

Coevolution and Maladaptation¹

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SYNOPSIS. Many of the most commonly cited examples of exquisite adaptation are of coevolved symbioses. As we learn more about the coevolutionary process, however, it is becoming increasingly evident that coevolution may also keep populations moderately maladapted much of the time. As a result, coevolving populations may only rarely occupy adaptive peaks, because the selective landscape is under continual change through reciprocal selection on the species themselves. These shifting patterns of coadaptation are further shaped by the geographic structure of most species. Selection mosaics across landscapes and coevolutionary hotspots can favor different evolutionary trajectories in different populations. The combined action of gene flow, random genetic drift, and local extinction of populations may then continually remold these local patterns, creating a geographic mosaic in the degrees of maladaptation found within local interactions. Recent mathematical models of the geographic mosaic of coevolution suggest that complex mosaics of maladaptation are a likely consequence of spatially structured species interactions. These models indicate that the spatial structure of maladaptation may depend upon the type of coevolutionary interaction, the underlying selection mosaic, and patterns of gene flow across landscapes. By maintaining local polymorphisms and driving the divergence of populations, coevolution may produce spatial patterns of maladaptation that are a source of ongoing innovation and diversification in species interactions.

INTRODUCTION

Many of the most commonly cited examples of exquisite adaptation are of symbioses that show evidence of tightly coevolved morphology, physiology, and behavior. The most extreme examples include mitochondria and chloroplasts (Chihade, 2000), but the array of symbiotic species showing coevolutionary adaptation continues to grow yearly. These examples showcase the effectiveness of coevolution in linking the genomes of interacting species, and they point to the central role of coevolution in organizing the earth's biodiversity.

As we learn more about the coevolutionary process, however, it is becoming increasingly evident that it may often also keep local populations moderately maladapted much of the time. The term maladaptation is used in a variety of ways by evolutionary biologists, but we use it here in the general sense of deviations from adaptive peaks, as have others (*e.g.*, Kirkpatrick and Barton, 1997; Crespi, 2000). Suggested examples of maladaptation in symbiotic interactions have included poorer parasite infectivity or performance on sympatric hosts than on allopatric hosts (*e.g.*, Kaltz *et al.*, 1999; Oppliger *et al.*, 1999; Koskela *et al.*, 2000) and mismatched profiles of local defenses and counterdefenses between hosts and parasites (Berenbaum and Zangerl, 1998; Burdon and Thrall, 1999).

Here we explore why moderate local maladaptation

may be a common and expected result of the coevolutionary process. As Crespi (2000) has argued, the study of maladaptation requires recognition and quantification of maladaptation and a determination of the causes. In this paper we focus on how one of the most common possible causes of local maladaptation—geographic structure—may shape patterns of maladaptation in species interactions across landscapes. Our goal is to begin to develop expectations on how maladaptation in coevolved interactions should be distributed across landscapes under different ecological and genetic conditions. Without such expectations, it will continue to be difficult to interpret the wide range of results obtained in studies of the outcomes of species interactions. Here we focus on the kinds of conditions that may prevent populations of interacting species from occupying local adaptive peaks. Used in this sense, local maladaptation corresponds to the deviation of a local population from its locally optimum fitness. Depending upon the geographic structure of an interaction, local maladaptation measured in this way may or may not correspond with interpretations of maladaptation measured in challenge experiments between sympatric vs. allopatric populations, which is another common way of assessing some aspects of geographic structure in local adaptation.

BACKGROUND: THE ECOLOGICAL STRUCTURE OF COEVOLUTIONARY MALADAPTATION

It is difficult enough for populations to adapt to their physical environments. Few environments are constant, and selection often varies on local populations over time. As a result, populations are genetic com-

¹ From the Symposium *Living Together: The Dynamics of Symbiotic Interactions* presented at the Annual Meeting of the Society for Integrative and Comparative Biology, 3–7 January 2001, at Chicago, Illinois.

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posites resulting from time-lagged variable selection around means that themselves shift over time.

