

On the role of enemies in divergence and diversification of prey: a review and synthesis¹

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Abstract: Understanding the contribution of ecological interactions to the origin and maintenance of diversity is a fundamental challenge for ecologists and evolutionary biologists, and one that is currently receiving a great deal of attention. Natural enemies (e.g., predators, parasites, and herbivores) are ubiquitous in food webs and are predicted to have significant impacts on phenotypic diversity and on speciation, and extinction rates of their prey. Spurred by the development of a theoretical framework beginning in the late 1970s, there is now a growing body of literature that addresses the effects of enemy–prey interactions on the evolution of prey. A number of theoretical models predict that enemies can produce phenotypic divergence between closely related species, even in the absence of interspecific competition for resources. Effects on diversification of prey are more variable, and enemies may either enhance or depress speciation and extinction rates of their prey. Empirical evidences from a number of study systems, notably those involving predators and prey in aquatic environments and interactions between insects and flowering plants, confirm both predictions. There is now considerable evidence for the role of enemies, especially those that are size-selective or use visual cues when identifying suitable prey, on phenotypic divergence of sympatric and allopatric taxa. Enemies may spur diversification rates in certain groups under some circumstances, and hinder diversification rates in other cases. I suggest that further research should focus on the role of enemies in diversification of prey, with significant insights likely to be the product of applying traditional experimental approaches and emerging comparative phylogenetic methods.

Résumé : La compréhension de la contribution des interactions écologiques à l'origine et au maintien de la diversité est un défi fondamental pour les écologistes et les biologistes de l'évolution; c'est une question qui reçoit beaucoup d'attention actuellement. Les ennemis naturels (c.-à.-d. les prédateurs, les parasites et les herbivores) sont omniprésents dans les réseaux alimentaires et ont, croit-on, un impact significatif sur la diversité phénotypique, ainsi que sur la spéciation et les taux d'extinction de leurs proies. Sous l'impulsion du cadre théorique développé à partir de la fin des années 1970, il existe actuellement un nombre croissant de publications qui s'intéressent aux effets des interactions ennemis–proies sur l'évolution des proies. Plusieurs modèles théoriques prédisent que les ennemis peuvent susciter une divergence phénotypique chez des espèces fortement apparentées, même en l'absence de compétition interspécifique pour les ressources. Les effets sur la diversification des proies sont plus variables et les ennemis peuvent augmenter ou réduire les taux de spéciation et d'extinction de leurs proies. Des données empiriques obtenues dans plusieurs systèmes d'étude, en particulier celles qui traitent de prédateurs et de proies dans les milieux aquatiques et des interactions entre les insectes et les plantes à fleurs, confirment ces deux prédictions. Il y a actuellement beaucoup d'information sur le rôle des ennemis, en particulier ceux qui font une sélection en fonction de la taille ou qui utilisent des signaux visuels pour identifier des proies adéquates, sur la divergence phénotypique des taxons sympatriques et allopatriques. Les ennemis peuvent accélérer les taux de diversification chez certains groupes sous certaines conditions et les ralentir dans d'autres cas. Les recherches futures devraient s'attaquer au rôle des ennemis dans la diversification des proies; les perspectives nouvelles significatives seront vraisemblablement le fruit de l'application des approches expérimentales traditionnelles et des méthodes de phylogénétique comparée qui se développent actuellement.

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Introduction

It is an almost universal rule that each animal either has enemies which seek to feed upon it, or that it seeks itself to feed upon other animals. In the first case, it has to escape its enemies or it cannot long continue to live. This it does either by its swiftness of flight, by its watchfulness, or by hiding itself from view. [Wallace 1879]

The effects of predation on the process of speciation are poorly understood. [McPhail 1969]

The study of interactions between individuals and their environment, both biotic and abiotic, is fundamental to our understanding of the origin and maintenance of biological diversity. There is much to be gained by examining the historical context of these interactions (Lack 1947; Simpson 1953; Schluter 2000). One fruitful approach has been to study the ecological factors responsible for, or at least associated with, adaptive radiations (e.g., Amadon 1950; Fryer and Iles 1972; Robichaux et al. 1990; Losos and Miles 2002). Adaptive radiations are characterized by the “more or less simultaneous divergence of numerous lines all from much the same ancestral adaptive type into different, also diverging adaptive zones” (Simpson 1953). An adaptive zone represents a “characteristic reaction and mutual relationship between environment and organism, a way of life and not a place where life is led” (Simpson 1953). Adaptive zones can be thought of as solutions to the problems associated with obtaining resources, attracting mates, and avoiding natural enemies (e.g., predators, parasites, pathogens). Surveys of the literature reveal that the vast majority of research conducted thus far on the role of ecological interactions in the evolution of biological diversity has focused on the former two aspects (e.g., Schluter and McPhail 1992; Boughman 2001; Seehausen and van Alphen 1999; Losos and Miles 2002).

The evolutionary consequences of interactions between prey and host species and their natural enemies, with the notable exception of members of fossil communities (e.g., Stanley 1973; Stanley et al. 1983; Vermeij 1977, 1987), have received considerably less attention. A notable exception focusing on contemporary species was a debate on the role of predators in the diversification of cichlid fishes in African rift valley lakes (see section Theoretical investigations). The founders of evolutionary biology were certainly well aware of the ubiquity of predators and other enemies (e.g., Müller 1879; Wallace 1879). Indeed, in what may have been the first application of a mathematical analysis to understanding evolution, Müller (1879) considered how the densities of two unpalatable species that resembled each other (i.e., formed a mimetic pair) affected the ability of predators to learn to avoid them (Joron and Mallet 1998). When interactions with enemies were acknowledged, they were typically invoked as agents of mortality that lowered population densities of potential competitors and, hence, reduced the strength of divergent selection. Similarly, Mayr (1963: 575) argued “an individual that attempts to shift into a novel niche is presumably far more vulnerable to predation than the member of a well-established population. Predators may well prevent populations from entering niches for which they are not particularly well adapted.” Significant progress

started in the mid-1970s, owing both to theoretical developments (Holt 1977) and to empirical investigations (e.g., Gilbert 1975; Ricklefs and O'Rourke 1975).

Here, I review and synthesize the present state of knowledge regarding the role of enemies in the divergence and diversification of their prey. Before proceeding, I would like to clarify three points. First, I use the term “prey” to refer broadly to the victims of natural enemies, whether or not they are killed by a single attack, as in classical predator–prey interactions. Second, competitors may also be considered natural enemies, through their effects on the quality and availability of shared resources. I exclude explicit consideration of competitors because of the wealth of reviews that have discussed the impacts of competition on evolution (Crombie 1947; Brown and Wilson 1956; Grant 1972; Stanley 1974; Smith and Skúlason 1996; Schluter 2000). Resource competition, both between natural enemies and between prey species, remains an important component of a number of the models and empirical systems I discuss (e.g., Gibbons 1979; Brown and Vincent 1992; Vamosi and Schluter 2004). Finally, lacking the space to properly elaborate on the incredible diversity of adaptations that have evolved in individual lineages to reduce the impacts of enemies (e.g., Tollrian and Harvell 1999), I focus instead on divergent traits among closely related prey species and a comparison of diversification rates of lineages with putative defensive traits with sister lineages lacking these defenses. In this context, I use “divergence” to refer to increased differences between related prey species in various aspects of their phenotypes (e.g., shells, spines, warning colours) and “diversification” to refer to speciation minus extinction rates of clades that are either spurred or hampered by natural enemies (Fig. 1). Because of space constraints, I do not discuss the remarkable diversity in the galls of various gall-inducing taxa. A number of recent reviews devote considerable attention to the role of enemies in gall diversity (Crespi et al. 1997; Stone et al. 2002; Stone and Schönrogge 2003). Finally, I do not consider the vast literature on the effects of natural enemies on the species richness of ecological communities (e.g., Paine 1966; Addicott 1974; Holt and Lawton 1994; Wellborn et al. 1996; Shurin and Allen 2001; Almany and Webster 2004), except to note that the ecological impacts of a natural enemy on prey community structure may be minor compared with its evolutionary role in promoting prey species diversity (Brown and Vincent 1992). This review has three main components. First, I review the major theoretical models and summarize their predictions. Second, I discuss case studies for which sufficient empirical evidence exists to test the predictions of theory. This is not intended to be an exhaustive list, but hopefully illustrates the diversity of systems in which the evolutionary consequences of enemy–prey interactions have been considered. Finally, I highlight emerging systems and approaches that offer promise of furthering our understanding of the effects of enemies on divergence and diversification in prey.

