

Competitive and Facilitative Evolutionary Diversification

Running Head: Evolutionary Diversification

Troy Day¹ & Kyle A. Young²

1. Departments of Mathematics and Biology
Jeffery Hall
Queen's University
Kingston, ON, K7L 3N6
Canada

Phone: 613-533-2431
Fax: 613-533-2964
Email: tday@mast.queensu.ca

2. Department of Biology
Simon Fraser University
Burnaby, BC, V5A 1S6
Canada

Phone: 604-291-4649
Fax: 604-291-3496
Email: kayoung@sfu.ca

September 29, 2003

FOR BIOSCIENCE

Abstract

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 via ecological character displacement, and more recently, that competition may play a role in both producing species and 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 on our planet at around 1.4 million (World Resource Institute 2001). Scientists continue to discover new species daily, and estimates suggest the total number of species on earth is somewhere between 2 and 100 million. More remarkable is that over the past 3-4 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 the history of the earth (Hutchinson 1959)? Why, for example, does a single hectare of tropical rain forest sometimes contain over 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 first looking to the *Origin of Species* (1859) 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, it was 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 biological species concept (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 sorts of adaptations under different conditions, gene flow must typically be reduced and even halted between areas of divergent selection pressures before morphological, behavioural, and physiological differences, the very 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 our 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 ingredient. Natural selection must be disruptive, favoring a diversity of phenotypes. It is under these conditions that we expect evolutionary diversification to occur. This is the topic of the present article. 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 we observe in nature. Evolutionary diversification might have proceeded randomly throughout the phenotypic “space” of possible organisms, in much the same way that a odours 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 towards 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, humidity, etc.), 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; MacArthur and

Levins 1964; Hardin 1960), 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 we observe today might have resulted in part from there being 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 then drives evolutionary diversification as more and more new niches are filled. Inherent in this idea is 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”. Note that this idea says nothing about the spatial distribution of different niches (although this might be, in part, how some niches are defined), but the reduction in gene flow thought to be required for substantial evolutionary divergence 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 the 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, a very 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 will 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 importantly in the present context, this work also led to the idea that as species are added to 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. They recognized that if species compete for resources, then we might expect evolutionary divergence in resource use 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, then many species might eventually be supported (after coevolution), whereas if it is very narrow, then relative 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 where the observational evidence for character displacement has been supplemented with an experimental demonstration of the hypothesized mechanism: that competition promotes evolutionary diversification. Threespine stickleback (*Gasterosteus aculeatus*) is small fish that inhabits high latitude coastal lakes and rivers of the northern hemisphere (Figure 1). There is a marine form of threespine stickleback that is believed to be the ancestor of these 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 (i.e. first marine invasion) with a broad range of phenotypes was created using various crossing techniques and placed into ponds with and without a limnetic competitor (i.e. second marine invasion). In the absence of competition all phenotypes had similar growth rates, whereas in the presence of the limnetic competitor, benthic-like phenotypes had a growth rate advantage over limnetic-type phenotypes (Figure 2). Thus, the presence of a limnetic competitor promoted diversification by increasing the fitness of phenotypes specializing on the benthic resources.

Intraspecific Competition and Evolutionary Diversification

The above perspective 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 then explores the extent to which competition for resources among these forms enhances pre-existing phenotypic differences. In a sense this is predominately 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 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 as well as for how they coevolve once they are present. It is a natural outgrowth and expansion of earlier

theory on ecological character displacement, but 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 towards specialization on the most abundant resource (Figure 3). At this stage, if the resource base is broad relative to the species-wide resource use spectrum, disruptive selection can act on phenotypic variation in this single 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, then 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 this is still a single species, some mechanism for the evolution of reproductive isolation between the different phenotypes is required before substantial evolutionary divergence will 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 that 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 occurs in two (or multiple) species models of interspecific competition and ecological character displacement (Slatkin 1980; Day 2000). Within-species evolutionary branching was not highlighted in previous results, however, because assumptions of sexual reproduction in earlier theory tended to ensure 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). Additionally, traits other than those directly related to resource extraction can undergo evolutionary diversification by similar processes (e.g., life history traits, sexually selected traits, etc.).

Examples

The theory of adaptive dynamics and evolutionary branching points are 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 post glacial fishes (Robinson and Wilson 1994; Schluter 1996), and 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 of 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). Importantly, 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 towards 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* did evolve towards being adapted to the most abundant resource, and populations that experienced stronger competition (as a result of a 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 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 simply 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 once 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.

There are a number of study systems that appear well equipped to test the role of NFDS in producing evolutionary branching points through disruptive selection (Travisano and Rainey 2000; Rainey et al. 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 *Escherichia 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; Trivisano and Rainey 2000). Similarly, in colonies of a single strain of *Pseudomonas* 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 Trivisano 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 is consistent with recent theoretical predictions (Trivisano and Rainey 2000). 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 evolutionary diversification.

