

Competitive and Facilitative Evolutionary Diversification

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A central goal of evolutionary ecology is to understand the role of different ecological processes in producing patterns of macroevolutionary diversification. Theory and empirical evidence have shown that competition between existing species can promote evolutionary diversification through ecological character displacement and, more recently, that competition may play a role both in producing species and in driving their subsequent evolutionary divergence. However, recent theory and experiments suggest that other ecological interactions, such as facilitation, may also be important in the evolutionary diversification of some taxa. Future research in this area will be invaluable in dissecting the relative roles of different ecological processes in producing and maintaining biodiversity.

Keywords: adaptive dynamics, adaptive radiation, competition, diversity, evolutionary branching

Current estimates place the number of named species at about 1.4 million (WRI 2001). Scientists continue to discover new species daily, and estimates suggest the total number of species on Earth is somewhere between 2 million and 100 million. More remarkable is that over the past 3 billion to 4 billion years, this enormous diversity of living creatures appears to have evolved from very few ancestral species (Freeman and Herron 2001). This poses a daunting but fundamental question for evolutionary biologists: How has such an astonishing level of evolutionary diversification taken place throughout Earth's history (Hutchinson 1959)? Why, for example, does a single hectare of tropical rain forest sometimes contain more than 300 species of trees instead of just a few?

Unfortunately (or perhaps fortunately, if you are a scientist), such questions do not yet have satisfactory answers. Indeed, the scale of the question is so large that it is difficult to know where or how to begin. Because evolution by natural selection is the most important unifying concept in biology, many scientists begin by looking to *The Origin of Species* ([1859] 1993) to see what Charles Darwin had to say on the subject. Although Darwin certainly recognized the origin of evolutionary diversification (i.e., species) as a central question in biology, he did not produce a fully compelling answer, despite the title of his most famous work.

With the advent of genetics, biologists realized that one fundamental issue involved in the evolutionary diversification of

sexual organisms is the evolution of reproductive isolation, the equivalent of speciation according to the concept of biological species (Dobzhansky 1951, Mayr 1963, Kondrashov and Mina 1986, Johnson and Gullberg 1998). This is typically viewed as an essential component of evolutionary diversification, because, even if divergent natural selection favors different kinds of adaptation under different conditions, gene flow must typically be reduced and even halted between areas of divergent selection pressures before morphological, behavioral, and physiological differences, the hallmarks of diversity, can take hold (Dobzhansky 1951, Kondrashov and Mina 1986, Johnson and Gullberg 1998). Much research has been carried out in this area, and scientists' understanding of the causes and consequences of reproductive isolation has progressed considerably since *The Origin of Species*.

Although reproductive isolation may set the stage for evolutionary diversification, there is another equally important

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ingredient. Natural selection must be disruptive, favoring a diversity of phenotypes. It is under these conditions that we expect evolutionary diversification to occur. What types of ecological processes give rise to diversifying selective pressure? Why does natural selection favor so many different kinds of organisms and modes of life? Of course, one possibility is that divergent natural selection has nothing to do with the diversity observed in nature. Evolutionary diversification could have proceeded randomly throughout the phenotypic “space” of possible organisms, in much the same way that odors diffuse randomly throughout the still air of a room. While this is certainly a reasonable null hypothesis, there is mounting evidence that natural selection has played an important role in many of the most spectacular evolutionary diversifications (Schluter 2000), and therefore it is of interest to know what ecological processes cause natural selection to favor diversity. In this article, we summarize historical progress on the topic and highlight some very modest steps that recent evolutionary theory has made toward answering this question.

Early ideas of evolutionary diversification

The concept of ecological opportunity played a central role in early ideas on the origin and maintenance of biological diversity (Simpson 1944, 1953). The concept is based on the notion that the environment is made up of different ecological niches (the variety of consumable resources and other factors such as temperature and humidity) and that the availability of these niches is a primary determinant of the number of species that are expected (Lack 1944, Dobzhansky 1951). Intuitively appealing, the idea was supported by early research (Elton 1933, Crombie 1945, MacArthur 1964) and led eventually to the well-known competitive exclusion principle. This principle states that no two species with the same niche can stably coexist (Volterra 1928, Hardin 1960, MacArthur and Levins 1964) and, by extension, that the number of coexisting species cannot exceed the number of distinct niches (as discussed in Armstrong and McGehee 1980).