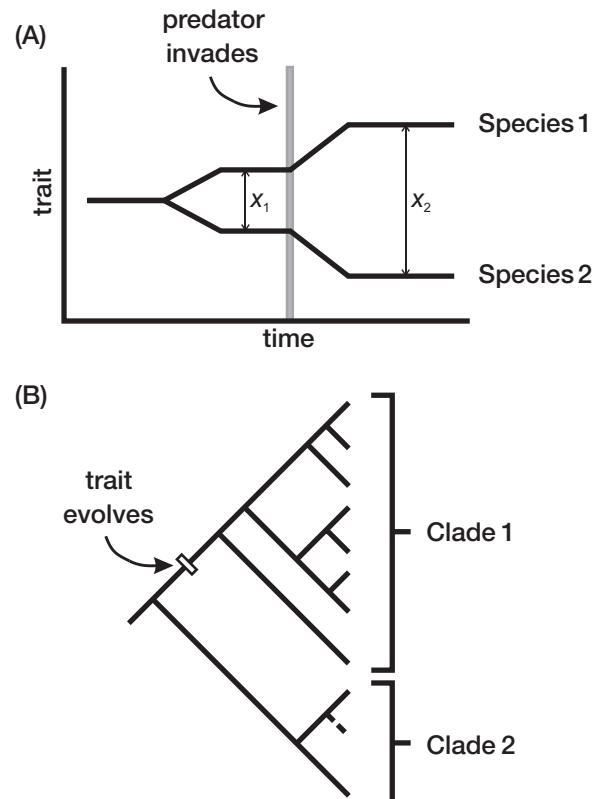
Theoretical investigations

Applying theory to examining the effects of enemies on diversity in prey has a long, albeit intermittent, history. Eighty years after Müller's (1879) treatment of the evolution

of mimicry between two unpalatable species, Fryer (1959) developed a graphical/verbal model to consider the effects of predators on the diversification of sibling species. His arguments were developed in response to proposals by Worthington (1937, 1940, 1954) and Jackson (1961) that radiations of cichlid fishes were retarded in Lake Albert and Lake Rudolph (= Lake Turkana) by the presence of predatory fish, especially tiger fish (*Hydrocynus vittatus* Castelnau, 1861) and the Nile perch (*Lates niloticus* (L., 1758)). Worthington (1940: 300) surmised that adaptation to new niches was hampered "because predators have acted as a steadying influence: unless the variants slipped immediately into vacant and suitable niches, they had short lives." Fryer (1959, 1965) and Fryer and Iles (1955) envisioned a different role for predation, arguing that predation may have actually accelerated speciation because spectacular radiations of cichlids had occurred in the presence of rich communities of predatory fish, including cichlids (species of *Haplochromis* Hilgendorf, 1888) and non-cichlids, such as the catfish *Bagrus meridionalis* Günther, 1894. In the verbal model, Fryer (1959: 444) presented the case of "a stock of fishes split into two (it could be more) populations ... suppose that population A begins to specialize in a certain direction X and population C begins to specialize in a different direction Y ... [and] genetical or behavioral differentiation had not proceeded to such a stage as would prevent interbreeding of these stocks, a hybrid population in which the antagonistic X and Y tendencies resulted in the production of ill-adapted offspring could arise at B." In other words, we are considering the early stages of speciation, with some ecological and (or) morphological differences having accrued between populations A and C. These two populations are still able to produce viable hybrid offspring ("population" B), which have intermediate phenotypes. Under these conditions, Fryer (1959: 444–445) argued that "such an ill-adapted hybrid population would be more easily eliminated by predation ... than either of the parent stocks, and such elimination would prevent the swamping and mixing of the X and Y tendencies which could then continue to increase until ultimately they became ... distinct species between which gene flow was impossible." Selective predation of hybrid individuals was thus envisioned as enhancing the evolution of reproductive isolation between diverging populations.

Holt (1977) advanced the field in a landmark paper on the role of predators in coexistence and habitat segregation of prey. Notably, he modeled alternate prey species that do not compete in the absence of the predator. In this way, he was able to explore the effects of what he labeled "apparent competition". Two species interact through direct competition when the presence of either species leads to a reduced population density for the other species at equilibrium because of a decrease in the amount of shared resources. In apparent competition, the reduction in population density of the other species at equilibrium is driven by an increase in predator population size in response to the presence of both species. In a short section at the end of the paper, Holt (1977) considered the effects of evolution and apparent competition on divergence among sympatric prey. Consider the case of two prey species that vary in a single phenotypic trait z . Furthermore, suppose that a_i , the per-predator per-unit prey rate of

Fig. 1. Evolution in prey species in response to interactions with their enemies. (A) Evolutionary branching produces species 1 and species 2, which are initially x_1 units divergent in a trait of interest. After a predator species invades the habitat (vertical shaded line), competition for enemy-free space drives further phenotypic divergence, resulting in the two species being x_2 units divergent in the trait. See also the description of the model by Holt (1977). (B) Differential diversification in sister clades in response to the evolution of a novel antipredator trait (e.g., resin canals) in the lineage that produces clade 1, which currently has more species than clade 2. Note that no extinction has occurred in clade 1, whereas one lineage (broken line) has become extinct in clade 2 as a consequence of lacking the antipredator trait.



encountering and capturing prey species i , is a function of z . The predator species, modeled as a food-limited generalist, is best at encountering and capturing prey at a single point \hat{z} (i.e., $a(z)$ is highest when $z = \hat{z}$) and becomes less adept as $|z_i - \hat{z}|$ increases. In other words, the efficiency of the predator drops as prey become more different from the phenotype that predators are best at encountering and capturing. Given prey species 1 has $z_1 - \hat{z}$ and species 2 has $z_2 - \hat{z}$, Holt (1977: 222) hypothesized "that natural selection should cause this species pair to diverge away from \hat{z} ." Thus, predation is expected to spur morphological divergence, provided that initial differences already exist between the two prey species. Holt (1977) then considered the ramifications of this divergence for the ability of a third species to invade this community. If $z_1 < z_3 < z_2$ and z_3 is sufficiently similar to \hat{z} (i.e., $|z_3 - \hat{z}| < |z_1 - \hat{z}| = |z_2 - \hat{z}|$), as might be expected for hybrid offspring between species 1 and 2, then species 3 will be excluded from the community. These results qualitatively

confirm Fryer's (1959) verbal model, and suggest that predation may enhance morphological divergence between existing community members while potentially reducing species richness of the community.

Brown and Vincent (1992) used evolutionary game theory to investigate the influence of predators on the diversity of prey species. Their approach addressed a limitation of the previous models, which considered the case of two prey species that were sufficiently divergent to (i) produce phenotypically distinct hybrids (Fryer 1959) or (ii) implicitly possess distinct gene pools (Holt 1977). The causes of the initial divergence were not explicitly modeled in either case. In the model by Brown and Vincent (1992), the evolutionary stable strategy (ESS) contained a single prey species in the absence of predators. Using this ESS as a starting point, they then explored the consequences of having predators with either broad or more narrow niche breadths (equivalent to the function $a(z)$ in Holt (1977)). The ESS with the addition of a predator with a very broad niche width also contained a single prey species. Here, disruptive selection exerted by the predator species is insufficient to overcome stabilizing selection of a higher carrying capacity on the single prey species. Changes in the prey's strategy away from the original ESS value result in large reductions in foraging success and comparatively minor reductions in predator attack rate. Brown and Vincent (1992) were able to generate an ESS containing two prey species and one predator species given a predator with a broad niche breadth. In this scenario, which is comparable to that in Holt (1977), reductions in predator attack rate drop significantly to overcome stabilizing selection that is due to higher carrying capacity. Unlike Holt's (1977) findings, communities containing three prey species could be an ESS provided that predators had very narrow niches. The primary reason for the different finding is that evolutionary changes in the predator(s) were explicitly modeled; indeed, an ESS containing three prey species was the result of the presence of either two or three predator species. In essence, the presence of two prey species results in sufficient disruptive selection on predators to favour two predator species, each specialized on a single prey species. This, in turn, vacates the phenotypic space near the original ESS that was obtained in the absence of predators, allowing the evolution or invasion of a third prey species. In the approach taken by Brown and Vincent (1992), increased morphological divergence and species richness of prey species can occur in the presence of predators, although each round of increase becomes ever more difficult, presumably placing limits on the total number of interacting predator and prey species (Schluter 2000).

