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LINKING LOCAL SPECIES INTERACTIONS TO RATES OF SPECIATION IN COMMUNITIES[1]

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Abstract. Regional species diversity limits the diversity of local communities by defining the pool of species that are available to colonize sites. Biogeographical processes that influence speciation and extinction rates determine the size and composition of this regional species pool. Community ecologists are beginning to recognize the importance of these biogeographical processes in influencing diversity patterns among local communities, but the potential for local interactions to influence biogeographical processes, especially speciation, has been little considered. In this paper I discuss one mechanism by which variation in the strengths of local interactions can influence the potential for population differentiation and thus for influencing speciation rates in the allopatric model of speciation. When more than one selective agent acts on the phenotype, the shape of the overall fitness surface depends critically on the relative strengths of the various selective agents. If one selective agent, which imparts strong selection, acts in all populations of a species, population differentiation via adaptation to local ecological conditions or via differentiation of sexual systems is retarded because the overall fitness surface in all populations strongly resembles the shape of the strongest selective agent. Consequently, the potential for speciation is reduced. Alternatively, if selective agents in various populations impart relatively equitable strengths of selection, the potential for differences in the overall fitness surfaces among populations is enhanced, which will enhance the potential for population differentiation and thus speciation. Analogous results obtain when multiple selective agents impact genetically correlated characters. Because the strength of selection generated by a species interaction should increase with the strength of the interaction, and because fewer species can usually coexist when the strengths of interactions are greater, the number of coexisting species and the potential for speciation in component taxa may covary among communities. This analysis indicates that the relative strengths of interactions can be as important to diversification in communities as the number of niche dimensions along which differentiation can occur.

Key words: biogeographic processes; multiple selective agents; natural selection; population differentiation; speciation; species diversity.

INTRODUCTION

Explaining patterns of species diversity is an enduring problem for community ecologists. Since Hutchinson (1958, 1959) questions concerning species diversity have been directed primarily at understanding the processes that regulate the number of coexisting species. In studying these processes, community ecologists generally assume a paradigm in which a defined pool of species exists, and each member of the pool can potentially colonize every site under consideration (e.g., as exemplified by the elegant laboratory experiments of Neill 1975, Robinson and Dickerson 1987, Drake 1991, Lawlor and Morin 1993). Once the potential pool of species is defined, ecological studies are directed at examining why only a subset of species in the pool can coexist in any particular ecological setting, and why different numbers of species coexist in different settings (e.g., marine intertidal: Connell 1961, Paine 1966, 1969, 1974, 1980, Lubchenco 1978, 1980; freshwater lakes: Brooks and Dodson 1965, Hall et al. 1970, Dodson 1970, 1974, Sprules 1972, Addicott 1974, Post and Cucin 1984, Vanni 1986, 1988, McPeek 1990; freshwater streams: Griffiths 1981, Flecker 1992; terrestrial plants: Harper 1969, Whittaker 1975, Tilman 1982, 1988).

This paradigmatic approach is appropriate for examining the processes that promote or retard species coexistence once the pool is defined, but it begs the question of how the species pool was created in the first place. The pool of potential species in a given biogeographic area is increased by speciation of existing taxa or by dispersal into the area by new taxa; species are lost from the pool by extinction or by mi-

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[1] For reprints of this Special Feature, see footnote 1, page 1319.

gration out of the area (Rosenzweig 1975, Platnick and Nelson 1978, Stanley 1979, Humphries and Parenti 1986, Eldredge 1989). Community ecologists are beginning to recognize that local diversity patterns are greatly influenced by regional processes such as speciation, extinction, and biogeographic history (Ricklefs 1987, 1989, Brown and Nicoletto 1991, Cornell and Lawton 1992, Cadle and Green 1993, Ricklefs and Schluter 1993). The importance of macroevolutionary and biogeographic processes are most clearly apparent in systems where local species interactions have little or no influence on local diversity (e.g., Strong et al. 1984, Cornell 1985*a, b,* 1993, Cornell and Lawton 1992), but macroevolution and biogeography can similarly influence species diversity in communities where strong species interactions regulate coexistence. For example, in a particular ecological setting many interacting species may be capable of coexisting, but few may exist there at any one time, because either low speciation rates, high extinction rates, or lack of dispersal constrain species richness. Consequently, interpreting diversity patterns from a purely ecological perspective is flawed.

Extinction is already an integral part of the conceptual framework of community ecology, since population extinction is a predictable and understandable outcome of species interactions on a local scale (e.g., competitive exclusion) that is easily generalizable to regional scales. Additionally, much of the present effort in conserving biological diversity is directed at understanding the processes that lead to extinction (e.g., Boecklin and Simberloff 1985, Soulé 1987, Lawton and May 1995), because of extinction's immediate and irreparable impacts.

In contrast, the links between species interactions and speciation are rarely considered. Many speciation mechanisms may operate largely autonomously of the ecological setting, e.g., vicariance (Cracraft 1982, 1985), hybridization and polyploidy (Grant 1981), mating system evolution (Barrett 1989). When these modes of speciation predominate, new species will be introduced "at random" into local communities via speciation and dispersal from other biogeographic areas, and extinctions caused by local interactions will be the primary ecological contributor to regulating local diversity (MacArthur and Wilson 1967, Rummell and Roughgarden 1985).

Shifts in habitat occupancy or host use by lineages commonly create new species (Rice 1985, 1987, Feder and Bush 1991, Tauber and Tauber 1989, Futuyma and McCafferty 1990, McPeek 1995*a, b*). These habitat or host shifts are thought to create new species when a founder population of a species adapted to one community type is established and subsequently adapts to a new community type. Species interactions can influence the potential for successful habitat shifts by affecting the likelihood that founder populations will adapt to their new ecological milieu before becoming extinct (Gomulkiewicz and Holt 1995). Key innovations to the new ecological environments may heighten speciation rates in lineages following habitat shifts (Simpson 1953, Mitter et al. 1988, Farrell et al. 1991), but the conditions that cause certain phenotypes in novel environments to be key innovations are unknown and may be unpredictable (Mitter et al. 1988, Farrell et al. 1991, Allmon 1992).

Ecologists have long postulated that species interactions, especially competition leading to character displacement, can generate diversification of a taxon into multiple niches within the same local community (e.g., Pimm 1978, Rosenzweig 1978, Wilson and Turelli 1986, Wilson 1989). Although mechanisms such as character displacement have contributed to the evolutionary divergence of already existing species to promote their coexistence in areas of sympatry, clear examples demonstrating that these mechanisms have caused speciation sympatrically in one lineage are however rare (see recent reviews by Schluter and MacPhail 1993, Robinson and Wilson 1994).