Coevolution adds another, fundamentally different, level of complexity to the problem. Unlike adaptation to the physical environment, adaptation to another species may induce a reciprocal genetic response, as the other species itself evolves in specific ways to enhance or mitigate those evolutionary changes. Hosts evolve to decrease the effectiveness of their parasites' adaptations, and parasites evolve to decrease the effectiveness of their hosts' defenses. Even mutualisms are not immune from this process, because cheaters force changes that push coevolving mutualisms in novel directions. By its nature, then, the coevolutionary process tugs local populations in different evolutionary directions over time, and it is likely to shift different populations in different directions. These coevolutionary dynamics may produce patterns of maladaptation ranging from local and ephemeral to widespread and permanent.

How maladaptation in species interactions is distributed across landscapes in space and time will depend upon at least six properties of populations and the forces acting on them. The first five of these all introduce time lags into the coadaptation of species within local communities.

Frequency-dependent selection automatically generates temporal patterns of local maladaptation in interactions between parasites and hosts. As natural selection continues to favor rare host genotypes to which the parasite is poorly adapted, it creates temporal mismatches between host and parasite genotype frequencies within local communities. How much of the time parasites or hosts appear to be locally maladapted will depend upon the rates at which each species can track changes in the other species (Morand *et al.*, 1996). A number of simulation models have now shown that a combination of differences in generation times and strengths of frequency-dependent selection often result in time lags in the adaptation of species to each other. Interacting parasites and hosts should therefore commonly be at least slightly to moderately mismatched in defenses and counter-defenses much of the time due to time-lagged selection (*e.g.*, Dybdahl and Lively, 1998; Kaltz and Shykoff, 1998; Lively, 1999). Differences among populations in the length of time lags will in themselves generate different local temporal patterns in degree of maladaptation of locally interacting species.

Density-dependent selection may favor different levels of virulence and defense at different host and parasite densities. Models of predator/prey interactions have indicated that regions of high prey productivity (*e.g.*, prey birth rates) will favor different coevolutionary dynamics than regions of low productivity (Hochberg and van Baalen, 1998). Consequently, rapidly fluctuating population densities could potentially create time delays in response to selection, thereby generating temporal patterns of maladaptation in the degree of matching among traits. In addition, mismatches

can result within fluctuating populations even in the absence of direct density-dependent selection, if the interacting populations are driven through genetic bottlenecks during epidemic cycles (Burdon and Thompson, 1995).

Dormancy/diapause in one of the species has the potential to introduce time lags into coevolving interactions and thereby create local maladaptation. Recent studies have suggested that the timing of diapause in some prey species is related to the seasonal pattern of intensity of predation, and that selection for diapause timing is subject to fluctuating selection (Ellner *et al.*, 1999). Similar fluctuating selection must certainly occur in interactions between symbionts and hosts. Studies of local adaptation in sister species or populations that differ in dormancy/diapause length would be useful in developing our understanding of the dynamics of maladaptation.

Genetic architecture of interactions in itself can have important effects on the coevolutionary process (*e.g.*, Thompson and Burdon, 1992; Frank, 1993b, 1996; Burdon *et al.*, 1996; Doebeli, 1996; Abrams, 2000; Roy and Kirchner, 2000). Recent models have indicated that host resistance governed by quantitative genetic effects may create different patterns of selection and dynamics on parasite virulence than host resistance governed by major gene effects (Gandon and Michalakis, 2000). Nevertheless, quantitative genetic theory on how additivity of traits, epistasis, and pleiotropy affect the temporal dynamics of coevolutionary maladaptation is still developing. Moreover, there are major gaps in our understanding of some of the most fundamental questions on the genetic dynamics of coevolution. For example, we know that most plants are polyploid and that polyploidy can have major effects on some plant/insect interactions (Thompson *et al.*, 1997; Segraves and Thompson, 1999; Nuismer and Thompson, 2001), but we know nothing about how polyploidy affects coevolutionary dynamics.

Adaptation to multiple hosts or symbionts creates potential compromises in selection that can make a pairwise interaction appear maladapted (Combes, 1997). In some cases the maladaptation may be real, depending upon the temporal dynamics of coevolution involving all the interacting species. In other cases, the adaptations of symbionts or hosts may be the locally weighted outcomes of selection imposed by their enemies. The few studies of adaptive landscapes created by multispecific interactions show evidence of complex fitness surfaces (*e.g.*, Simms and Rausher, 1993). Studies of a number of symbiont/host interactions have indicated that adaptation to different hosts can create either negative trade-offs, positive correlations, asymmetric effects on performance on different hosts, or no clear correlations in host-related adaptations (*e.g.*, Via, 1994; Fry, 1996; Thompson, 1996; Kraaijeveld *et al.*, 1998; Fellowes *et al.*, 1999; Crill *et al.*, 2000; Turner and Elena, 2000). Moreover, the structure of these correlations may change over time (Joshi and Thompson, 1995). How the dynamics of these positive and nega-

tive correlations relate to the overall adaptation and maladaptation of populations remains largely unresolved.