Abrams (2000) also employed an ESS approach, but considered instead how the antipredator traits of a focal prey species evolve in response to the addition of second prey species. Furthermore, the evolutionary dynamics of the quantitative traits were explicitly modeled. A number of models were considered with the two major classes of scenarios involving either a single predator or two predators. Predation by a single predator species was again found to lead to shifts in antipredator traits of sympatric species to minimize risk of being preyed upon. Departing from the findings of previous models, however, divergence in antipredator traits was

not the only outcome observed: convergence, parallel increases, and parallel decreases in antipredator traits are all possible outcomes in sympatry (Abrams 2000). Divergence was most likely when the presence of two prey species in sympatry led to increased predation risk through a strong numerical response of predators and species 1 (2) had a trait optimum lower (greater) than the most vulnerable trait value. The mechanism is analogous to apparent competition considered by Holt (1977). Alternatively, "apparent mutualism" may emerge in sympatry, leading to parallel decreases or convergence in sympatry (Abrams 2000). These shifts are most likely if the presence of two consumer species lowers the rate of predation experienced by both of them below that experienced when each occurs alone with the same predators. Parallel decreases are expected when predation rate is reduced in sympatry and both species have trait optima less than the most vulnerable trait value, which may be most likely with energetically costly structures.

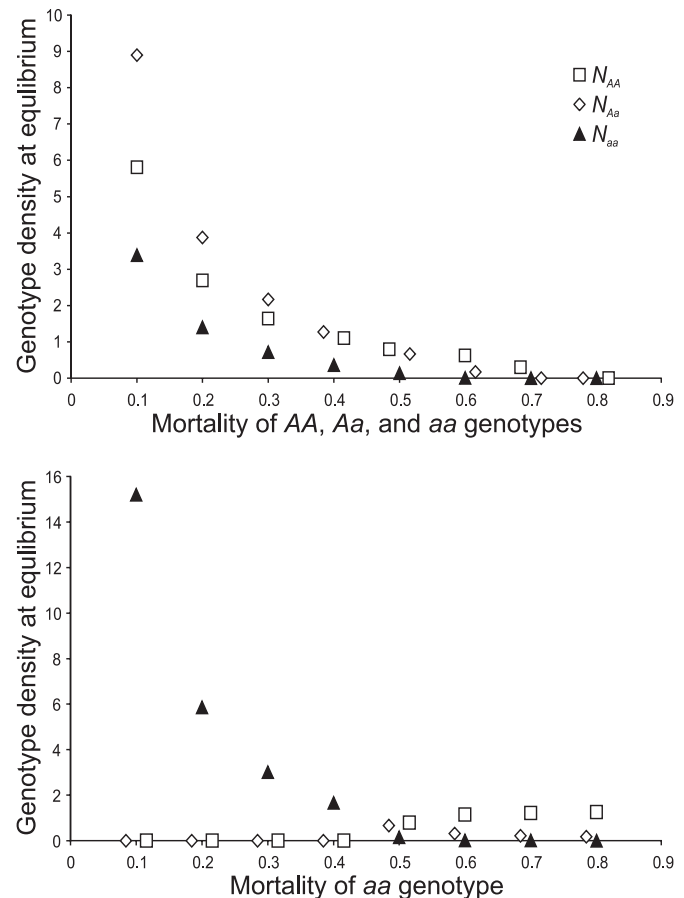
For food webs containing two predators, Abrams (2000) considered only those cases where adaptations to one of the predators result in increased vulnerability to the other predator. For example, increased values of the antipredator trait may make prey better able to evade predator species 1 and more vulnerable to capture by predator species 2. Such a scenario may be most likely when (i) prey species evolve to exploit different habitats under the influence of resource competition only (i.e., ecological character displacement) and (ii) habitats contain different predators or favor different modes of defence (Abrams 2000). Divergence appears to be the most likely outcome of habitat-specific predation risk, although convergence and parallel shifts are also possible (Abrams 2000).

The theory of adaptive dynamics, which incorporates evolutionary game theory approaches and evolutionary branching, can be used to model the evolution of quantitative traits subject to frequency-dependent selection (Geritz et al. 2004). Adaptive dynamic approaches have recently been applied to examine evolutionary branching in predator-prey systems (Doebeli and Dieckmann 2000; Bowers et al. 2003). Doebeli and Dieckmann (2000), for example, demonstrated that evolutionary branching in the prey trait is most likely in prey species when predation efficiency decreases sufficiently with increasing distance between prey and predator traits. The resulting community contains two prey species and a generalist predator with reduced attack success on each of the two prey species than it had on the original single prey species. Bowers et al. (2003) also demonstrated evolutionary branching in a predator-prey system when the carrying capacity of prey was an emergent property of individual-level processes (in response to crowding) but not when an explicit carrying capacity was imposed on prey. From these results, they conclude that branching (i.e., phenotypic divergence) can readily occur when there are trade-offs between predator avoidance and growth rates. One caveat is that these results strictly apply only to haploid populations, requiring assortative mating in sexual populations for the branching to lead to reproductively isolated populations (i.e., diversification) (Doebeli and Dieckmann 2000). It largely remains to be seen whether and under what circumstances branching or divergence in antipredator traits influences mate choice.

A final approach that holds promise considers the impact of mortality on the ability of density- and frequency-dependent selection to produce stable polymorphisms. Wilson and Turelli (1986; see also Wilson 1989) explicitly modeled the following verbal scenario. Initially, there is a single consumer population (AA) adapted to niche 1 (= resource 1), and there exists a second niche that is unexploited. A mutant (aa) arises that is crudely adapted to niche 2, but at the cost of very poor performance on the original niche. The mutant, thus, is poorly adapted to both niches, but may invade and persist because niche 2 is “empty” (Wilson 1989). It was shown that stable polymorphisms with heterozygote (Aa) advantage readily emerged from their model, setting the stage for subsequent evolution to eliminate the intermediate forms. The finding of stable polymorphisms was not a trivial one: although natural selection acted against heterozygotes, random mating among all genotypes recreated them every generation. Another strength of this modeling approach is that it explicitly incorporates resource dynamics, which are absent from all of the models previously discussed. The effects of genotype-specific mortality or variations in overall mortality, which were not the focus of Wilson and Turelli’s (1986) approach, are now being considered (S.M. Vamosi and S.A. Richards, unpublished results). When mortality (m) is low and equal among genotypes, stable polymorphisms readily emerge, although they are often accompanied by heterozygote advantage. Increasing m of all genotypes has little effect on the ability of the aa genotype to invade and persist on resource 2 unless m is high (Fig. 2, top panel). In contrast, when $m_{AA} = m_{Aa}$ and fixed at an intermediate level, changing m_{aa} has significant impacts on the ability of the mutant genotype to invade and persist (Fig. 2, bottom panel). When $m_{aa} < m_{AA} = m_{Aa}$, only the aa genotype is present at equilibrium. Conversely, when $m_{aa} > m_{AA} = m_{Aa}$, the AA genotype becomes dominant and the aa genotype is present at extremely low densities at equilibrium only because of matings between AA and Aa individuals.