Although designed to explain which ecological processes limit present diversity, the combination of ecological opportunity and competitive exclusion also served as a guide for understanding how that diversity might originate. In particular, the enormous diversity observed today may have resulted in part from the existence of an enormous number of ecological niches (Dobzhansky 1951). Perhaps groups of individuals from an existing species colonize and establish populations in particular niches, and selection drives evolutionary diversification as more and more new niches are filled. Inherent in this idea is the assumption that tradeoffs occur: Having high fitness in one niche comes at the cost of having low fitness in other niches. Diversification through specialization ensues, because “a jack of all trades is master of none.” This theory does not incorporate the spatial distribution of different niches (although the spatial location of a niche might be, in part, one of its defining features), but the reduction in gene flow thought to be required for substantial evolutionary

divergence to occur would undoubtedly be more pronounced if different niches were isolated in space.

These early ideas focused on the role of competition for resources and tradeoffs in structuring communities and laid the groundwork for subsequent research. Although the competitive exclusion principle focused attention on an idealized relationship between the number of niches and the number of species, it was clear that different species share the same collection of resources and that species’ niches are properly defined by the extent to which they use the different resources that make up the axes of a multidimensional niche space (Hutchinson 1957, 1959). As a result, an influential idea related to the competitive exclusion principle was formalized: the principle of limiting similarity (MacArthur and Levins 1967, May and MacArthur 1972, May 1974; see Abrams 1983 for a review and critique of these results). Although species can partition the different resources along the axes of the total niche volume, we might still expect that, when integrated over the different resources present, some species would be able to competitively exclude others. In fact, the more similar two species are in their resource requirements, the more intensely they will compete, and the more likely it is that one will exclude the other through competition for resources. Thus, the principle of limiting similarity postulates that there is a limit to how similar species can be and still coexist (MacArthur and Levins 1967, May and MacArthur 1972, May 1974).

Together, the concepts of niche dimensionality, competitive exclusion, and limiting similarity highlighted the fact that there are countless ways in which evolutionary diversification might fill up available niche space, but that coexisting species still must somehow differ in their resource use (Tilman 1982). More important in the present context, this work also led to the idea that as species are added to a community and evolve suitable adaptations, the species already present in the community are expected to undergo some degree of coevolutionary modification as well (Lack 1944, Futuyma and Slatkin 1983). Although the environment was originally envisaged as determining the collection of niches to which species must evolve, each species in fact modulates the relative abundance of the various resources and so affects the evolutionary trajectory of competing species. One of the clearest conceptual statements of this general idea is the theory of ecological character displacement, which was explicitly developed to explain the role of interspecific competition for resources in driving evolutionary diversification (Schluter 2000).

Interspecific competition for resources and character displacement

The original notion of character displacement was developed by Brown and Wilson (1956), Hutchinson (1959), and MacArthur and Levins (1964), even before the concept of limiting similarity was completely formalized. These authors recognized that if species compete for resources, evolutionary divergence in resource use might be expected where

similar species come into geographic contact. This would reduce the degree of competition and thereby promote the coexistence of a diversity of organisms. This phenomenon was called “character displacement” because it should result in phenotypic characters related to resource use in similar species being displaced from one another where their geographic ranges overlap. Indeed, Brown and Wilson (1956) put forward a number of empirical examples to support this idea (see Grant 1972 for an incisive examination).

One of the key features of the theory of character displacement is the importance of interactive coevolution: Each species affects the resource distribution in the environment and thus modifies the selective regime affecting its own evolution as well as that of other species. Using a particular resource might be beneficial in the absence of competition, but the presence of competitors might well alter the situation. In effect, it is the ecological community itself that is a primary determinant of its own evolutionary diversification. Still, we might expect the competitive exclusion principle to limit diversity. If the resource base in a given location is very broad, many species might eventually be supported (after coevolution), whereas if it is very narrow, relatively few species might be able to coexist (Roughgarden 1983, Taper and Case 1992).

There are dozens of putative examples of character displacement from a wide variety of taxa (Schluter 2000). Here we consider one particularly illustrative example in which the observational evidence for character displacement has been supplemented with an experimental demonstration of the hypothesized mechanism (competition promotes evolutionary diversification). The threespine stickleback (*Gasterosteus aculeatus*) is a small fish that inhabits high-latitude coastal lakes and rivers of the Northern Hemisphere (figure 1). A marine form of threespine stickleback is believed to be the living ancestor of the freshwater forms. In a few lakes in British Columbia, there are two species (or morphs) of freshwater stickleback that have evolved morphological adaptations for consuming two very different resources: planktonic prey (limnetic morph) and benthic prey (benthic morph). This is in contrast to most other lakes, in which there is a single morph that is intermediate in its resource use (Schluter and McPhail 1992). Molecular evidence suggests that the coexisting species pairs arose from two separate invasions of the lakes by limnetic-like marine sticklebacks (Taylor and McPhail 1999).