Evolutionary biologists generally acknowledge that allopatric speciation via divergent selection in different regions of a species range is one of the most common and potentially most powerful mechanisms for generating new species, especially in animals (Mayr 1942, 1963, Lynch 1989, Allmon 1992, Rice and Hostert 1993, Coyne 1994). Rice and Hostert (1993) reviewed laboratory experiments that simulate the major mechanisms of speciation and concluded that the allopatric model of speciation in which "multifarious, strong, discontinuous, divergent" selection in different parts of a species' range can relatively rapidly generate reproductive isolation even with gene flow. Consequently, any mechanism that can influence the disparity in natural selection experienced by populations across the range of a species will regulate to a substantial degree the potential for speciation in that species.

Although the importance of allopatric speciation has long been recognized, community ecologists have been surprisingly silent about how ecological interactions in general and species interactions in particular could influence the potential for allopatric speciation. Since species interactions are major ecological forces determining the form of natural selection experienced by most organisms (Endler 1986), variation in the types and strengths of interactions across a species' range may critically determine its potential for undergoing speciation. Moreover, speciation rates for many taxa in a given environment could be strongly influenced by the scope of large-scale geographic variation in species interactions.

In this paper I describe one way in which species interactions operating in local communities may influence the potential for speciation by influencing the potential for generating differentiation across the range of a species as hypothesized in the allopatric speciation model with regional differences in selection. The relative strengths of selection experienced by a population can have profound effects on the shape of the overall fitness surface. Using a simple model of fitness I show that even when the same trait values are favored by various agents of natural selection, the relative strengths of selection imposed by various selective agents will modulate the degree of population differentiation that can be generated by natural selection, and thus the potential for allopatric speciation via response to local selection pressures that vary across the range of a species. This analysis indicates that the relative strengths of selection imparted by various niche axes can be as important to diversification as the number of niche axes along which populations can differentiate. Because the strength of ecological interactions can also influence the number of coexisting species, and if the strength of an interaction is positively related to the strength of selection imposed by that interaction, this mechanism suggests a possible link between the ecological processes regulating local species diversity and the macroevolutionary processes generating new species.

LOCAL INTERACTIONS AND POPULATION DIFFERENTIATION

Can local interactions influence regional processes which affect the potential for population differentiation and thus allopatric speciation? A number of authors have argued that the primary force preventing population differentiation that would lead to allopatric speciation is the similarity in selection pressures experienced by different populations across the range of a species (e.g., Ehrlich and Raven 1969, Lande 1980). Conversely, if populations in different parts of a species' range experience different selection regimes, populations in these different areas may evolve to the point of differentiation that can lead to speciation (Ehrlich and Raven 1969, Endler 1977). The results of laboratory experiments indicate that such differences in selection pressures across a species' range could rapidly generate reproductive isolation via pleiotropic or genetic hitchhiking effects, even with substantial gene flow (reviewed by Rice and Hostert 1993). In this section I outline how the relative strengths of local selective agents can influence the potential for population differentiation across the range of a species by influencing the shape of the fitness surfaces experienced by different populations.

Local ecological interactions will influence the potential for speciation by generating variation in the shapes of fitness surfaces experienced by populations across the range of a species. The distribution of a species is a mosaic of local populations embedded in local communities. For example, for a species inhabiting lakes, each lake supports a separate population, and the species range is the geographic area encompassing the collection of lakes inhabited by the species. The fitnesses of individuals in a particular population are influenced by the local abiotic environment and interactions with resources, competitors, predators, diseases, etc., in the local community. Each ecological interaction, which is also potentially an agent of natural selection, may generate a unique relationship between some component of fitness (survival or fecundity schedules) and the phenotype (i.e., fitness components of Arnold and Wade 1984). The overall fitness surface experienced by a population is then a function of all the component interactions that contribute to determining overall fitness (Lande 1979, 1980, Arnold and Wade 1984).

Some ecological interactions may be regular features of all local communities inhabited by a species and in fact may define species composition of the community (e.g., keystone species sensu Paine [1966, 1980]), whereas other types of interactions may vary in importance across a species' range. Each population will be evolving according to the fitness surface generated by local ecological conditions. Although current theoretical development of how multiple selective agents may influence selection dynamics is sparce, I use a simple model of fitness surfaces to illustrate how variation in the strengths of selection from various selective agents acting in local populations can profoundly influence the degree of differences between fitness surfaces experienced by populations and thus the potential for population differentiation and speciation.

For simplicity I will consider the case in which only two selective agents act on one phenotypic character in any one population. One phenotypic character may often simultaneously experience selection from multiple selective agents. For example, in many prey species activity level will influence both survival under predation and feeding rates, which should both be strong determinants of fitness (e.g., Sih 1980, 1982, Kohler and McPeek 1989, Werner and Anholt 1993, Werner and McPeek 1994). Growth rate can also be simultaneously under selection generated by both predation and competition (e.g., Wilbur 1984, Travis et al. 1985). Germination date in plants may experience selection via competitive interactions and abiotic factors such as the timing of frosts (Kalisz 1986, Miller 1987, van der Toorn and Pons 1988, Biere 1991, Stratton 1992). Arnold and Wade (1984) have examined how total lifetime fitness is decomposable into separate fit-