To summarize, a number of theoretical models suggest that sympatric prey may experience character shifts as readily from interactions with enemies as from interactions with competitors (Holt 1977; Brown and Vincent 1992; Abrams 2000; Doebeli and Dieckmann 2000; Bowers et al. 2003). The diversity of assumptions and modeling approaches suggests that this conclusion is likely robust and character shifts, especially divergence, may be a common evolutionary response in prey species that share predators. The predicted effects on diversification of prey species are more variable and appear to depend largely on whether predators evolve in response to trait shifts in prey species. In the absence of appreciable evolution in predators, morphological divergence between coexisting prey species may hamper the evolution or invasion of additional prey species (Holt 1977). When predator traits experience sufficient disruptive selection as a consequence of two (or more) divergent prey species, two (or more) predator strategies or species may be favoured, which may then spur further divergence and diversification of prey species (e.g., Brown and Vincent 1992). Finally, a model incorporating resource dynamics suggests that enemies may spur sympatric diversification if differential survival is coupled with assortative mating between prey genotypes that possess similar values of the antipredator trait (S.M. Vamosi and S.A. Richards, unpublished results).

Fig. 2. Invasion and persistence of mutant genotype (aa) in model incorporating frequency- and density-dependent selection. Illustrated are the outcomes of two scenarios. Top panel: all three genotypes have the same mortality. Bottom panel: mortality of AA and Aa genotypes is kept constant ($m = 0.5$) and mortality of the aa genotype varies from $m = 0.1$ – 0.8 .



Empirical investigations

Having established that, at least in theory, interactions between prey species and their natural enemies are predicted to lead to character shifts in coexisting prey species and potentially to changes in the number of prey species, I now shift my attention to empirical investigations of these phenomena. The number of studies on the effects of enemies on diversification and phenotypic divergence in prey has largely lagged behind that of the effects of resource competition between consumers. Schluter (2000), for example, presented 61 cases of putative ecological character displacement alone. Thus, our ability to make general conclusions about whether character shifts are as readily observed in response to interactions between prey species and their natural enemies, as in response to direct competition, is limited at present (Abrams 2000). It is, however, possible to discuss the range of likely responses and confirm whether modeling approaches adequately capture the essence of real systems. The subdivisions used throughout this section are provided merely to help guide the reader through the evidence and should not be taken to imply, for example, that the processes driving the

evolution of leaf-shape diversity in plants and mimicry of wing colour patterns in butterflies necessarily differ.

Marine assemblages

Origin of multicellularity

There is a considerable body of work on the macroevolutionary effects of predators on the divergence and diversification of prehistoric lineages, especially in marine environments (e.g., Vermeij 1977; Stanley et al. 1983; Vermeij 1987; Stone 1998; Hautmann and Golej 2004). Indeed, it has been hypothesized that unicellular predation spurred the origin of multicellular forms in the late Precambrian and their subsequent “explosive” diversification as they colonized new adaptive zones during the Cambrian era (Stanley 1973). Prior to the origin of unicellular predation, it is thought that competition for limited resources favoured phototrophs with a high surface-to-volume ratio (i.e., small, unicellular forms). The advent of phagotrophy (ingestion of whole prey) tipped the balance in favour of individuals with larger body sizes (Stanley 1973; Boraas et al. 1998). Recently, Boraas et al. (1998) demonstrated the plausibility of this hypothesis with an experimental system, that of a phagotropic protist (*Ochromonas vallescia* [currently spelled *vallesiaca*] Chodat) preying upon a population of algae (*Chlorella vulgaris* Beijerinck, 1890). Based on over 20 years of culturing *C. vulgaris* in the laboratory, Boraas et al. (1998) were able to ascertain that the multicellular form is a rare genetic mutant in predominantly unicellular culture. In the presence of *O. vallesiaca*, however, the multicellular form (typically eight-celled at equilibrium) successfully invaded the culture within 20 generations. To date, this study has largely escaped the attention of researchers studying the evolutionary impacts of enemies (but see Rainey and Rainey 2003).

Mesozoic marine revolution

During this protracted event, which spans the Mesozoic and Cenozoic eras, the habits and composition of benthic marine communities changed dramatically (Vermeij 1977; Checa and Jiménez-Jiménez 2003). Two major trends that have been well documented, especially in bivalve and gastropod molluscs, are increasing thickness and ornamentation of shells and infaunal (living within sediment) forms becoming more common than epifaunal (living on surfaces) forms. Stanley et al. (1983), for example, present evidence that extinction rates of nonsiphonate (epifaunal) bivalves have increased dramatically compared with siphonate (infaunal) bivalves. As a consequence, the latter group is now represented by 10× as many species as the former group. Although other factors are likely involved, there is considerable evidence suggesting that these trends are correlated with escalating predation intensity during this time. Vermeij (1977) listed 14 major groups of molluscivores, of which 11 arose and (or) evolved the habits of crushing, drilling, or swallowing whole their prey during the Mesozoic era. An accompanying trend has been an increase in drill holes and shell breakage during this time (Palmer 1979; Kowalewski et al. 2000; Leighton 2001; and references therein). Concurrent trends have been documented in other marine taxa. Palmer (1982), for example, argued that a reduction in the number of plates of barnacles, which started in the late Cretaceous, was correlated with the rise of drilling gastropods. Starting

in the late Triassic, the coralline subgroup of calcareous red algae underwent a radiation while another subgroup, the solenopores, declined in diversity and eventually became extinct (Stanley et al. 1983). It is thought that defenses present in the former group, but lacking in the latter one, allowed them to radiate alongside the radiation of herbivores (e.g., urchins and limpets) that excavate calcareous substrata and, hence, potentially damage unprotected tissues.

Freshwater communities

Threespine sticklebacks (species of *Gasterosteus* L., 1758)

Research on sympatric divergence has focused largely on the benthic and limnetic species pairs in southwestern British Columbia (but see Doucette et al. 2004). To a large extent, these studies have been made possible by a vast body of research on functional morphology and predator–prey relationships within allopatric populations (e.g., Hagen and Gilbertson 1973; Reimchen 1980, 1994, 1995; Bell and Richkind 1981; Foster et al. 1988; Bergstrom 2002). Using an approach analogous to that used in tests of ecological character displacement in trophic traits (e.g., Schluter and McPhail 1992), three patterns of character shifts in defensive armour of sympatric species have been found (Vamosi and Schluter 2004). Total armour of limnetics was significantly greater than that of benthics, with no overlap between the two species in their distributions of population means. Interestingly, the average amount of armour, averaged over both species, was reduced in sympatry compared with allopatric populations. Finally, differences between sympatric benthics and limnetics in total armour were greater than expected from comparisons with allopatric populations. In addition to differences in defensive armour, benthics and limnetics differ in a number of other putative antipredator defenses, including schooling behaviour (Vamosi 2002) and fast-start performance (Law and Blake 1996).

Three studies have tested the effects of divergent habitat preferences and antipredator traits on survival and growth of sympatric sticklebacks. In experimental arenas, limnetics were more susceptible to predators found in the habitat occupied by benthics, and the converse was true for benthics (Vamosi 2002). In experimental ponds that contained juvenile benthics, limnetics, and F₁ hybrids, the addition of cutthroat trout (*Oncorhynchus clarkii* (Richardson, 1836)) primarily had an impact on the survival of limnetics. As a result, the relative survival of benthics and limnetics was reversed in the presence of cutthroat trout. F₁ hybrids survived poorly relative to benthics and limnetics regardless of treatment (Vamosi and Schluter 2002; see also Vamosi et al. 2000). A related investigation explored the contributions of both competition and predation to character divergence (Rundle et al. 2003). Divergent selection on the target population tended to be stronger in the predator-added treatment than in the predator-reduced treatment. Somewhat unexpectedly, this trend occurred even though competition was strongest in the predator-reduced treatment. Overall, the strength of divergent selection was best predicted by stickleback mortality being strongest where mortality was highest.

A single study has examined the role of predators, along with a number of abiotic and biotic factors, on diversification of sympatric stickleback species pairs (Vamosi 2003). A

Scatter plot showing the relationship between Log (surface area) (X-axis) and Number of other fish species (Y-axis). The X-axis ranges from 0.0 to 3.0, and the Y-axis ranges from 0 to 9. Data points are represented by open circles (○) and filled circles (●). The plot shows a positive correlation, with the number of other fish species increasing as the log of surface area increases. There is a notable outlier at approximately (2.9, 8.0).