These findings led researchers to postulate that the divergent phenotypes observed in lakes with species pairs are the evolutionary result of competition for resources and ecological character displacement between the two groups of colonizing marine sticklebacks (Schluter and McPhail 1992). Experiments conducted in artificial ponds support this hypothesis (Schluter 1994, 2003). An experimental population (corresponding to the first marine invasion) with a broad range of phenotypes was created using various crossing techniques and placed in ponds with and without a limnetic competitor (corresponding to the second marine invasion). In the absence of competition, all phenotypes had similar growth rates, whereas in the presence of the limnetic com-



Figure 1. The two forms of freshwater stickleback found in some lakes in coastal British Columbia, Canada. Photograph: Dolph Schuller, University of British Columbia.

petitor, benthic phenotypes had a growth rate advantage over limnetic phenotypes (figure 2). Thus, the presence of a limnetic competitor promoted diversification by increasing the fitness of phenotypes specializing on the benthic resources.

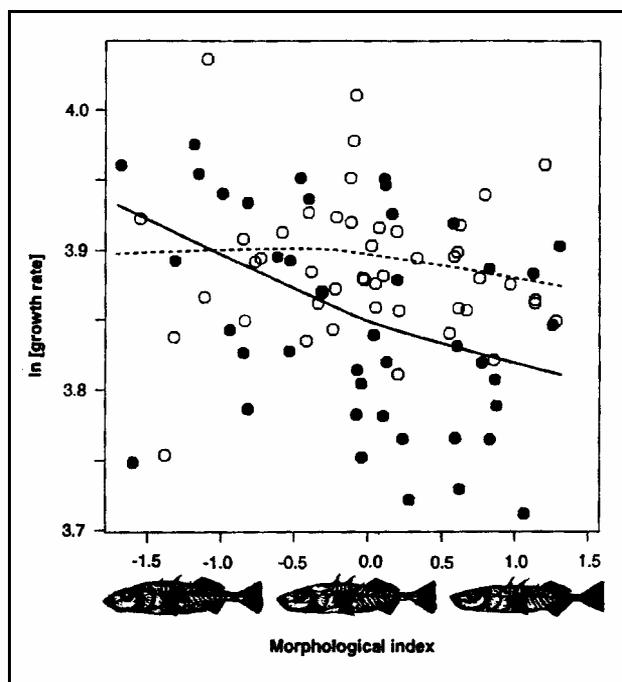


Figure 2. Growth rate (in millimeters) of different morphs of stickleback along a continuum from benthic to limnetic types (left to right on the x-axis). Open circles and dotted line show results from an experimental control; filled circles and solid line show results when competitors of the limnetic species were added. The addition of limnetic competitors appears to generate a growth rate advantage for the benthic morphs. Reprinted from Schluter (1994).

Intraspecific competition and evolutionary diversification

The perspective discussed above treats the evolutionary diversification resulting from competition largely as a phenomenon of interspecific interactions. As such, it tends to view species (or at least differentiated races) as given and explore the extent to which competition for resources among these forms enhances preexisting phenotypic differences. In a sense, this is predominantly a process of allopatric diversification: One form colonizes a habitat and evolves to best utilize the resource base. Then a second, and typically somewhat different, species colonizes the habitat, and coevolutionary diversification ensues. Though it has produced invaluable insights, this body of work does not provide an answer to our original question: What types of ecological processes give rise to the divergent selection that drives evolutionary diversification?

One of the most interesting recent theoretical developments postulates a mechanism through which evolutionary diversification into distinct phenotypes might occur in sympatry (i.e., within a single species), thereby providing an evolutionary explanation for how selection favors the origin of different species and how they coevolve once they are present. It is a natural outgrowth and expansion of earlier theory on ecological character displacement, but it also considers how diversifying selection acts on phenotypic variation at an intraspecific level (Roughgarden 1972, Bolnick et al. 2003). Suppose that a single species colonizes a habitat and evolves toward specialization on the most abundant resource (figure 3). At this stage, if the resource base is broad relative to the species-wide spectrum of resource use, disruptive selection can act on phenotypic variation within this species (Eshel 1983, Abrams et al. 1993, Geritz et al. 1998). Natural selection favors diversification, because strong competition for what was initially the most abundant resource now makes specialization on other resources more profitable (figure 3; Rosenzweig 1978).

Points in phenotypic space that are approached as a result of directional natural selection but that, once reached, experience disruptive selection have been termed *evolutionary branching points*, because they are the points at which evolutionary diversification is favored by natural selection. Notice, however, that because a population at a branching point is still a single species, some mechanism for the evolution of reproductive isolation between the different phenotypes is required before substantial evolutionary divergence can take place (Taylor and Day 1997, Dieckmann and Doebeli 1999, Geritz and Kisdi 2000, Abrams 2001). This phenomenon of endogenously generated disruptive selection has been the focus of a great deal of recent theory on evolutionary diversification, which is sometimes referred to as the theory of adaptive dynamics (Geritz et al. 1998).