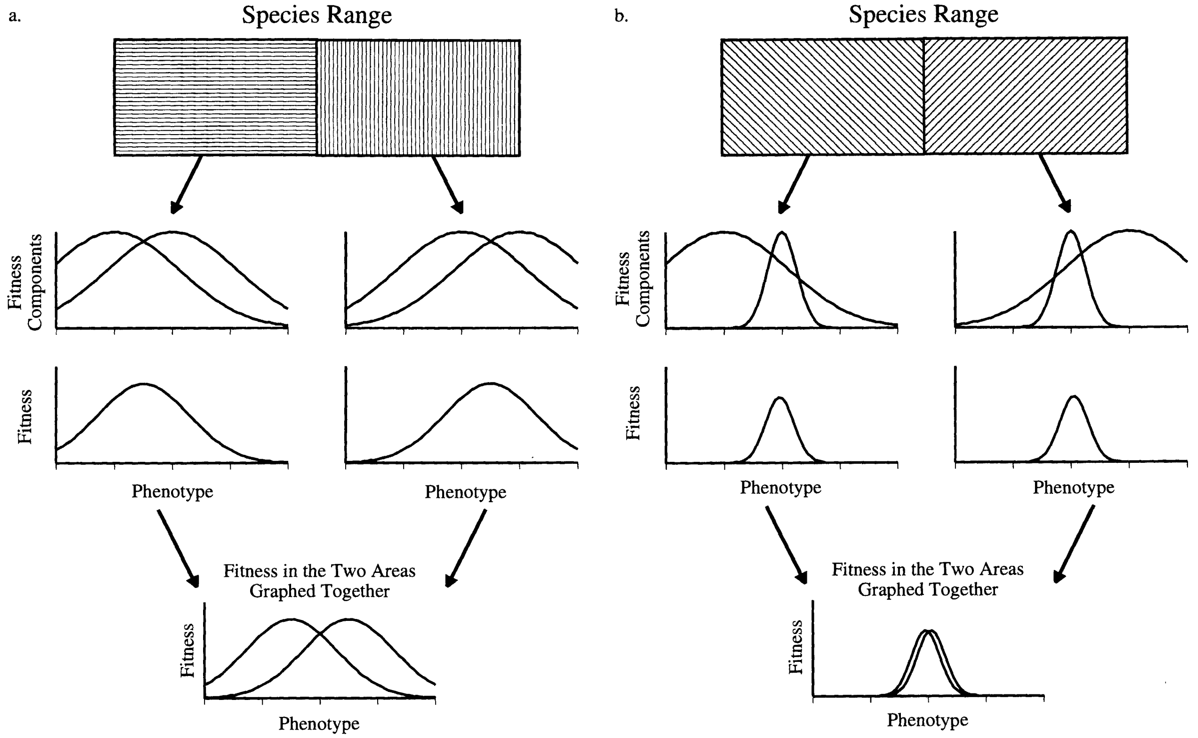

FIG. 1. The potential for population differentiation caused by differences in the strengths of selection from multiple selective agents on one phenotypic character. The panels of this figure present an idealized scenario of two species living in two different communities. For one species in one community (a), two areas exist across the range of this species. In one area (the area of its range designated by horizontal lines), two selective agents, which favor different values but impose similar strengths of selection, act on one phenotypic trait. The relationships between the fitness components for the two selective agents and the phenotype are given by the left panel in the first row of graphs in (a). The optimum in the overall fitness surface in this area is intermediate to the two optima of the individual fitness components; this is illustrated in the left panel in the second row of graphs in (a). In another area (the area of its range designated by vertical lines), two selective agents that impose similar strengths of selection also act on the phenotypic trait; one selective agent found in the first area also operates here, but the other is replaced by a different selective agent that favors another trait value. The relationships for the two fitness components and for overall fitness for this second area of the species range are given in the right column of graphs in (a). Selection favors very different phenotypic values in these two areas (the overall fitness surfaces for the two regions are illustrated in the same graph in the bottom-most panel of (a). Significant differentation between the two areas of the species range can therefore be generated by these divergent selection regimes, which could result in allopatric speciation. Now consider another species in another community (b) experiencing similar spatial variation in selection regimes in two areas of its range. Selective agents in the two areas favor the same trait values as for the species described in (a), but the selective agent common to both areas imposes much stronger selection than the selective agents that are unique to each area [cf. the panels in the first row of graphs of (b)]. Consequently for this species, the overall fitness surfaces for the two areas are very similar [second row of graphs and the bottom-most panel of (b)]. Little differentation between the two regions can be generated for this species because the phenotypes favored in the two areas are very similar, and the fitness curves largely overlap. Thus the potential for allopatric speciation is greatly reduced.

ness components. When fitness components are multiplicative, the fitness component generating the largest strength of selection will have the greatest effect on the overall fitness function (Arnold and Wade 1984). This result is important for understanding changes in the fitness surfaces experienced by populations as selective agents vary across the range of a species.

To illustrate how differences in the type and strength of different selective agents acting on one character can influence the potential for population differentiation, consider the following scenario. A species occupies one community type and has two areas to its range (Fig. 1a); these areas may be different geographic regions or the main body of the range and some peripheral populations. In the first area, two selective agents act on one character to determine overall fitness (Fig. 1a). Each selective agent imposes optimizing selection, and both impose similar strengths of selection, but the optimal phenotypic value differs for the two agents (Fitness Components in Fig. 1a). With optimizing selection the strength of selection characterizes the change in fitness as the phenotype is changed away from the optimum (Lande 1979). (The curves for the two fitness components pictured in Fig. 1a are both Gaussian in form, where the formula for each is Fitness Component = $\exp[-(z - \mu)^2/2\omega]$: z is the phenotypic value; μ is the optimal phenotype; ω is the parameter that defines the width of the curve and quantifies the strength of selection. $\omega=20$ for both of these fitness components. All of the results pictured in Fig. 1 and discussed in the text are easily derived analytically.) Overall fitness, which is a multiplicative function of the two fitness components (Lande 1979, Arnold and Wade 1984), is maximized at a phenotypic value that is exactly intermediate in this case to the two separate fitness component optima (Fitness in Fig. 1a). (Note that this intermediate optimum is the evolutionary characterization of what community ecologists discuss as trade-offs [cf. Lubchenco 1978, Schoener 1986, Tilman 1987].) In contrast, in the other area of the range one of the selective agents found in the first area is also present (this may be a keystone interaction that defines the community's species composition), but the other selective agent is replaced by a new selective agent that favors another trait value (Fig. 1a). Again, the strength of selection for both selective agents is the same (again $\omega = 20$). Overall fitness in this area is maximized at a trait value that is substantially different from that of the first area (Fig. 1a). Differences in selection regimes between these two areas should promote population differentiation, because different trait values are favored in the two areas of the species range. This difference in selection regimes between the two regions of the species range should therefore be conducive to generating allopatric speciation (Rice and Hostert 1993).

Now consider another species that exists in another community type (Fig. 1b). This species has similar differences in selective agents among populations, but the selective agents also differ in the strength of selection they impose. One agent imposes strong selection on the trait and is common to both areas (the ubiquitous fitness component pictured in Fig. 1b has $\omega = 1$: note that the strength of selection increases as ω decreases), while other selective agents are unique to each area and impose much weaker selection ($\omega = 20$ for these selective agents in Fig. 1b). The optima for the fitness components are at the same trait values as in the previous example; only the strengths of selection differ (Fig. 1b). Again in each area, the optimal trait value in overall fitness is intermediate to the separate fitness component optima, but now the overall optimum is very near the optimum for the component with strong selection. Consequently, the optima for the two areas are very near to one another, and the fitness curves for the two areas largely overlap (Fig. 1b). Little or no population differentiation will occur between the two areas; even though the agents of selection are quite different in the two areas, the adaptive topographies are almost identical because their shapes are predominantly defined by the strong selective agent that is common to both areas. Consequently, little potential exists for speciation via allopatric differences in selection in this environment.

The results of simulations (M. A. McPeek, *unpublished data*) indicate that similar outcomes of population differentiation can be achieved when separate selective pressures act independently on two phenotypic characters that are genetically correlated because of shared pleiotropic loci and the genetic correlation is also allowed to evolve.

DISCUSSION

Natural selection may constrain or enhance the potential for population differentiation that can lead to allopatric speciation. It has been argued that natural selection is the primary evolutionary force determining whether populations of a species remain a cohesive unit or are disrupted onto separate evolutionary trajectories (Ehrlich and Raven 1969, Lande 1980). If populations experience similar selective surfaces, cohesion is likely since the same relationship between fitness and phenotype will exist in all populations. Populations may explore the adaptive surface by undergoing shifts between adaptive peaks, but any resulting new adaptation can be dispersed throughout the species range to generate peak shifts in the rest of the populations (Wright 1932, Lande 1980, Crow et al. 1990, Phillips 1994). Population differentiation should be much more likely when populations experience different selective surfaces (Ehrlich and Raven 1969, Endler 1977). In this case, selection is a consistent evolutionary force generating different adapted phenotypes among populations. This is true even with significant gene flow (Endler 1977, Rice and Hostert 1993). However, selection on dispersal propensity generated by spatial variation in fitness should also favor a reduction in gene flow between areas with different selection surfaces (Gadgil 1971, Balkau and Feldman 1973, Hastings 1983, Holt 1985, McPeek and Holt 1992), which will further promote differentiation. Therefore, any mechanism that causes populations of a species to experience different selection surfaces should have a tremendous impact on the potential for speciation (Endler 1977, Rice and Hostert 1993).