Evidence that differential predation regimes contribute to the remarkable divergence observed among allopatric populations (McPhail 1969; Hagen and Gilbertson 1972; Moodie 1972; Reimchen 1980, 1984, 1988) has been shown in a number of studies. Walker (1997) and Walker and Bell (2000), for example, demonstrated consistent differences in body shape between stickleback populations from lakes with and without native predatory fish. Sticklebacks from lakes with native predatory fish, for example, tended to have longer median fins, which are thought to increase thrust during evasive maneuvers (Walker 1997).

A number of fish assemblages have been studied from the perspective of attempting to understand the role of enemies,

The role of predators in allopatric divergence and diversification of the damselfly *Enallagma* Charpentier, 1840 (Odonata: Coenagrionidae) has been examined by McPeck and colleagues in a comprehensive series of papers. Within the North American representative of this genus, there are two groups of species: one that is associated with fish lakes ($N = 34$ species) and the other that is associated with fishless lakes ($N = 4$ species). In the latter group of lakes, large dragonflies have been identified as important predators (McPeck 1990a) and are typically referred to as dragonfly lakes. Coexistence with fish predators has been inferred to be the ancestral state for North American *Enallagma* (McPeck 1995; Brown et al. 2000; McPeck and Brown 2000), and the simplest explanation for the disparity in species richness is that the genus *Enallagma* has only recently invaded the dragonfly lake habitat. Considerable evidence demonstrates the existence of adaptations that permit coexistence with the two types of predators. Furthermore, adaptations to dragonflies result in higher vulnerability to fish predators, and vice versa. The shift from fish to dragonfly lakes is correlated with increases in caudal lamella size, abdominal segment lengths and widths, and leg length (McPeck 1995). Together, these traits increase swimming performance of *Enallagma* damselflies. Being more active and attempting to swim away from predators appear to be effective antipredator strategies when the predators are dragonflies, but make damselflies

more conspicuous to fish (McPeck 1990b). Conversely, fish lake *Enallagma*, which use crypsis as their main antipredator defense, were often captured by dragonflies without having attempted any evasive maneuvers (McPeck 1990b). Interestingly, not only has the shift to dragonfly lakes been accompanied by evolution of a suite of characters related to swimming performance (e.g., McPeck 1995), dragonfly predation continues to exert considerable selection on dragonfly lake *Enallagma* species (McPeck 1997).

Other freshwater organisms

The ecological literature is replete with descriptions of putative adaptations of freshwater organisms, especially benthic invertebrates and zooplankton, which reduce predator-induced mortality (e.g., Wellborn et al. 1996). Here, I restrict my attention to a few systems with intra- and inter-specific variation in phenotypic traits attributable to differential predation. Two different ecomorphs have been identified in the amphipod *Hyalella azteca* Saussure, 1858 species complex (Crustacea: Hyalellidae). Lakes with fish predators tend to contain a small-bodied form, whereas fishless ponds and marshes are predominated by large-bodied forms (Wellborn 1994, 1995). Stomach content analyses and predation trials reveal that different patterns of size-selective predation are maintaining, and have likely driven, differences in body size and correlated life-history traits in the two habitats. Recent allozyme data suggest that the coexistence of sympatric cryptic species in fish lakes may also be the result of size-selective predation (Wellborn and Cothran 2004). Vertebrate predators removing large individuals and invertebrate predators preying selectively on smaller individuals are also common themes in zooplankton communities (e.g., Zaret 1980). In a classic experiment, Spitze (1991) demonstrated evolution in *Daphnia pulex* (De Geer, 1778) (Crustacea: Daphnidae) towards larger body size and increased and earlier reproduction in the presence of *Chaoborus americanus* (Johannsen, 1903) (Diptera: Chaoboridae). Finally, the coexistence of hybrid *D. pulex* with their parental species may be facilitated by within- and among-year variation in levels of fish predation (Spaak and Hoekstra 1997). Hybrids were selectively favoured over one of the parental species when fish predation was high, and the other parental species at other times. These findings do not support the assumption that interspecific hybrids are always more susceptible to predation than the parental species (Fryer 1959; see also Fritz et al. 1999; Vamosi and Schluter 2004).

Interactions between hosts and pathogens

Spatial niche evolution in bacteria

The bacterium *Pseudomonas fluorescens* has become a model system for studies of the evolution of diversity (e.g., Buckling et al. 2000; Kassen et al. 2000; Rainey and Rainey 2003). Buckling and Rainey (2002) examined the effect of a naturally virulent phage on diversification of *P. fluorescens* in experimental microcosms. Their design allowed them to test two predictions of the theories described earlier (e.g., Holt 1977; Brown and Vincent 1992). First, phages may drive sympatric (within-population) diversification if there are a variety of phage-resistance strategies or fitness costs associated with resisting phages. Second, allopatric (among-

population) diversification may be the result of different mutations that confer phage resistance sweeping to fixation in different populations. In the absence of phages, bacteria rapidly diversified into spatial niche specialists (smooth, wrinkly spreader, and fuzzy spreader morphotypes) with similar patterns of diversity across replicate populations. The observed diversification was attributed to the effects of resource competition. In the presence of phages, sympatric diversity was greatly reduced, as a result of phage-imposed reductions in host density decreasing competition for resources. Interestingly, in 2 of the 12 cultures grown in the presence of phages, a new form (mucoid colonies that colonized the sides of vials) evolved. In contrast, allopatric diversity was greatly increased as a result of phage-imposed selection for resistance, which caused populations to follow divergent evolutionary trajectories. These results confirm Abrams' (2000) prediction that enemies can drive diversification among populations even if they do not interact with each other through apparent competition. The within-population results suggest that, under some conditions, enemies may inhibit sympatric diversification by opposing diversifying selection which arises from direct competition for resources (Buckling and Rainey 2002).

More recently, Brockhurst et al. (2004) extended the scope of the original experiment by considering sympatric and allopatric diversification of *P. fluorescens* in the presence of phage in two types of environments: spatially heterogeneous (cultures not shaken, as in the original) and spatially homogeneous (cultures shaken). Contrary to what was observed in spatially heterogeneous environments (Buckling and Rainey 2002; Brockhurst et al. 2004), phage did not reduce sympatric diversification in spatially homogeneous environments. Indeed, for much of the experiment, sympatric diversity was higher in the presence of phage. The most likely explanation for these results is that trade-offs between phage resistance and competitive ability allow the invasion and persistence of inferior competitors (Brockhurst et al. 2004; see also reviews by Chase et al. 2002; Kneitel and Chase 2004).

Diversification of primates

In a recent comparative study of the correlates of species richness in primate taxa, Nunn et al. (2004) arrived at the somewhat unexpected conclusion that the diversity of primate clades is positively correlated with the number of parasite species harboured by each host. In other words, parasite diversity for a given host species was higher for primate species that belong to species-rich clades. This association was due largely to viruses, with some protozoan species also showing similar patterns. Unfortunately, the likely cause of this association is still poorly understood. Nunn et al. (2004) were able to exclude the possibility that sexual selection in response to host-parasite interactions was spurring parasite species richness or diversification of primate lineages. Additionally, they were able to find only partial support for the notion that species-rich primate lineages would provide greater opportunities for host shifts and host sharing among parasites, thus spurring parasite diversification. It is hoped that further research will help elucidate the mechanisms responsible for this intriguing association between parasite and host species richness.

Interactions between plants and insects

Latex and resin canals in vascular plants

A long-standing belief in evolutionary biology is that the radiations of insects and flowering plants have spurred, and been spurred by, one another (e.g., Ehrlich and Raven 1964; Gilbert 1975; Futuyma 1983; Grimaldi 1999). The underlying interactions hypothesized as driving such patterns have been termed "escape and radiation". Plant lineages with effective herbivore defense may be released from the negative effects of herbivory (the escape component), potentially increasing their ability to colonize new habitats, which may then facilitate further phenotypic evolution and (or) the evolution of reproductive isolation (the radiation component). One such trait complex hypothesized to be a key innovation allowing for escape and radiation, especially in angiosperms, is laticiferous (i.e., latex-bearing) and resinous (i.e., resin-bearing) canals. Such canals have been demonstrated to reduce feeding rates and increase mortality of herbivores in a number of plant species (Dillon et al. 1983; Becerra 1994; Dussourd 1995). The aptly named "evil woman" (*Cnidoscolus urens* (L.) Arthur; Euphorbiaceae), for example, has stinging trichomes and "sticky latex sap, which flows out of any break in the epidermis and effectively deters both piercing and chewing insects" (Dillon et al. 1983: 113).