There is an interesting relationship between the results from adaptive dynamics and previous theory. Perhaps not surprisingly, the conditions under which evolutionary branching points occur are the same as those under which

evolutionary divergence and coexistence occur in two-species or multiple-species models of interspecific competition and ecological character displacement (Slatkin 1980, Day 2000). Evolutionary branching within species was not highlighted in previous results, however, because assumptions of sexual reproduction in earlier theory tended to lead to the conclusion that evolutionary branching within a single species did not occur, even in the face of disruptive selection (Slatkin 1980, Taylor and Day 1997). The recent theory of adaptive dynamics, on the other hand, most often assumes that reproduction is asexual (Abrams 2001). Therefore, it is better able to identify the role of diversifying selection, because gene flow does not prevent evolutionary divergence from occurring at branching points. In essence, no new ecological process is being described by this recent theory on competitive diversification (Rosenzweig 1978). However, recent research has also demonstrated that ecological interactions other than competition can give rise to such evolutionary branching points (Doebeli and Dieckmann 2000). In addition, traits other than those directly related to resource extraction can undergo evolutionary diversification by similar processes (e.g., life-history traits, sexually selected traits).

Examples of experimental evolutionary diversification

The theory of adaptive dynamics and of evolutionary branching points is very recent, and therefore there are still few explicit tests of its predictions. Circumstantial evidence for evolutionary branching in sympatry comes from the repeatable trophic polymorphisms observed in numerous species of postglacial fishes (Robinson and Wilson 1994, Schluter 1996) and from a well-documented case of sympatric speciation in African cichlids (Schliewen et al. 1994, 2001). Opportunities exist for testing the predictions experimentally, however, and some steps have been taken in this direction. Perhaps the most direct attempt is a study involving artificial selection experiments, using *Drosophila* as a model system (Bolnick 2001).

To mimic the theory as closely as possible, a continuous resource base (similar to that shown in figure 3) was created by making a range of resources of different qualities available to the flies through the addition of different concentrations of cadmium chloride in an otherwise standard cornmeal *Drosophila* medium. The concentrations were chosen to result in a unimodal resource distribution across the various cadmium levels (figure 4). As assumed by the theory, the requisite tradeoff in resource specialization occurs in this experimental system; flies that are adapted to resources with high cadmium concentrations show poor fitness on cadmium-free resources (Bolnick 2001).

The experiment was run over several generations to test the prediction that flies should evolve toward specialization on the most abundant resource, and that selection for this evolutionary change should be stronger when competition for resources is stronger. Consistent with this prediction, experimental populations of *Drosophila* evolved toward adaptation