Studies of community organization suggest that some selection pressures will be consistent environmental features of a community type and others may vary from locality to locality. Two of the best studied systems are the rocky intertidal and freshwater lakes. Paine (1980) in his review of rocky intertidal community structure shows that *Pisaster* seastars are a consistent organizing force influencing species richness all along the western North American coast, but the composition and importance of other species as well as abiotic factors change with latitude. In freshwater lakes characteristic zooplankton communities develop in the presence and absence of fish (Hrbácek et al. 1961, Brooks and Dodson 1965, Hall et al. 1970, Zaret 1980, Vanni 1986, 1988): small-bodied species with fish, and large-bodied species in fishless lakes. In these communities, fish predation defines species composition and contributes to the regulation of coexisting species, but other ecological features, such as productivity (Carpenter et al. 1985, McQueen et al. 1986, 1989), algal and zooplankton abundances (Stemberger and Lazorchak 1994), and structural complexity (Tessier and Welser 1991), can vary greatly among lakes. Some ecological interactions, such as *Pisaster* predation in the intertidal or fish predation in fish lakes, strongly influence species composition and thereby define the community type; these "keystone" interactions (Paine 1966, 1974) and their associated selection pressures will be ubiquitous selective agents acting on all populations of a species in a given community type. Other interactions, which are not primary determinants of species composition but rather primarily influence the abundances of species within the community, and their associated selection pressures can vary in importance among local populations.

The relative strengths of selection imposed by ubiquitous interactions and interactions that vary substantially among populations will influence the degree to which population differentiation can develop within a species (Fig. 1). If the ubiquitous and local selection pressures are relatively similar in strength, local populations will be able to adapt along niche dimensions that vary among populations; this will promote population differentiation and therefore allopatric speciation. If, however, the ubiquitous selective agents impose much stronger selection than local selective agents, populations will be constrained from adapting to local conditions that vary among populations, and the potential for speciation will be retarded. The potential for speciation is enhanced as selection strengths become more similar because greater variation in the overall fitness surfaces experienced by different populations can be achieved (Fig. 1).

Selective agents that vary among local populations need not only be environmental factors, but could also be sexual selection pressures. Natural and sexual selection are generally thought to act on the same traits or correlated sets of traits (Fisher 1958, Lande 1981, Thornhill and Alcock 1983, Kodric-Brown and Brown 1984, Lande and Kirkpatrick 1988). Weaker natural selection may allow sexual selection to generate greater differences in mating preferences among local populations which could lead to speciation (West-Eberhard 1983). Alternatively, sexual selection may reinforce niche differentiation, permitted by weaker selection from ubiquitous selective agents, to enhance synergistically the potential for speciation (Lande and Kirkpatrick 1988). Speciation due to differentiation of mate choice or sexual recognition may therefore not be independent of changes in the strength of natural selection within communities.

These considerations generate a number of testable predictions about how ecological and evolutionary processes interact to influence species diversity in communities structured by species interactions. (1) Species in less diverse communities should display less population differentiation across their ranges in ecologically important phenotypic characters, because less local adaptation should be possible. This is because (2) greater disparities should exist among the strengths of selection imposed by various selective agents in less diverse communities, and consequentially (3) the shapes of fitness surfaces should vary less among populations for species in less diverse communities (Fig. 1). (4) Speciation rates in component taxa should be higher in more diverse communities. It is somewhat disheartening to realize that almost no data are available to evaluate these predictions. Testing these predictions will require combining ecological and evolutionary methodologies to study community structure, and therefore should foster cross-discipline exchanges and collaborations. Measuring the strengths of species interactions and the resulting selection can be combined in the same experimental manipulations of competitors, resources, predators, etc. (e.g., Miller et al. 1994). Observational and experimental studies quantifying the fitness surfaces in multiple populations will be invaluable for interpreting the causes of population differentiation (Wade and Kalisz 1990). Finally, phylogenetic studies of component taxa can not only provide estimates of diversification rates for comparison among communities (e.g., Mitter et al. 1988, Farrell et al. 1991), but also for reconstructing the history of community structure development over time (Futuyma and McCafferty 1990, McPeek 1995*a, b*).

The number of local niche dimensions is often cited as influencing the potential for diversification within communities (Begon et al. 1990, Ricklefs 1990, Krebs 1994). This analysis shows that the relative strengths of selection imposed by various selective agents (i.e., along various niche dimensions) can have as much or more to do with the potential for diversification as the number of axes along which diversification can occur. In the example discussed above (Fig. 1), the number of "niche axes" available for populations to diversify along was always the same. The potential for differentiation among populations is governed by the relative strengths of selection imposed by the various ecological interactions defining the niche axes. Differentation of taxa could be greater in a community type with relatively few local niche dimensions, weak interactions and weak selection pressures than in a community type with many local niche dimensions but one strong interaction and consequently one strong selection pressure.

Coexistence and speciation.—Do the ecological conditions that promote the coexistence of many species also foster high speciation and/or low extinction rates? We must begin to address such questions theoretically and empirically if we are to understand fully patterns of species diversity. For the mechanism I discuss in this paper, a loose congruency could potentially exist between the number of coexisting species and the potential for generating new species in a community. The strength of selection generated by an ecological interaction should be related to the magnitude of effects the interaction has on overall birth and death rates, i.e., the "strength" of the ecological interaction (Paine 1980). For example, in a study of 16 populations over 4 yr, Weis et al. (1992) found that the strength of selection on the gall-making insect *Eurosta solidaginins* was positively correlated with the mortality imposed by parasitoid wasps. Mechanisms of competition should operate in an analogous fashion; as competitor abundances increase, resource levels will decrease, which will place a premium on having competitively superior phenotypes. The strength of selection on emergence date in plants has been shown to increase as conspecific density (Miller et al. 1994) and heterospecific density (van der Toorn and Pons 1988, Stratton 1992) increases, presumably as a result of increases in the strength of competition.

A common pattern observed in nature is that the number of coexisting species decreases as the strength of interactions among species increases (Paine 1966, 1969, 1974, 1980, 1988, Harper 1969, Addicott 1974, Lubchenco 1978, Duggins and Dethier 1985, Turner 1985, Gibson 1988), and ecological theories that encapsulate various mechanisms of interactions among species can generate this relationship (e.g., May 1973, Holt 1977). For example under the keystone predator hypothesis (Paine 1966, 1969, 1974), species diversity should be low in areas where the keystone predator is absent, because the strength of competition with the dominant competitor should be greatest in the absence of the predator and thus drive all other species extinct via competitive exclusion. Diversity should also be low when the keystone predator is very abundant; the strength of predation under this condition drives most prey species locally extinct. Diversity is predicted to be highest at intermediate predator densities where the strengths of competition and predation are both much weaker than their potential maxima. General food web theory also predicts that the number of coexisting species should decrease as the average strength of species interactions in a community increases (May 1973). The frequency and intensity of disturbance can also generate such diversity patterns (e.g., Connell 1978, Huston 1979).