To investigate the correlation between possessing canals and diversification rates, Farrell et al. (1991) used the method of sister-group comparisons to examine the species richness of canal-bearing clades. Sister-group comparisons control for the effects of shared ancestry (Vamosi and Vamosi 2005). Farrell et al. (1991) surveyed the botanical literature and identified 16 sister-group pairs, 13 of which were angiosperm taxa, in which the focal group possessed laticiferous and (or) resinous canals and its sister group lacked these structures. For example, the canal-bearing family Sapotaceae (800 species) was found to have more species than its presumed sister group Ebenaceae (450 species), which lacks canals. A significant effect of resinous and laticiferous canals was found, with the canal-bearing clade having more species than its sister group in 13 of the 16 sister-group pairs (one-tailed sign test, $P = 0.011$). This study has been largely accepted as providing evidence that putative key innovations may indeed spur diversification rates (e.g., Heilbuth 2000; Schluter 2000; Sargent 2004).

Although a thorough reconsideration of the pattern is beyond the scope of this review, preliminary indications suggest that modifications to existing contrasts and the inclusion of additional sister-group pairs may potentially weaken, rather than strengthen, the reported associations. In all cases, information on phylogenetic affinities and species-richness values was obtained from Stevens (2001–2005). First, rearrangements within the "Alismatiflorae" change the original contrast of ((Alismataceae (90 species) + Limnocharitaceae (11 species)) vs. Butomaceae (1 species)) to ((Alismataceae (81 species) + Limnocharitaceae (7 species)) vs. (Butomaceae (1 species) + Hydrocharitaceae (116 species))). Similarly, the contrast among members of the family Araceae presented "Pothoideae in part" as lacking canals and having ≤ 995 species, which was less than the canal-bearing focal group (1350 species). This contrast now appears to be between members of the Pothoideae, with the latex-bearing clade Monstereae (360 species) having fewer species than its

sister clade Potheae (900 species). In other words, the canal-bearing clade is now shown to be larger than its sister group in only 11 of the original contrasts, a pattern that is not significantly different from random (one-tailed sign test, $P = 0.105$). Second, it was suggested that another contrast which would support the hypothesis would be between the liliaceous genera *Allium* L. (450 species) and *Nothoscordum* Kunth (35 species). Rahn's (1998: 71) treatment of Alliaceae, however, includes the statement that "laticifers have been found in all Alliaceae screened by Sterling and Huang (1972) (*Allium*, *Nothoscordum*, *Tristagma*, and *Tulbaghia*).". The laticiferous family Eucommiaceae was another excluded taxon, because its assignment even to subclass was unclear. However, this family contains only a single species (*Eucommia ulmoides* Oliv.) and its sister group Garryaceae (17 species) has more species.

Why might laticiferous and resinous canals not always spur increased diversification rates? One possible explanation invokes the escape and radiation hypothesis itself. Herbivores that are able to overcome the defense of a plant lineage will now be able to access a new niche, leaving the plants with the costs but not the initial benefits of the defense. Vein severing, petiole constriction, and leaf trenching, which may reduce the effectiveness of laticiferous and resinous canals, have been recorded in a number of insect taxa (e.g., Dillon et al. 1983; Becerra 1994; Dussourd 1997, 1999). A phytophagous habit in insects is correlated with increased diversification rates in insects (Mitter et al. 1988), although to the best of my knowledge the macroevolutionary consequences of possessing behaviours that circumvent these plant defenses have not been examined explicitly. An alternative explanation is that the evolution of canals reduces herbivory on individuals, which results in higher population densities, but has little effect on speciation and extinction rates of lineages (cf. Schluter 2000).

Leaf-shape diversity

Coevolution between species of passion flower (*Passiflora* L.; Passifloraceae) and of *Heliconius* Kluk, 1802 (Heliconiidae) butterflies is a classic example of phenotypic divergence among hosts that may be driven by their enemies (Gilbert 1975). One aspect of this system that has received the most attention in subsequent reviews is that of leaf-shape diversity among sympatric species of *Passiflora* (e.g., Schluter 2000). Female *Heliconius* butterflies use visual cues to detect suitable hosts on which to lay their eggs, which subsequently produce larvae that can be significant herbivores of the host plant. Thus, natural selection is thought to drive competition for enemy-free space in leaf shape. Three other aspects of this system further implicate visual selection in the evolution of diversity in species of *Passiflora*. First, *Passiflora* leaf shapes are often convergent on that of common tropical plants that are not suitable hosts for *Heliconius* butterflies (Killip 1938; cited in Gilbert 1975). Second, despite the fact that there are ca. 350 species of *Passiflora* in the Nearctic and Neotropical regions, the number of sympatric species rarely exceeds 10. Gilbert (1975) suggests that this reflects a limit on the number of shape categories (a measure of enemy-free space) that can be discriminated by female *Heliconius* butterflies. In other words, *Passiflora* species with a leaf shape too similar to ex-

isting species in a “packed” community are hypothesized to experience increased apparent competition, which would limit their ability to colonize and persist in that habitat. Finally, a number of *Passiflora* species possess butterfly-egg mimics on their stipules that may reduce the incidence of attack because female *Heliconius* butterflies are under selection to choose hosts that are not already parasitized (Gilbert 1975; Williams and Gilbert 1981). Unfortunately, because of the difficulties with conducting the proper experiments in the field, the hypothesis that leaf-shape variation (and correlated species richness) in sympatry is driven by visual selection has not been properly tested in this system (L. Gilbert, personal communication). However, experiments with the butterfly *Battus philenor* (L., 1771) demonstrate that visual selection is a plausible mechanism for leaf-shape divergence between two host-plant species in the genus *Aristolochia* L. (Aristolochiaceae) (Rauscher 1978, 1981). Analogous to some *Passiflora* species, it appears that the leaf shape of one of the *Aristolochia* species is not only divergent from its congener in sympatry, but may also be convergent with that of local grass species genus.

Remarkable similarity of leaf shape of Australian mistletoes (Loranthaceae) to their hosts has been attributed to protective mimicry (Barlow and Wiens 1977). There are thought to be 64 species of Loranthaceae in Australia, with as many as 36 of these displaying varying degrees of resemblance to their primary host plants. Visual selection by herbivorous mammals, particularly possums (genus *Trichosurus* Lesson, 1828), appears to be the selective agent for convergence. The geographic restriction of such cases of mimicry in Loranthaceae may stem from host characteristics. In Australia, their hosts are primarily *Acacia* P. Mill. (Fabaceae) and *Eucalyptus* L'Hér. (Myrtaceae) species, which tend to be highly defended against herbivores (e.g., Milewski et al. 1991; Marsh et al. 2003). In this example, herbivores are potentially driving phenotypic divergence among species, whereas the species richness (i.e., diversification) of the group is likely the result of the rich diversity of potential *Acacia* and *Eucalyptus* hosts.