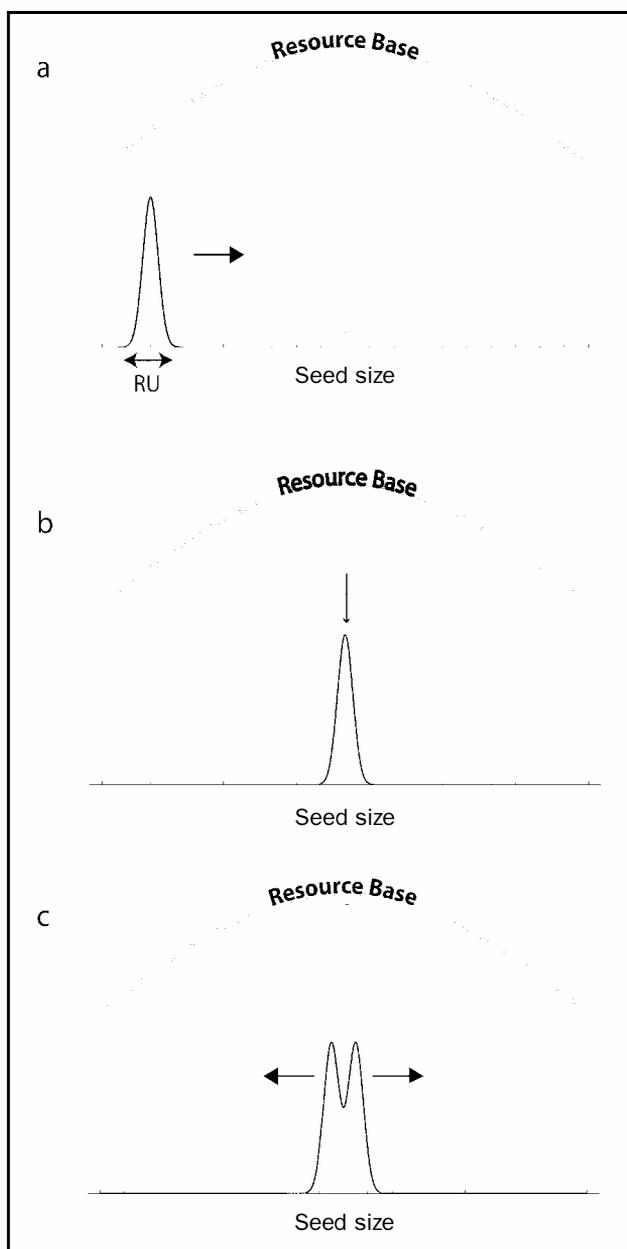


Figure 3. Graphic portrayal of the underpinnings of the theory of competitive evolutionary branching. The curve labeled “resource base” illustrates the abundance of different resources in the environment. For illustrative purposes, the resources are taken to be seeds of different sizes. The blue curve represents the resource use spectrum of the species in question. (a) The resource use spectrum (labeled “RU”) of the species initially evolves toward utilization of the most abundant seed size. (b) Strong competition among those individuals that are best adapted to the resource that is initially most abundant (i.e., those under the arrow) results in a depression of their fitness. (c) If the resource use spectrum is substantially narrower than the resource base, disruptive selection can occur, favoring evolutionary diversification.

to the most abundant resource, and populations that experienced stronger competition (as a result of lower total resource density per fly) evolved more quickly, suggesting that selection was stronger under these conditions (figure 4). While these results are interesting and are the first to test recent theoretical predictions, the crucial prediction of the theory (that disruptive selection is generated through competition for resources) was not explicitly tested. Therefore, the extent to which this example should be viewed as strong support for the theory of competitive diversification is unclear.

One hallmark of the hypothesized mechanism of competitive diversification is a phenomenon referred to as negative frequency-dependent selection (NFDS). This is a situation in which the direction of natural selection depends on the frequency of different phenotypes in the population in such a way that rare types have a fitness advantage (positive frequency-dependent selection occurs if common types have a selective advantage). The fitness of the different phenotypes changes as a function of their frequency, such that variation is maintained. For example, it is only after the most abundant resource is heavily utilized (as a result of a high frequency of types specializing on this resource) that specializing on other resource types becomes beneficial enough that such morphs can increase in frequency.

A number of study systems appear to be well equipped to test the role of NFDS in producing evolutionary branching points through disruptive selection (Rainey et al. 2000, Travisano and Rainey 2000, Kassen 2002). Microbial organisms such as *Pseudomonas* and *Escherichia coli* are ideal for testing this theory, because their rapid generation times make evolutionary experiments feasible. Also, because such organisms are asexual, they represent the most conducive systems for finding evolutionary branching. Several experiments have documented evolutionary diversification along with a clear pattern of NFDS. In single strains of *E. coli* propagated in a glucose medium, evolutionary diversification eventually took place, resulting in the stable maintenance of two distinct physiological types (Turner et al. 1996, Travisano and Rainey 2000). Similarly, in colonies of a single strain of *Pseudomonas* that were propagated in a complex liquid medium, evolutionary diversification eventually took place, resulting in three well-defined types that appear to coexist indefinitely (the fuzzy spreader, wrinkly spreader, and smooth types; Rainey and Travisano 1998). These morphs appear to exploit different spatial niches in the liquid medium. Perhaps even more remarkably, these patterns of evolutionary diversification are highly repeatable between experiments.

These results are extremely exciting, and it has been noted that these experiments have inadvertently provided empirical data that are consistent with recent theoretical predictions (Travisano and Rainey 2000). Evolutionary diversification occurred as expected, and the presence of clear NFDS in these experiments has been taken as evidence that, in accord with theory, competition for resources played the primary role in driving this diversification.

Competitive or facilitative diversification?

The examples above clearly show evolutionary diversification in experimental systems. However, it is important to ask whether competition for resources was actually the primary

mechanism driving this diversification. It is worth considering whether a pattern of NFDS is sufficient to rule out other possible ecological interactions as explanations for the diversification.

Unfortunately, the answer is no. Consider, instead, the possibility that facilitation played an important role in these experiments (Whittaker 1977, Bruno et al. 2003). Facilitation is an ecological interaction in which the presence of one species (say type A) enhances the fitness of another (say type B). Negative frequency-dependent selection can occur under this type of interaction as well, because the greater the frequency of type A, the greater is its facilitative effect on type B.