Consequently, in a community in which a strong ecological interaction dominates, few species are expected to coexist; and if this dominant interaction imposes much stronger selection than other interactions, the potential for allopatric speciation in component taxa should be impeded (Fig. 1b). Conversely, if the populations of component taxa in a community are regulated by relatively weak interactions and interactions impose relatively similar strengths of selection, many species may be able to coexist, and the potential for allopatric speciation in component taxa may be enhanced. Obviously, not all strong selection pressures will necessarily result from strong ecological interactions, just as not all strong ecological interactions will necessarily generate strong selection on the phenotype. However, abundant evidence indicates that ecological interactions generate natural selection (see Endler 1986 for a general review) and that the strength of selection can covary with the strengths of interactions (reviewed by Travis 1990).

At present, the data needed to evaluate whether the strengths of ecological interactions and the strengths of selection are positively correlated across communities, and whether these processes interact to influence species diversity, do not exist. Ideally, one would correlate (1) the changes in birth or survival rates associated with manipulations of major predators or competitors in field experiments with (2) the strengths of selection gradients on phenotypic characters determining performance in these ecological interactions in natural populations in communities that vary in species diversity. Studies of interaction strengths and selection strengths are commonly being conducted separately to many systems (field experiments of species interactions: see reviews by Connell 1983, Schoener 1983, Sih et al. 1985, Hairston 1989, Goldberg and Barton 1992; quantifying natural selection in the field, e.g., Kalisz 1986, Brodie 1992, King 1994), but few studies simultaneously evaluate the strength of an ecological interaction and natural selection imposed by that interaction (see above references). Therefore, relating any covariance among them to diversity patterns is presently impossible. Also, more explicit theory linking mechanisms of various types of ecological interactions to the phenotypes of component species and thereby to the mechanisms generating the shapes of individual fitness surfaces is sorely needed.

Other mechanisms linking ecology and speciation.— Obviously, the process I have described is only one of many by which ecological interactions could influence speciation rates. The mechanisms described above will be most applicable in environments where species interactions strongly influence species composition in local communities and temporal variation in local environmental conditions is relatively small (e.g., marine intertidal, and freshwater lentic and lotic communities). My goal in this paper is not to develop a complete framework for these linkages under all possible conditions, but rather to stimulate thought on the general topic and explore the problem in one set of environmental conditions. I briefly mention two others.

"Key innovations" are often invoked as a reason why some communities have more species than others. "Key innovations" are phenotypes that are associated with higher diversification rates in certain lineages (Bock 1985). The mechanisms presented above may also be relevant to why key innovations may lead to higher speciation rates. Implicit in discussions of key innovations is the idea that possessing a new phenotypic trait alters selection pressures on the entire phenotype (Simpson 1953, Stanley 1979, Benton 1988, Eldredge 1989), but how changing the selection regime alters the potential for speciation remains unclear (Mitter et al. 1988, Allmon 1992). In lineages that do not possess the key innovation, strong selection pressures on one set of characters may prevent adaptation along other niche axes or to sexual selection pressures that could lead to population differentiation (i.e., Fig. 1b). However, if the new phenotypic trait relaxes selection from a strong selective agent, populations may be better able to respond to other selection pressures that may promote differentiation (Fig. 1a). In this case the important feature to relaxing selection is a difference in the phenotype rather than a difference in the external environment; key innovations may be associated with habitat shifts, but it is possession of the new phenotype that is thought to promote higher speciation rates. Farrell et al. (1991) have shown that plant lineages possessing latex and resin canals have higher diversification rates than sister groups lacking canals. They concluded that the relaxation of selection due to herbivores was probably the cause of higher diversification rates. Other hypotheses exist for why key innovations may lead to greater diversification (Mitter et al. 1988, Allmon 1992, Brooks and McLennan 1993). However, if the relaxation of one selection pressure promotes diversification via responses to others, not only should speciation rates increase in lineages possessing the key innovation, but also these lineages should cover a much wider range of phenotype space than sister clades without the key innovation.

The degree of temporal variation in environmental conditions may also substantially influence speciation rates in communities (Sanders 1968, Slobodkin and Sanders 1969, Jackson 1974, Jablonski 1986). Temporal variation will influence the evolution of both adaptations to local environmental conditions and dispersal rates between populations (Levins 1964, Holt 1987, McPeek and Holt 1992). In this paper, I have considered only the case where interactions and the resulting fitness surfaces in local populations do not vary substantially through time. Under these conditions, greater spatial variation in environmental conditions will promote greater levels of differentiation, if ubiquitous selection pressures for the community type are not relatively strong. Spatial but no temporal variation will concomitantly select for decreased dispersal among populations (Gadgil 1971, Balkau and Feldman 1973, Hastings 1983, Holt 1985, McPeek and Holt 1992), which will reduce gene flow. Consequently, both local adaptation and the evolution of dispersal should promote population differentiation under these conditions.

In contrast, temporal variability in ecological conditions will favor strategies that can survive over the range of conditions experienced in local populations: either individuals with phenotypes that are a compromise of those most favored under each separate set of conditions experienced (i.e., a "jack-of-all-trades": Levins 1968, MacArthur 1972, Felsenstein 1979) or individuals that are phenotypically plastic (Levins 1968, Smith-Gill 1983, Via and Lande 1985, Sultan 1987, Moran 1992). Spatial and temporal variability also favor high dispersal rates and therefore potentially high gene flow rates among populations (Gadgil 1971, Kuno 1981, McPeek and Holt 1992). With spatial and temporal variation both adaptation to local conditions and the evolution of dispersal should retard population differentiation. The potential for speciation via population differentiation should therefore decrease as the degree of temporal variability in local conditions increases (Slobodkin and Sanders 1969, Jablonski 1986).

The mechanisms generating and maintaining species diversity may be as numerous as the types of environments that exist in nature, and there is no reason to believe that only one mode of speciation will operate in one system. Species diversity may be regulated to varying degrees by species interactions in different systems (e.g., terrestrial insect communities vs. invertebrates in freshwater lakes). Speciation and extinction rates may also be influenced to varying degrees by ecological processes in different systems; in some systems speciation may proceed predominantly by polyploidy, vicariance events, or drift, while ecological processes such as the strength of selection or variability in environmental conditions may have primacy in others. Processes governing coexistence and processes governing diversification may also be integrated to varying degrees in different systems. Moreover, multiple mechanisms may simultaneously operate to create new species in systems. Our goal should not be to derive one general model to cover all situations. Rather, models encapsulating properties associated with different systems are required. Generality will emerge when we understand which properties cause different mechanisms to operate in different systems. Development of such a theory will build strong mechanistic links between community ecology and macroevolution.

