have consequences for the scale at which trade-offs are important. Sorting these problems for herbivorous insects or for any system requires an understanding of the relative importance of the various processes regulating the abundances of coexisting and segregating species and an understanding of the abilities of species to deal with these various processes (see also Strong et al. 1984; Bernays and Graham 1988).

Enough is known about species interactions in two systems to suggest that each may be structured along the lines of the model presented in this article. The first system is the zooplankton assemblages in high-altitude ponds in the Rocky Mountains (Dodson 1970, 1974; Sprules 1972). Some ponds have larval *Ambystoma* salamanders and phantom midge larvae (*Chaoborus americanus*) as the primary predators and *Daphnia rosea* as the primary prey of these predators. Other ponds have a large copepod (*Diaptomus shoshone*) as the primary predator and *Daphnia middendorffiana* and fairy shrimp (*Branchinecta coloradensis*) as the primary prey for this predator. In spite of the strong segregation of these species between ponds, a small copepod (*Diaptomus coloradensis*) is "ubiquitous" in both pond types (Dodson 1970). Although not conclusive, the results of Dodson (1970, 1974) and Sprules (1972) do suggest that *D. coloradensis* may coexist with the *Daphnia* and fairy shrimp specialists in both pond types because it is better at acquiring resources but poorer at avoiding predators. Because of its smaller size, *D. coloradensis* is relatively more susceptible to *Chaoborus* predation (Dodson 1970; Sprules 1972); little is known about the relative susceptibilities of the grazers to *D. shoshone* predation, but its small size is likely to make it more susceptible to this predator. Also, in spite of experiencing higher predation rates, *D. coloradensis* is the most abundant grazer for most of the summer in both pond types (Dodson 1974), which suggests that *D. coloradensis* may be more effective than the other grazers at using algal resources and converting them into offspring. Obviously, more focused experiments are required to test this model definitively in this system, but these results, which were gathered to test other hypotheses, are suggestive.

I have been studying the coenagrionid damselfly assemblages that inhabit lakes with fish as top predators and lakes with large dragonflies as top predators (e.g., McPeck 1989, 1990a, 1990b, 1995; McPeck et al. 1996). Species in the genus *Enallagma* segregate between these two lake types because they possess different behavioral and morphological phenotypes that make them differentially susceptible to fish and dragonflies (Pierce et al. 1985; McPeck 1990a, 1990b, 1995; McPeck et al. 1996). In contrast, species in the genus *Ischnura* are abundant in both lake types (McPeck 1990a). The results of field experiments demonstrate that *Ischnura* species experience greater mortality rates than native *Enallagma* species from both predators in both lake types; *Ischnura* species also have substantially higher growth rates than all *Enallagma* species, and when competitive effects are detected, growth rates of *Enallagma* are more affected by *Ischnura* densities than *Ischnura* growth rates are by *Enallagma* densities (M. A. McPeck, unpublished data). Also, *Ischnura* individuals from fish and dragonfly lakes are behaviorally and morphologically indistinguishable (M. A. McPeck, unpublished data). These results suggest that *Ischnura* occupies the "superior resource exploiter but poor predator avoider" niche in both lake types, while the *Enallagma* specialist in each lake type possesses a superior antipredator adaptation against one predator that comes at the expense of resource acquisition ability (the within-community trade-off) and defenses against the other predator (the between-community trade-off).

Throughout this article I have used an Eltonian definition of the niche, focusing on the abilities of a species to engage in various interactions—essentially how a

species is adapted to its environment (Elton 1927). In contrast to Elton, Hutchinson (1957) focused his niche concept on the environmental variables that limit the distribution of a species and ignored the differential abilities of species to engage in those interactions. Obviously, these are complementary concepts, and both are useful for understanding species interactions and coexistence (Leibold 1995). Any trade-off that promotes coexistence cannot be understood mechanistically without determining both the interactions affecting species abundances and the properties of species that define their abilities to engage in those interactions. This involves thinking about community structure in a multidimensional framework involving not only the multiple interactions that simultaneously affect species abundances (Leibold 1995) but also the multiple phenotypic properties of species that constrain and enhance their abilities to engage in these multiple interactions (e.g., McPeck 1990b, 1995; McPeck et al. 1996). This conceptual expansion also applies to thinking about the processes influencing the distributions of species in the environment. Considering how the nature of trade-offs promoting coexistence within communities changes across communities provides a broad framework for predicting which species will be detrimentally impacted and which species will be largely unaffected by alterations in environmental conditions.

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