The demonstration that other ecological interactions, such as facilitation, can give rise to NFDS is not merely a theoretical result. Facilitation has been implicated in the aforementioned microbial experiments. For example, in the experiments in which *E. coli* diversified during propagation in glucose, the new variants that arose specialized on acetate, which is a metabolite produced by the consumption of glucose by the original strain. This example of cross-feeding demonstrates that evolutionary diversification in this case occurred primarily as a result of the first species having a facilitative effect on the second through its introduction of additional resources into the environment (Turner et al. 1996). Facilitative interactions may be important in the *Pseudomonas* system as well. For example, the fuzzy spreader type cannot invade a population of the wrinkly spreader type without the smooth type also being present (see figure 4 in Travisano and Rainey 2000).

These findings suggest that ecological interactions other than competition can create diversifying selection and promote evolutionary diversification. Under facilitation, the addition of new species creates new niches (Levins and Lewontin 1985) and thereby represents a fundamentally different type of ecological interaction that may play an important role in evolutionary diversification (Doebeli 2002). To better understand the relative roles of competition and facilitation in diversification, we require a clear approach for distinguishing between the two.

Consider first the question of what maintains current diversity. If competition is the primary mechanism, then we expect to find a pattern of NFDS. There are two different ways one might test for NFDS in a focal species (which we term type B): (1) by decreasing the density of type B while increasing that of type A, so that total density remains constant, or (2) by holding the density of type B fixed while increasing the density of type A. If competition is important, the absolute fitness of type B will increase under the first type of manipulation (increasing type A while decreasing type B), because of a decrease in the strength of competition: The total number of individuals will not change, but fewer of them will be similar in resource use to type B. Conversely, under the second type of manipulation (increasing type A while holding the density of type B constant), the absolute fitness of type B will decrease, because although the number of

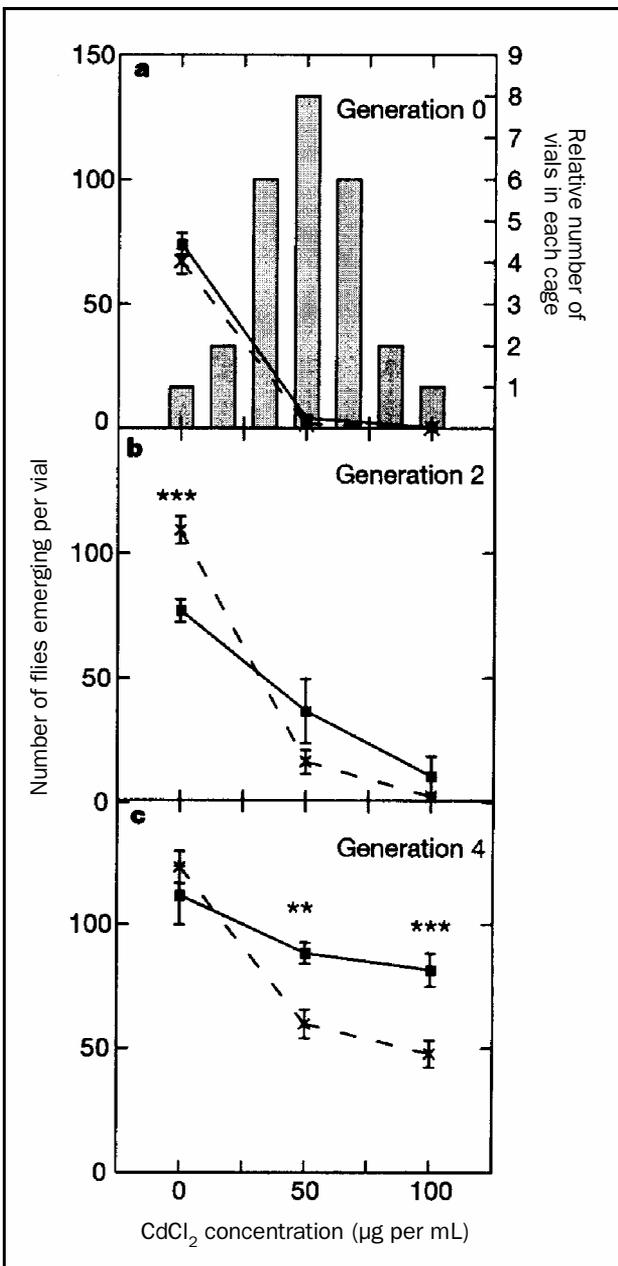


Figure 4. Populations of fruit flies with high levels of competition (squares) adapt to cadmium more rapidly than populations with low levels of competition (crosses). (a) Histograms show the relative abundance of resources with different cadmium concentrations (in micrograms of cadmium chloride [CdCl₂] per milliliter). Lines depict the fecundity of flies in the two treatments at different cadmium concentrations at the beginning of the experiment. (b) Fecundity after two generations of selection. (c) Fecundity after four generations of selection. Reprinted from Bolnick (2001).