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LITERATURE CITED

Addicott, J. F. 1974. Predation and prey community structure: an experimental study of the effect of mosquito larvae on the protozoan communities of pitcher plants. Ecology **55**:475–492.

Allmon, W. D. 1992. A causal analysis of stages in allopatric speciation. Oxford Surveys in Evolutionary Biology **8**: 219–258.

Arnold, S. J., and M. J. Wade. 1984. On the measurement of natural and sexual selection: theory. Evolution **38**:709–719.

Balkau, B. J., and M. W. Feldman. 1973. Selection for migration modification. Genetics **74**:171–174.

Barrett, S. 1989. Mating system evolution and speciation in heterostylous plants. Pages 257–283 *in* D. Otte and J. A. Endler, editors. Speciation and its consequences. Sinauer, Sunderland, Massachusetts, USA.

Begon, M., J. L. Harper, and C. R. Townsend. 1990. Ecology: individuals, populations and communities. Second edition. Blackwell Scientific, Boston, Massachusetts, USA.

Benton, M. J. 1988. The nature of an adaptive radiation. Trends in Ecology and Evolution **3**:127–128.

Biere, A. 1991. Parental effects in *Lychnis flos-cuculi.* II. Selection on time of emergence and seedling performance in the field. Journal of Evolutionary Biology **3**:467–486.

Bock, W. J. 1985. Adaptive inference and museological research. Occasional Papers of the British Columbia Provincial Museum **25**:123–138.

Boecklin, W. J., and D. Simberloff. 1985. Area-based extinction models in conservation. Pages 247–276 *in* D. K. Elliott, editor. Dynamics of extinction. John Wiley & Sons, New York, New York, USA.

Brodie, E. D., III. 1992. Correlational selection for color pattern and antipredator behavior in the garter snake *Thamnophis ordinoides.* Evolution **46**:1284–1298.

Brooks, J. L., and S. I. Dodson. 1965. Predation, body size, and composition of plankton. Science **150**:28–35.

Brooks, J. L., and D. A. McLennan. 1993. Comparative study of adaptive radiations with an example using parasitic flatworms (Platyhelminthes: Cercomeria). American Naturalist **142**:755–778.

Brown, J. H., and P. F. Nicoletto. 1991. Spatial scaling of species composition: body masses of North American land mammals. American Naturalist **138**:1478–1512.

Cadle, J. E., and H. W. Green. 1993. Phylogenetic patterns, biogeography, and the ecological structure of Neotropical snake assemblages. Pages 281–293 *in* R. E. Ricklefs and D. Schluter, editors. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, Illinois, USA.

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience **35**:634–639.

Connell, J. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus.* Ecology **42**:710–723.

———. 1978. Diversity in tropical rainforests and coral reefs. Science **199**:1302–1310.

———. 1983. On the prevalence and importance of interspecific competition: evidence from field experiments. American Naturalist **122**:661–696.

Cornell, H. V. 1985*a*. Local and regional richness of cynipine gall wasps on California oaks. Ecology **66**:1247–1260.

———. 1985*b*. Species assemblages of cynipid gall wasps are not saturated. American Naturalist **126**:565–569.

———. 1993. Unsaturated patterns in species richness: the role of regional processes in setting local species richness. Pages 243–252 *in* R. E. Ricklefs and D. Schluter, editors. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, Illinois, USA.

Cornell, H. V., and J. H. Lawton. 1992. Species interactions, local and regional processes, and the limits to the richness of ecological communiites: a theoretical perspective. Journal of Animal Ecology **61**:1–12.

Coyne, J. A. 1994. Ernst Mayr and the origin of species. Evolution **48**:19–30.

Cracraft, J. 1982. A nonequilibrium theory for the rate-control of speciation and extinction and the origin of macroevolutionary patterns. Systematic Zoology **31**:348–365.

———. 1985. Biological diversification and its causes. Annals of the Missouri Botanical Garden **72**:794–822.

Crow, J. F., W. R. Engels, and C. Denniston. 1990. Phase three of Wright's shifting-balance theory. Evolution **44**: 233–247.

Dodson, S. I. 1970. Complementary feeding niches maintained 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 mechanisms and the structure of an experimental species ensemble. American Naturalist **137**:1–26.

Duggins, D. O., and M. N. Dethier. 1985. Experimental studies of herbivory and algal competition in a low intertidal habitat. Oecologia (Berlin) **67**:183–191.

Ehrlich, P. R., and P. H. Raven. 1969. Differentiation of populations. Science **165**:1228–1232.

Eldredge, N. 1989. Macroevolutionary dynamics: species, niches, and adaptive peaks. McGraw-Hill, New York, New York, USA.

Endler, J. A. 1977. Geographical variation, speciation, and clines. Princeton University Press, Princeton, New Jersey, USA.

———. 1986. Natural selection in the wild. Princeton University Press, Princeton, New Jersey, USA.

Farrell, B. D., D. E. Dussourd, and C. Mitter. 1991. Escalation of plant defense: do latex and resin canals spur plant diversification? American Naturalist **138**:881–900.

Feder, J. L., and G. L. Bush. 1991. Genetic variation among apple and hawthorn host races of *Rhagoletis pomonella* across an ecological transition zone in the Mid-Western United States. Experimental and Applied Entomology **59**: 249–265.

Felsenstein, J. 1979. Excursions along the interface between disruptive and stabilizing selection. Genetics **93**:773–795.

Fisher, R. A. 1958. The genetical theory of natural selection. Second edition. Dover, New York, New York, USA.

Flecker, A. S. 1992. Fish trophic guilds and the structure of a tropical stream: weak direct vs. strong indirect effects. Ecology **73**:927–940.

Futuyma, D. J., and S. S. McCafferty. 1990. Phylogeny and the evolution of host plant associations in the leaf beetle genus *Ophraella* (Coleoptera: Chrysomelidae). Evolution **44**:1885–1913.

Gadgil, M. 1971. Dispersal: population consequences and evolution. Ecology **52**:253–261.

Gibson, D. J. 1988. The maintenance of plant and soil heterogeneity in dune grassland. Journal of Ecology **76**:497–508.

Goldberg, D. E., and A. M. Barton. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. American Naturalist **139**:771–801.

Gomulkiewicz, R., and R. D. Holt. 1995. When does evolution by natural selection prevent extinction? Evolution **49**:201–207.

Grant, V. 1981. Plant speciation. Columbia University Press, New York, New York, USA.

Griffiths, R. W. 1981. The effect of trout predation on the abundance and production of stream insects. Master's thesis. University of British Columbia, Vancouver, British Columbia, Canada.

Hairston, N. G. 1989. Ecological experiments : purpose, design, and execution. Cambridge University Press, New York, New York, USA.

Hall, D. J., W. E. Cooper, and E. E. Werner. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. Limnology and Oceanography **15**:839–928.