Seed dispersal mechanisms

Seed predators and dispersers exert significant selection pressures on plants (Janzen 1971; Hulme 1998; Strauss and Irwin 2004; Tiffney 2004). In at least two genera of flowering plants, divergent seed dispersal mechanisms are correlated with variation in predation risk. Within the genus *Viola* L. (Violaceae), there appear to be two major seed dispersal syndromes, myrmecochory and diplochory (Beattie and Lyons 1975). The majority of the approximate 400 species of *Viola* use diplochory, with ballistic ejection of seeds (autochory) followed by attraction of, and dispersal by, ants (myrmecochory). Diplochorous species also tend to possess strong, tall peduncles (stalks) that keep seed capsules away from the ground before dispersal. Together, these traits are thought to be adaptations that minimize pre-dispersal seed predation, especially by caterpillars and slugs, and post-dispersal seed predation, by reducing aggregations of seed predators directly around the parental plant (e.g., Janzen 1970). Eleven myrmecochorous species, which are restricted to parts of Eurasia, have weak, trailing peduncles that keep seed capsules at ground level. After dehiscence of the cap-

sules, the seeds form large clumps around the parental plant (Beattie and Lyons 1975). These clumps of seeds are thought to represent a rich food source that attracts ants prior to mobilization of other seed predators. Beattie and Lyons (1975) argue that the presence of mound-building ants, which exhibit rapid and monopolistic exploitation (= dispersal), and the absence of harvester ants, which destroy seeds, are required for the evolution and maintenance of myrmecochory. Armbruster (1982) studied capsule development and seed dispersal in 16 Neotropical species of *Dalechampia* L. (Euphorbiaceae), a predominantly Neotropical genus that contains approximately 100 species. All species relied on ballistic dehiscence of capsules for seed dispersal. One of the species, *Dalechampia spathulata* (Scheidw.) Baill., was found in low-light environments and had capsules that developed sequentially within an inflorescence, whereas the other species were found in high-light environments and had capsules that developed simultaneously. In low-light environments, the rate of capsule development was markedly slower when two or three capsules were developing simultaneously, which increased the amount of time that the entire seed crop was vulnerable to predation by larvae of nymphalid butterflies, notably species of *Dynamine* Hübner, 1819 (Armbruster 1982). Thus, the interactive effects of light environment and predation risk are thought to have selected for divergent seed capsule development strategies.

Diversity of sympatric parasitoids

Larvae of the pigeon tremex (*Tremex columba* (L., 1763)), a siricid wasp, develop in the trunks of various hardwood species in North America (Gibbons 1979). In northeastern and central USA and southeastern Canada, *T. columba* is host to three closely related species of ichneumonid wasps (*Megarhyssa atrata* (Fabricius, 1781), *Megarhyssa macrurus lunator* Fabricius, 1781 and *Megarhyssa greeni* Viereck, 1911). The three species occur sympatrically, and have been frequently observed to attack pigeon tremex larvae in the same tree or log (Gibbons 1979). Although the congeneric species have very similar life histories, coexistence is apparently mediated via differences in ovipositor lengths and corresponding oviposition behaviour (Heatwole and Davis 1965). *Megarhyssa greeni* females have the shortest ovipositors and, consequently, parasitize larvae that are present at the shallowest depths. *Megarhyssa atrata*, conversely, have the longest ovipositors and can parasitize larvae at depths up to 140 mm (Le Lannic and Nénon 1999). Oviposition times mirror these differences, with successful oviposition taking 7 min, 12 min, and over 1 h in *M. greeni*, *M. macrurus*, and *M. atrata*, respectively (Heatwole et al. 1963). Ovipositing females are unable to escape while their ovipositors are inserted into the wood, and Heatwole et al. (1963) frequently observed birds preying on ovipositing *M. atrata* females. The origin and maintenance of sympatric *Megarhyssa* wasps may be driven by intra- and inter-specific competition for hosts (Gibbons 1979), with increasing risk of predation with longer ovipositor lengths potentially limiting the diversity of coexisting species.

Aposematism and mimicry

Aposematism and mimicry have long been the subjects of theoretical (e.g., Müller 1879) and empirical (e.g., Bates

1862) investigations. Aposematism refers to the case of unpalatable prey that have associated conspicuous colouration, which serves to advertise their unpalatability to potential predators (Härlin and Härlin 2003). In mimetic systems, an unpalatable model species may be imitated by palatable (Batesian mimicry) or other unpalatable species (Müllerian mimicry). Neotropical poison frogs and *Heliconius* butterflies are familiar examples of aposematism and mimicry, respectively. Although not all aposematic species are mimicked by other species, most cases of mimicry involve an aposematic model (but see Ruxton et al. 2004). More detailed characterizations of aposematism and mimicry can be found in recent reviews (Mallet and Joron 1999; Härlin and Härlin 2003).

Species richness of aposematic lineages

Although the original workers (e.g., Bates, Darwin, Müller, and Wallace) believed that aposematism and mimicry influenced diversification, most subsequent works have focused on the difficulties associated with the evolution of these phenomena (reviewed by Mallet and Joron 1999). Certainly, the invasion of a conspicuous mutant, even if it is unpalatable, may be hindered by the probability of increased attack by naïve predators (Guilford 1988; Joron and Mallet 1998; Lindström et al. 1999; Mallet and Joron 1999). Aposematic lineages, thus, may be expected to be relatively rare. But what happens to diversification rates of lineages after aposematism successfully invades? The evolution of colours that act as honest signals of unpalatability may reduce predation pressure and lead to increased diversification, either through increased speciation and (or) reduced extinction. An examination of aposematic lineages of anurans confirms the first, but not the second, prediction (Table 1). Using traditional relationships within the dendrobatid frogs, aposematism has four independent origins in anurans, with the aposematic clade being larger than its sister clade in only two sister-group comparisons. Recent evidence from molecular phylogenies of the family Dendrobatidae suggests that aposematism has evolved a number of times from cryptic ancestors in the paraphyletic genus *Colostethus* (Vences et al. 2003). The numbers of species that will be assigned to the different "*Colostethus*" lineages are not known at the present time (M. Vences, personal communication). Given that there are approximately twice as many cryptic species as aposematic species within the family Dendrobatidae (Table 1), few arrangements would affect the overall conclusion of a lack of a strong correlation, at least in anurans, between aposematism and enhanced diversification rates. Clearly, more evidence is desirable, although a recent sister-group analysis incorporating a number of additional groups (including beetles, spiders, and wasps) has uncovered few taxa that are aposematic and comparatively species rich (K. Przecek, C. Mueller, and R. Meyers, unpublished results). Aposematism, thus, may not be a key innovation in the same sense as other defenses (e.g., spines and thorns) because the alternate state (i.e., crypsis) may be equally effective in reducing predation pressure and promoting speciation. For example, adaptation to different backgrounds, and increased predation against migrants, has produced a variety of locally adapted colour pattern morphs in the cryptic walking-stick genus *Timema* Scudder, 1895 (Crespi and Sandoval 2000; Nosil 2004).

Table 1. Species richness of aposematic anuran taxa and their sister groups.

| Family | Aposematic group* | Aposematic group species richness | Sister group† | Sister group species richness | References‡ |
|----------------|--|-----------------------------------|---|-------------------------------|---|
| Bufonidae | <i>Melanophryniscus</i> | 18 | <i>Dendrophryniscus</i> (7) or <i>Dendrophryniscus</i> + <i>Oreophrynella</i> (6) | 7 or 13 | Graybeal (1997); Cannatella (1986) |
| Dendrobatidae | <i>Cryptophylllobates</i> (1) + <i>Dendrobates</i> (41) + <i>Epipedobates</i> (30) + <i>Phylllobates</i> (5) | 77 | <i>Allobates</i> (2) + <i>Aromobates</i> (1) + <i>Colostethus</i> (128) + <i>Mannophryne</i> (12) + <i>Nephelobates</i> (8) | 151 | Clough and Summers (2000); Vences et al. (2003) |
| Mantellidae | <i>Mantella</i> | 15 | <i>Mantidactylus</i> | 85 | Wilkinson et al. (2002) |
| Myobatrachidae | <i>Pseudophryne</i> | 13 | <i>Arenophryne</i> (1) + <i>Metacrinia</i> (1) + <i>Myobatrachus</i> (1) | 3 | Read et al. (2001) |

Note: Values for species richness obtained from the American Museum of Natural History's *Amphibian Species of the World* version 3.0 (Frost 1998–2004).

* Authority names and dates for genera listed are as follows: *Melanophryniscus* Gallardo, 1961; *Cryptophylllobates* Lötters, Jungfer and Widmer, 2000; *Dendrobates* Wagler, 1830; *Epipedobates* Myers, 1987; *Phylllobates* Duméril and Bibron, 1841; *Mantella* Boulenger, 1882; *Pseudophryne* Fitzinger, 1843.

† Authority names and dates for genera listed are as follows: *Dendrophryniscus* Jiménez de la Espada, 1871; *Oreophrynella* Boulenger, 1895; *Allobates* Zimmermann and Zimmermann, 1988; *Aromobates* Myers, Paolillo O. and Daly, 1991; *Colostethus* Cope, 1866; *Mannophryne* La Marca, 1994; *Mantidactylus* Boulenger, 1895; *Arenophryne* Tyler, 1976; *Metacrinia* Parker, 1940; *Myobatrachus* Schlegel, 1850.