Competitive or Facilitative Diversification?

The above examples clearly show evolutionary diversification in experimental systems and are thus quite remarkable. 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 plays 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). NFDS 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.

Importantly, 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 *Escherichia 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 third, “smooth” type also being present (Figure 4 in Trivisano and Rainey 2000).

These findings suggest 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 NFDS. There are two different ways one might test for NFDS in a focal species (which we term type B): (i) by decreasing the density of type B while increasing that of type A so that total density remains constant, or (ii) 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 manipulation (i) because of a decrease in the strength of competition (the total number of individuals does not

change but fewer of them are similar in resource use to type B). Conversely, under manipulation (ii), the absolute fitness of type B will decrease because, although the number of individuals similar in resource use to type B does not change, the total number of competitors nevertheless increases (Figure 5a).

If facilitation is the primary mechanism maintaining diversity, then under manipulation (i) again we expect the absolute fitness of type B to increase because now the facilitative effect of type A on type B (per individual of type B) has increased. The distinguishing prediction comes from manipulation (ii). If facilitation is important we expect an increase in the absolute fitness of type B under manipulation (ii) 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). Importantly, these predictions assume that the resource changes that come about from changes in density of different types have equilibrated. Also notice that these manipulations are purely “ecological” in the sense that we don’t allow any evolutionary change to occur (as far as possible).

Consider now 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 (call it type A) initially adapts to the most valuable/abundant resource in the environment. Over time, a new mutant (call it type B) may appear which has a positive absolute growth rate, but their fitness is nevertheless lower than 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 approach zero (by definition).

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 rare enough, type B gains a relative fitness advantage over type A and thus increases in frequency. The reason for this is that 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, then things work somewhat differently. Again, because of intra-type competition, the absolute fitness of type A is expected to decline as its density increases (Figure 5b). In contrast to competition, however, 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 such 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 these two fundamentally different ecological processes that can give rise to evolutionary diversification. Importantly, they are not mutually exclusive, and indeed within-type competition plays an important role in facilitative evolutionary diversification. Additionally, the interactions between difference species need not be symmetric. For example type A can have a facilitative effect on type B but type B might nevertheless have a largely competitive effect on type A.

Conclusions

Recent theoretical developments have made important steps towards 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 support for this contention, 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 currently at least two main challenges on the road to further developing this area of research. From an empirical standpoint, we 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 undoubtedly important and may lead to different predictions. Moreover, the perspective taken here is largely an equilibrium one, assuming 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 complimentary 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 is 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 has yet to receive sufficient theoretical and experimental attention.

It is also unclear at this stage if 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, etc). No

doubt some interesting reasons for such differences might be imagined, but at this stage it remains an open question. It is important to recognize, however, that it is also possible for there to be different types of facilitative interactions in microbes versus other taxa.

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, chapt. 6). There is increasing evidence for the role of facilitation in systems other than micro-organisms (Callaway et al. 2002), and this presents an exciting area for future research (Bruno et al. 2003).

Acknowledgements

We thank Peter Abrams, Anurag Agrawal, Rees Kassen, Laura Nagel and Dolph Schluter for comments. T.D. is supported by a grant from the Natural Science and Engineering Research Council (NSERC) of Canada and a Premier's Research Excellence Award. K.A.Y. is supported by a NSERC Post-Doctoral Fellowship.

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Figure Captions

Figure 1. The two forms of freshwater stickleback found in some lakes in coastal British Columbia, Canada.

Figure 2. Experimental results showing the growth rate of different morphs of stickleback along a continuum from benthic types to limnetic types (left to right on the horizontal axis). Open symbols and dotted line are results from an experimental control, and filled symbols and solid line are 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 *Science* 266:798-801).

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

Figure 4. High competition populations (squares) adapt to cadmium more rapidly than low competition populations (crosses). (a) histograms show the relative abundance of resources with different cadmium concentrations. Lines depict the fecundity of flies in the two treatments at different cadmium concentrations at the beginning of the experiment. (b) Fecundity after 2 generations of selection. (c) Fecundity after 4 generations of selection. (reprinted from *Nature* 410:463-466)

Figure 5. Top Panels: The absolute fitness of a resident type or species (solid line-type A in the text) and that of an invading mutant type or species (dashed line-type B in the text) plotted against increasing density of the resident type under manipulation (ii) of the text (i.e., with the density of the mutant type held constant at a small value). Bottom Panels: 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. (a) Predictions under competitive diversification. Absolute fitness of both types decreases as density of resident increases, but that of the resident does so more quickly. NFDS is seen by the fact that the mutant has a greater relative fitness when its frequency is small enough (i.e., density of resident is large enough). (b) Predictions under facilitative diversification. Absolute fitness of resident decreases as its density increases, but that of the mutant actually increases owing to type A's facilitative effect. NFDS is seen by the fact that the mutant has a greater relative fitness when its frequency is small enough (i.e., density of resident is large enough).