Harper, J. L. 1969. The role of predation in vegetational diversity. Brookhaven Symposium in Biology **22**:48–62.

Hastings, A. 1983. Can spatial variation alone lead to selection for dispersal? Theoretical Population Biology **24**: 244–251.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology **12**:197–229.

———. 1985. Population dynamics in two-opatch environments: some anomalous consequences of an optimal habitat distribution. Theoretical Population Biology **28**:181–208.

———. 1987. Population dynamics and evolutionary processes: the manifold roles of habitat selection. Evolutionary Ecology **1**:331–347.

Hrbácek, J., M. Dvorakova, V. Korlnek and L. Procházkóva. 1961. Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen **14**:192–195.

Humphries, C. J., and L. Parenti. 1986. Cladistic Biogeography. Clarendon Press, Oxford, England.

Huston, M. 1979. A general hypothesis of species diversity. American Naturalist **113**:81–101.

Hutchinson, G. E. 1958. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology **22**:415–427.

———. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? American Naturalist **93**:145–159.

Jablonski, D. 1986. Background and mass extinctions: the alternation of macroevolutionary regimes. Science **231**: 129–133.

Jackson, J. B. C. 1974. Biogeographic consequences of eurytopy and stenotopy among marine bivalves and their evolutionary significance. American Naturalist **108**:541–560.

Kalisz, S. 1986. Variable selection on the timing of germination in *Collinsia verna* (Scrophulariaceae). Evolution **40**: 479–491.

King, R. B. 1994. Color-pattern variation in Lake Erie water snakes: prediction and measurement of natural selection. Evolution **47**:1819–1833.

Kodric-Brown, A., and J. H. Brown. 1984. Truth in advertising: the kinds of traits favored by natural selection. American Naturalist **124**:309–323.

Kohler, S. L., and M. A. McPeek. 1989. Predation risk and the foraging behavior of competing stream insects. Ecology **70**:1811–1825.

Krebs, C. J. 1994. Ecology: the experimental analysis of distribution and abundance. Fourth edition. Harper Collins, New York, New York, USA.

Kuno, E. 1981. Dispersal and the persistence of populations in unstable habitats: a theoretical note. Oecologia (Berlin) **49**:123–126.

Lande, R. 1979. Quantitative genetic anaysis of multivariate evolution, applied to brain:body size allometry. Evolution **33**:402–416.

———. 1980. Genetic variation and phenotypic evolution during allopatric speciation. American Naturalist **116**:463–479.

———. 1981. Models of speciation by sexual selection on polygenic traits. Proceedings of the National Academy of Sciences (USA) **78**:3721–3725.

Lande, R., and M. Kirkpatrick. 1988. Ecological speciation by sexual selection. Journal of Theoretical Biology **133**: 85–98.

Lawlor, S. P., and P. J. Morin. 1993. Food web architecture and population dynamics in laboratory microcosms of protists. American Naturalist **141**:675–686.

Lawton, J. H., and R. M. May. 1995. Extinction rates. Oxford University Press, Oxford, England.

Levins, R. 1964. The theory of fitness in a heterogeneous environment. IV. The adaptive significance of gene flow. Evolution **18**:635–638.

———. 1968. Evolution in changing environments. Princeton University Press, Princeton, New Jersey, USA.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. American Naturalist **112**:23–39.

———. 1980. Algal zonation in the New England rocky intertidal community: an experimental analysis. Ecology **61**:333–344.

Lynch, J. D. 1989. The gauge of speciation: on the frequencies of modes of speciation. Pages 527–553 *in* D. Otte and J. A. Endler, editors. Speciation and its consequences. Sinauer, Sunderland, Massachusetts, USA.

MacArthur, R. H. 1972. Geographical ecology. Princeton University Press, Princeton, New Jersey, USA.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.

May, R. M. 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton, New Jersey, USA.

Mayr, E. 1942. Systematics and the origin of species. Columbia University Press, New York, New York, USA.

———. 1963. Animal species and evolution. Belknap Press of Harvard University, Cambridge, Massachusetts, USA.

McPeek, M. A. 1990. Determination of species composition in the *Enallagma* damselfly assemblages of permanent lakes. Ecology **71**:83–98.

———. 1995*a*. Testing hypotheses about evolutionary change on single branches of a phylogeny using evolutionary contrasts. American Naturalist **145**:686–703.

———. 1995*b*. Morphological evolution mediated by behavior in the damselflies of two communities. Evolution **49**:749–769.

McPeek, M. A., and R. D. Holt. 1992. The evolution of dispersal in spatially and temporally varying environments. American Naturalist **140**:1010–1027.

McQueen, D. J., M. R. S. Johannes, J. R. Post, T. J. Stewart, and D. R. S. Lean. 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. Ecological Monographs **59**:289–308.

McQueen, D. J., J. R. Post, E. L. Mills. 1986. Trophic relationships in freshwater pelagic ecosystems. Journal of the Fisheries Research Board of Canada **43**:1571–1581.

Miller, T. E. 1987. Effects of emergence time on survival and growth in an early old-field plant community. Oecologia (Berlin) **72**:272–278.

Miller, T. E., A. A. Winn, and D. E. Schemske. 1994. The effects of density and spatial distribution on selection for emergence time in *Prunella vulgaris* (Lamiaceae). American Journal of Botany **81**:1–6.

Mitter, C., B. F. Farrell, and B. Wiegmann. 1988. The phylogenetic study of adaptive zones: has phytophagy promoted insect diversification? American Naturalist **132**:107–128.

Moran, N. A. 1992. The evolutionary maintenance of alternative phenotypes. American Naturalist **139**:971–989

Neill, W. E. 1975. Experimental studies of microcrustacean competition, community composition and efficiency of resource utilization. Ecology **56**:809–826.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist **100**:65–75.

———. 1969. A note on trophic complexity and community stability. American Naturalist **103**:91–93.

———. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principle predator. Oecologia **15**:93–120.

———. 1980. Food webs: linkage, interaction strength and community infrastructure. Journal of Animal Ecology **49**: 667–685.

———. 1988. Food webs: road maps of interactions or grist for theoretical development? Ecology **69**:1648–1654.

Phillips, P. C. 1994. Peak shifts and polymorphisms during phase three of Wright's shifting-balance process. Evolution **47**:1733–1743.

Pimm, S. L. 1978. Sympatric speciation: a simulation model. Biological Journal of the Linnean Society **11**:131–139.

Platnick, N. I., and G. Nelson. 1978. A method of analysis for historical biogeography. Systematic Zoology **27**:1–16.

Post, J. R., and D. Cucin. 1984. Changes in the benthic community of a small precambrian lake following the introduction of yellow perch, *Perca flavescens.* Canadian Journal of Fisheries and Aquatic Sciences **41**:1496–1501.

Rice, W. R. 1985. Disruptive selection on habitat preference and the evolution of reproductive isolation: an exploratory experiment. Evolution **38**:735–742.