‡ References indicate source(s) used to identify the sister group to focal aposematic taxa.

Analogous to the case of latex and resin canals, aposematic lineages may be better able to persist in a greater diversity of habitats without necessarily experiencing higher speciation rates (cf. Schluter 2000).

Mimicry in butterflies

Mimicry may drive the diversification of models and mimics through a number of mechanisms. First, coevolutionary chase between models and Batesian mimics has been proposed (Huheey 1988; Gavrillets and Hastings 1998). Batesian mimics are harmful to their models, thus models may benefit from evolving new warning colouration. Escape in this interaction is likely to be short-lived because the new model is expected to attract new mimics. Although an appealing scenario, relatively more rapid evolutionary rates in the mimic and selection against novel variants in the model make it unlikely that mimicry diversification will be driven by coevolutionary chase (Joron and Mallet 1998). Second, there is better evidence that the evolution of a novel warning colouration, coupled with increased predation on poorly adapted hybrids between different forms, can result in reproductive isolation and speciation. *Heliconius melpomene* (L., 1758) and *Heliconius cydno* Doubleday, [1847] are recently diverged unpalatable sister species and tend to mimic different species (*Heliconius erato* (L., 1764) and *Heliconius sapho* (Drury, [1782]), respectively) that differ in their warning colours (Jiggins et al. 2001). Sympatric *H. melpomene* and *H. cydno* from Panama did not mate with each other in choice experiments. Interestingly, *H. melpomene* males from French Guiana, which are allopatric to *H. cydno*, courted *H. cydno* females much more vigorously, and occasionally mated with them, than *H. melpomene* males from sympatry with *H. cydno* in Panama. This observation suggests that mate discrimination has been enhanced in sympatry, possibly owing to reinforcement (Jiggins et al. 2001). Finally, there are a number of instances of multiple mimicry rings, groups of sympatric species that share a common warning pattern, within one area. The reasons for the coexistence of multiple mimicry rings that are broadly sympatric with one another are not clear, although they may partially be the result of different predators in different habitats (Mallet and Gilbert 1995; Beccaloni 1997).

Prospectus

The evolutionary effects of interactions between enemies and their prey, long postulated to have significant consequences (Müller 1879; Worthington 1940; Fryer 1959; Askew 1961; McPhail 1969; Gilbert 1975), are now the focus of intensive research. Indeed, a number of studies were published after I began composing this review (e.g., Horth 2004; Nunn et al. 2004; Schmidt and Van Buskirk 2005). There now exists a substantial body of theory that, although not as extensive as that addressing the effects of resource competition, forms a framework for empirical investigations. Furthermore, evidence that enemies may drive allopatric and sympatric phenotypic shifts and diversification of their prey is beginning to accumulate.

Given the empirical findings that are currently available, we can begin to evaluate the models that have addressed the role of enemies in diversification and divergence of prey

(Holt 1977; Brown and Vincent 1992; Abrams 2000; Doebeli and Dieckmann 2000; Bowers et al. 2003). Data from a number of the systems discussed here demonstrate that the presence of predators increases morphological divergence among closely related prey lineages, either through habitat-specific predation risk or apparent competition mediated via shared predators (e.g., Wellborn 1994; McPeck 1995; Vamosi and Schluter 2004). Under some environmental conditions, the presence of enemies may reduce morphological diversity in sympatry (e.g., Buckling and Rainey 2002). Given the differences between various systems, conclusively identifying the factors underlying these patterns may prove challenging. Simulation results suggest that invasion of a mutant genotype into a novel niche depends greatly on its foraging behaviour (i.e., ability to discriminate among alternate resources of different quality; S.A. Richards and S.M. Vamosi, unpublished results). Accordingly, the most parsimonious explanation for the results of Rundle et al. (2003) is that juvenile sticklebacks altered their foraging behaviour and (or) habitat use in response to the presence of predators and density of competitors (see also Svanbäck and Persson 2004). In contrast, there is little evidence for adaptive decision-making by the bacteria or phage used by Buckling and Rainey (2002). One pattern that appears to hold across multiple systems is that phenotypic divergence in enemy-free space is most likely when predators are size-selective and (or) hunt visually (e.g., Gilbert 1975; Ricklefs and O'Rourke 1975; Spitze 1991; Wellborn 1994; Horth 2004).

Empirical evidence also suggests that natural enemies may have a significant impact on diversification in their prey, although the typical direction of their effects is not clear at the present time. The fossil record registers dramatic reductions in the diversity of some groups of prey and the radiation of others that correspond with the rise and diversification of enemies (e.g., Stanley 1973; Vermeij 1977; Stanley et al. 1983). Experiments with contemporary members of some of these lineages confirm that enemy-prey interactions have contributed to these trends (Palmer 1982; Boraas et al. 1998; Stone 1998). Within-lake diversification of benthics and limnetics has occurred despite, and likely been facilitated by, the presence of predators (Rundle et al. 2003; Vamosi 2003). Contrary to Fryer's (1959) verbal model, however, increased vulnerability of hybrids to predators has not been found (Vamosi and Schluter 2002). Furthermore, stickleback species pairs are not found in lakes that contain fish species other than cutthroat trout (Vamosi 2003). Vascular plant lineages with resinous and laticiferous canals may be more species rich than their sister groups that lack these defenses (Farrell et al. 1991), although this pattern warrants reconsideration. Aposematism and mimicry are also expected to increase diversification rates, although the data are scanty at present. Finally, avian predation may be limiting the numbers of parasitoid wasps coexisting in sympatry (Gibbons 1979).

Future directions

Overall, there appears to be more evidence supporting the role of enemies in the phenotypic differentiation of prey than in affecting their diversification rates. Rather than trying to

decide whether natural enemies typically hamper or facilitate diversification, I believe significant insights will instead be gained by characterizing the conditions leading to the various outcomes. Here, I highlight a few study systems and approaches, in hopes of stimulating further research. In my estimation, the debate concerning the role of predators in the adaptive radiations of cichlids was never properly resolved. Specifically, Fryer (1959) pointed out that during the course of cichlid radiations, a number of species evolved that were themselves predators of other cichlids, yet their role has been largely ignored. The suggestions that visual predators may drive aspect diversity in moths (Ricklefs and O'Rourke 1975) and leaf shape in passion vines (Gilbert 1975) have remained largely untested for 30 years (but see Rausher 1978, 1981; Bond and Kamil 2002). Aposematic and mimetic systems are natural laboratories for testing a number of theoretical predictions regarding the impacts of enemies on divergence and diversification, yet most investigations thus far have posed the question "how does it evolve?" rather than "what happens after it evolves?" Mallet and Joron (1999), in a comprehensive review of these phenomena, were able to dedicate less than a single page to the connections between mimicry and speciation. Finally, seed dispersal and seedling survival are important in determining rates of spread in flowering plants (Heilbut et al. 2001), yet we know almost nothing about how seed predation and herbivory affect the origin and maintenance of dioecy (Ashman 2002).

I further suggest that experimental documentation of behaviour, growth, and survival of prey in the presence of enemies should be accompanied by comparative phylogenetic methods. Sister-group comparisons, for example, may allow a test of the tantalizing suggestion that aposematic signals (i.e., conspicuous thorns) are correlated with high species richness in certain taxa of flowering plants (Lev-Yadun 2001). A better understanding of the effects of laticiferous and resinous canals on diversification (Farrell et al. 1991) may be aided by constructing lineages-through-time plots (Nee et al. 1996) and measuring the degree of tree imbalance in phylogenies of closely related lineages that either possess or lack these structures (Chan and Moore 2002). These methods allow one to estimate birth and death rates of lineages over time, and also to pinpoint lineages within larger clades that are associated with particularly high or low diversification rates. Applied to the case of latex and resin canals, for example, one could elucidate whether the benefits of these defenses are manifested early or late in the history of given clades. Together with phylogenies of their major enemies, one could further test whether the amount of time that a particular lineage was freed from herbivore pressure tends to be reflected by current relative species richness. Using a variety of approaches and study systems, I trust we will be able to more conclusively answer McPhail's (1969) call to action before the passing of another 35 years.

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