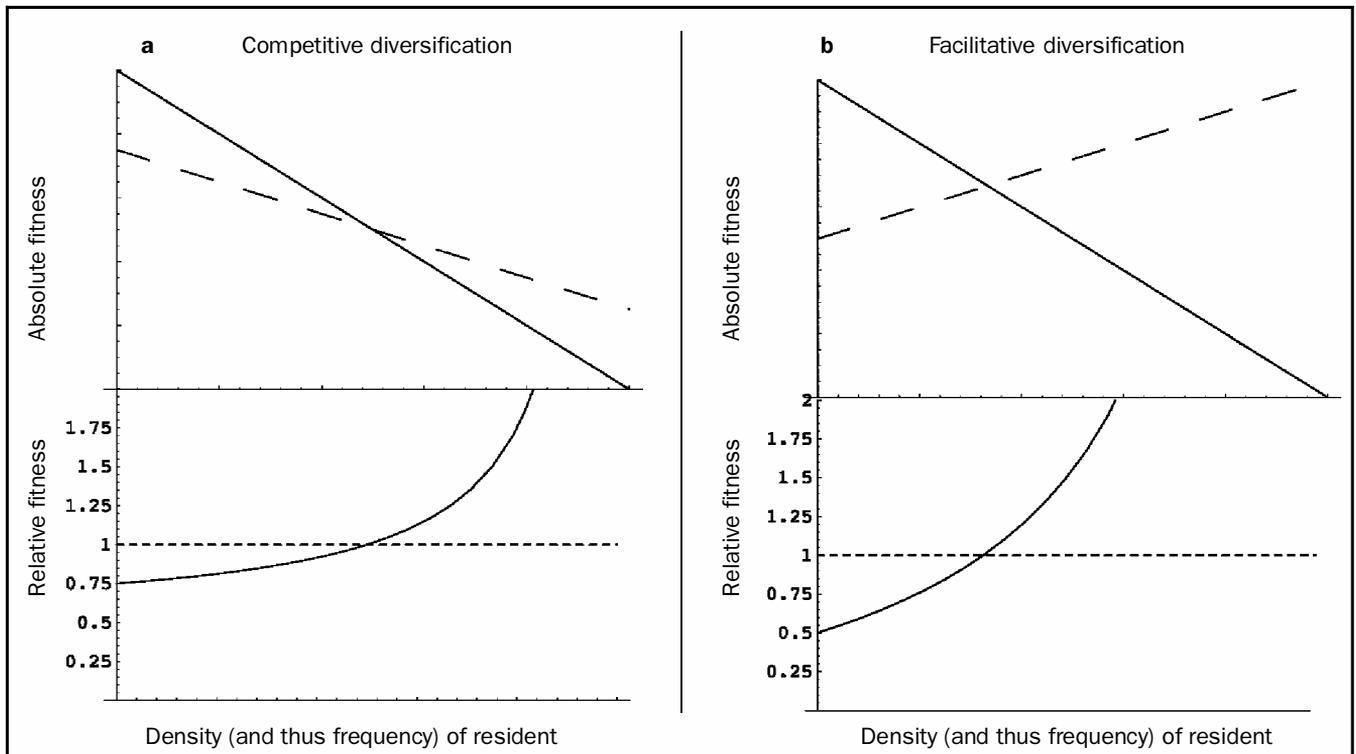


Figure 5. (a) Predictions under competitive diversification. Top panel shows the absolute fitness of a resident type or species (type A; solid line) and that of an invading mutant type or species (type B; dashed line) plotted against increasing density of the resident type, with the density of the mutant type held constant at a small value. The absolute fitness of both types decreases as the density of the resident type increases, but that of the resident does so more quickly. Bottom panel shows the relative fitness of the mutant type or species plotted against the same increasing density of the resident type [i.e., (mutant absolute fitness)/(resident absolute fitness)]. A value of unity implies equal fitness. Negative frequency-dependent selection (NFDS) is shown by the increase in the mutant's relative fitness when its frequency is small enough (i.e., when the density of the resident species is large enough). (b) Predictions under facilitative diversification. The absolute fitness of the resident type decreases as its density increases, but that of the mutant actually increases, owing to type A's facilitative effect. NFDS is shown by the increase in the mutant's relative fitness when its frequency is small enough (i.e., when the density of the resident species is large enough).

individuals similar in resource use to type B will not change, the total number of competitors will nevertheless increase (figure 5a).

If facilitation is the primary mechanism maintaining diversity, then under the first type of manipulation (increasing type A and decreasing type B), again we expect the absolute fitness of type B to increase, because the facilitative effect of type A on type B (per individual of type B) has increased. The distinguishing prediction comes from the second manipulation (increasing type A). If facilitation is important, we expect an increase in the absolute fitness of type B under this manipulation, because type A is essentially helping type B persist through facilitation. Thus, increasing the density of type A will increase the absolute fitness of type B (figure 5b). These predictions assume that the resource changes that come about from changes in density of different types have equilibrated. The manipulations are purely ecological in the sense that (as far as possible) no evolutionary change is allowed to occur.