———. 1987. Speciation via habitat specialization: the evolution of reproductive isolation as a correlated character. Evolutionary Ecology **1**:301–314.

Rice, W. R., and E. E. Hostert. 1993. Laboratory experiments on speciation: what have we learned in 40 years? Evolution **47**:1637–1653.

Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. Science **235**:167–171.

———. 1989. Speciation and diversity: the integration of local and regional processes. Pages 599–622 *in* D. Otte and J. A. Endler, editors. Speciation and its consequences. Sinauer, Sunderland, Massachusetts, USA.

———. 1990. Ecology. Third edition. W. H. Freeman, New York, New York, USA.

Ricklefs, R. E., and D. Schluter. 1993. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, Illinois, USA.

Robinson, B. W., and D. S. Wilson 1994. Character release and displacement in fishes: a neglected literature. American Naturalist **144**:596–627.

Robinson, J. V., and J. E. Dickerson. 1987. Does invasion sequence affect community structure? Ecology **68**:587–595.

Rosenzweig, M. L. 1975. On continental steady states of species diversity. Pages 121–141 *in* M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts, USA.

———. 1978. Competitive speciation. Biological Journal of the Linnean Society **10**:274–289.

Rummell, J. D., and J. D. Roughgarden. 1985. A theory of faunal buildup for competition communities. Evolution **39**: 1009–1033.

Sanders, H. L. 1968. Marine benthic diversity: a comparative study. American Naturalist **102**:243–282.

Schluter, D., and J. D. MacPhail. 1993. Character displacement and replicate adaptive radiation. Trends in Ecology and Evolution **8**:197–200.

Schoener, T. W. 1983. Field experiments on interspecific competition. American Naturalist **122**:240–285.

———. 1986. Mechanistic approaches to community ecology: a new reductionism? American Zoologist **26**:81–106.

Sih, A. 1980. Optimal behavior: can foragers balance two conflicting demands? Science **210**:1041–1043.

———. 1982. Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmanni.* Ecology **63**:786–796.

Sih, A., P. Crowley, M. McPeek, 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.

Simpson, G. G. 1953. The major features of evolution. Columbia University Press, New York, New York, USA.

Slobodkin, L. B., and H. L. Sanders. 1969. On the contribution of environmental predictability to species diversity. Brookhaven Symposium in Biology **22**:82–95.

Smith-Gill, S. J. 1983. Developmental plasticity: developmental conversion versus phenotypic modulation. American Zoologist **23**:47–55.

Soulé, M. E. 1987. Viable populations for conservation. Cambridge University Press, Cambridge, United Kingdom.

Sprules, W. G. 1972. Effects of size-selective predation and food competition on high altitude zooplankton communities. Ecology **53**:375–386.

Stanley, S. M. 1979. Macroevolution: pattern and process. W. H. Freeman, San Francisco, California, USA.

Stemberger, R. S., and J. M. Lazorchak. 1994. Zooplankton assemblage responses to disturbance gradients. Canadian Journal of Fisheries and Aquatic Science **51**:2435–2447.

Stratton, D. A. 1992. Life-cycle components of selection in *Erigeron annuus*: I. phenotypic selection. Evolution **46**:92–106.

Strong, D. R., J. H. Lawton, and R. Southwood. 1984. Insects on plants: community patterns and mechanisms. Harvard University Press, Cambridge, Massachusetts, USA.

Sultan, S. E. 1987. Evolutionary implications of phenotypic plasticity in plants. Evolutionary Biology **21**:127–178.

Tauber, C. A., and M. J. Tauber. 1989. Sympatric speciation in Insects: perception and perspective. Pages 307–344 *in* D. Otte and J. A. Endler, editors. Speciation and its consequences. Sinauer, Sunderland, Massachusetts, USA.

Tessier, A. J., and J. Welser. 1991. Cladoceran assemblages, seasonal succession and the importance of a hypolimnetic refuge. Freshwater Biology **25**:85–93.

Thornhill, R., and J. Alcock. 1983. The evolution of insect mating systems. Harvard University Press, Cambridge, Massachusetts, USA.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.

———. 1987. The importance of the mechanisms of interspecific competition. American Naturalist **129**:769–774.

———. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, New Jersey, USA.

Travis, J. 1990. The interplay of population dynamics and the evolutionary process. Philosophical Transactions of the Royal Society of London, B **330**:253–259.

Travis, J., W. H. Keen, and J. Juilianna. 1985. The effects of multiple factors on viability selection in *Hyla gratiosa* tadpoles. Evolution **39**:1087–1099.

Turner, T. 1985. Stability of rocky intertidal surfgrass beds: persistence, preemption, and recovery. Ecology **66**:83–92.

van der Toorn, J., and T. L. Pons. 1988. Establishment of *Plantago lanceolata* L. and *Plantago major* L. among grass: II. Shade tolerance of seedlings and selection on time of germination. Oecologia (Berlin) **76**:341–347.

Vanni, M. J. 1986. Competition in zooplankton comunities: suppression of small species by *Daphnia pulex*. Limnology and Oceanography **31**:1039–1056.

———. 1988. Freshwater zooplankton community structure: introduction of large invertebrate predators and large herbivores to a small-species community. Canadian Journal of Fisheries and Aquatic Sciences **45**:1758–1770.

Via, S., and R. Lande. 1985. Genotype-environment interaction and the evolution of phenotypic plasticity. Evolution **39**:505–522.

Wade, M. J., and S. Kalisz. 1990. The causes of natural selection. Evolution **44**:1947–1955.

Weis, A. E., W. G. Abrahamson, and M. C. Anderson. 1992. Variable selection on *Eurosta*'s gall size. I. The extent and nature of variation in phenotypic selection. Evolution **46**: 1674–1697.

Werner, E. E., and B. R. Anholt. 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. American Naturalist **142**: 242–272.

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

West-Eberhard, M. J. 1983. Sexual selection, social competition, and speciation. Quarterly Review of Biology **58**: 155–183.

Whittaker, J. H. 1975. Communities and ecosystems. Second edition. Macmillan, New York, New York, USA.

Wilbur, H. M. 1984. Complex life cycles and community organization in amphibians. Pages 196–224 *in* P. W. Price, C. N. Slobodchikoff and W. S. Gaud, editors. A new ecology: novel approaches to interactive systems. John Wiley & Sons, New York, New York, USA.

Wilson, D. S. 1989. The diversification of single gene pools by density- and frequency-dependent selection. Pages 366–385 *in* D. Otte and J. A. Endler, editors. Speciation and its consequences. Sinauer, Sunderland, Massachusetts, USA.

Wilson, D. S., and M. Turelli. 1986. Stable underdominance and the evolutionary invasion of empty niches. American Naturalist **127**:835–850.

Wright, S. 1932. The roles of mutation, inbreeding, crossbreeding and selection in evolution. Proceedings of the Sixth International Congress on Genetics **1**:356–366.

Zaret, T. M. 1980. Predation and freshwater communities. Yale University Press, New Haven, Connecticut, USA.