Consider how these ecological interactions might initiate evolutionary diversification. In this context, we must distinguish between the absolute and relative fitnesses of our two types. We expect (and experiments confirm) that a single type (type A) initially adapts to the most valuable or abundant resource in the environment. Over time, a new mutant (type B) may appear that has a positive absolute growth rate, but its fitness is nevertheless lower than that of the type adapted to the most abundant resource. Because the new mutant has a lower relative fitness, it will decline in frequency and ultimately be driven to extinction. However, as the best adapted type (A) approaches carrying capacity, its mean absolute fitness (in terms of growth rate) must, by definition, approach zero.

If there are largely competitive interactions between type A and the new mutant (type B), then although both type A and type B fitness are expected to decrease with the increased abundance of type A, we might eventually expect their absolute fitnesses to become equal (figure 5a). This is the signature of

NFDS: Once it is rare enough, type B gains a relative fitness advantage over type A and thus increases in frequency, because within-type competition is stronger than between-type competition. Thus, as recent theory has predicted, competition produces NFDS and drives evolutionary diversification (figure 5a).

If there are largely facilitative interactions between type A and the mutant type B, things work somewhat differently. Again, because of intratype competition, the absolute fitness of type A is expected to decline as its density increases (figure 5b). However, in contrast to the scenario in which type A and type B are largely competitive, we might expect the absolute fitness of type B to increase as the density of type A increases (figure 5b). As before, NFDS is operating in such a way that there is some density of type A at which type B has a fitness equal to that of type A. Here, however, this occurs because a certain density of type A is required to provide the necessary facilitative effect. Thus, facilitation produces NFDS and drives evolutionary diversification because the positive effect of type A on type B allows type B to invade (figure 5b).

These considerations outline a simple conceptual approach for distinguishing between two fundamentally different ecological processes, competition and facilitation, that can give rise to evolutionary diversification. These processes are not mutually exclusive, and indeed within-type competition plays an important role in facilitative evolutionary diversification. In addition, the interactions between different species need not be symmetric. For example, type A may have a facilitative effect on type B, but type B may nevertheless have a largely competitive effect on type A.

Conclusions

Recent theoretical developments have made important steps toward explaining how ecological interactions among individuals can give rise to endogenously generated disruptive selection. This provides a potentially important part of the explanation for why such a tremendous evolutionary diversification has taken place throughout the history of life. To date, the primary focus of this theory has been on the effect of competition for resources in driving evolutionary diversification. Although there is some empirical support for this focus, recent theoretical and empirical studies have revealed that other types of ecological interactions, such as facilitation, can also play a fundamental role in producing evolutionary diversification.

There are at least two main challenges on the road to further developing this area of research. From an empirical standpoint, researchers must devise ways to distinguish between various types of ecological interactions as evolutionary generators of diversity. For example, we might distinguish between competition and facilitation by comparing how the absolute fitness of a rare mutant (type B above) depends on the density of another type. Other interactions, such as predation, parasitism, and mutualism, are also important and may lead to different predictions. Moreover, the perspective taken here largely assumes that communities are at (or near) their equilibrium level of diversity. This ignores

important historical factors that undoubtedly have large effects on patterns of diversity (Ricklefs and Schluter 1993), and teasing apart these complementary explanations poses an interesting challenge.

From a theoretical standpoint, the importance of ecological interactions such as facilitation in generating disruptive selection has only recently been explored (Doebeli and Dieckmann 2000). Using the competitive exclusion principle as a guide, one might expect that evolutionary branching would be more likely to occur as a result of facilitation, because this interaction increases the number of resources and thus the number of niches in the environment. This conjecture, that diversity begets diversity, has long been proposed as an explanation for the remarkable levels of diversity in tropical rain forests, but it has yet to receive sufficient theoretical and experimental attention.

It is also unclear at this stage whether the importance of facilitation extends beyond the experimental microbial systems explored to date. It is entirely possible that the factors governing evolutionary diversification in microbes are unlike those governing diversification in other taxa (e.g., Darwin's finches, sticklebacks, fruit flies). Facilitation in microbes appears to be the result of cross-feeding, but facilitation in other species might also be mediated through complex and often indirect ecological interactions involving several species on different trophic levels (Schluter 2000). There is increasing evidence for the role of facilitation in organisms other than microbes (Callaway et al. 2002), which presents an exciting area for future research (Bruno et al. 2003).

Acknowledgments

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