The geographic structure of interactions is the final crucial component of interactions, shaping the pattern of both temporal and spatial maladaptation. Almost all widespread symbiotic interactions that have been studied show some geographic structure, varying across landscapes in the traits and outcomes that shape coevolutionary trajectories (e.g., Berenbaum and Zangerl, 1998; Parker and Spoerke, 1998; Burdon *et al.*, 1999; Lively, 1999; Parker, 1999; Thompson, 1999a; de Jong *et al.*, 2000). Because spatial structure is so prevalent, its role in adaptation and coadaptation is becoming one of the fundamental problems in evolutionary biology (e.g., Wade and Goodnight, 1998; Thompson, 1999b; Avise, 2000).

Developing predictions about the geographic structure of maladaptation requires consideration of three widespread phenomena, which together comprise the core of the geographic mosaic theory of coevolution: selection mosaics, coevolutionary hotspots, and trait remixing across landscapes (Thompson, 1994, 1999b). Selection mosaics arise when the type or strength of selection on interactions varies across the geographic range of an interaction. The interactions between the pollinating floral parasite *Greya politella* and its host plants, for instance, have the potential to shift between mutualism and antagonism across habitats. This variation in outcome is driven largely by the availability of co-pollinators, such that the interaction is mutualistic in environments where co-pollinators are rare or relatively inefficient but antagonistic in environments where co-pollinators are abundant (Thompson and Pellmyr, 1992; Pellmyr and Thompson, 1996; Thompson, 1997).

These selection mosaics can, in turn, result in a mosaic of coevolutionary hotspots and coldspots across landscapes. Coevolutionary hotspots are those communities where selection acting on an interaction is truly reciprocal. Crossbills and lodgepole pines, for example, have coevolved only in those parts of the Rocky Mountains of North America where pine squirrels, which are the major biotic driver of lodgepole pine evolution in the Rockies, are rare or absent (Benkman, 1999). Because many interactions may be coevolutionary within only a fraction of their geographic range, spatial variation between coevolutionary hotspots and coldspots may drive much of the observed dynamics of maladaptation.

Metapopulation dynamics and complex patterns of gene movement across broader geographic landscapes are the additional important components of geographically structured coevolution. (e.g., Gandon *et al.*, 1996; Burdon and Thrall, 1999; Burdon *et al.*, 1999). Local metapopulation dynamics may sometimes occur within a similar coevolutionary selection regime, but those dynamics are in turn embedded in larger geographic groups of populations that may be under different evolutionary and coevolutionary pressures. The

longterm study of the geographic dynamics of gene-for-gene coevolution between wild flax and flax rust in Australia exemplifies how coevolution between species can be continually reshaped by metapopulation dynamics and gene movement across local and broader geographic landscapes (Burdon and Thrall, 2000). These studies have demonstrated that the ongoing coevolution of species may, in fact, often require complex geographic structure.

THE DYNAMICS OF COEVOLUTIONARY MALADAPTATION

Recent mathematical models of the geographic mosaic of coevolution have begun to suggest that complex mosaics of maladaptation are a likely consequence of geographically structured species interactions. The models suggest that selection mosaics, coevolutionary hotspots, and trait remixing through gene flow and metapopulation dynamics are capable of acting together to create novel patterns of local and regional maladaptation in coevolving species.

Metapopulation structure and broader geographic structure

Coevolutionary models incorporating gene flow and metapopulation structure among populations have shown that coevolutionary dynamics in spatially structured populations connected by gene flow differ from the dynamics of locally coevolving species. These novel dynamics and patterns of maladaptation can be especially pronounced when relative gene flow rates differ between hosts and parasites, as has now been demonstrated in some symbiotic interactions (e.g., Dybdahl and Lively, 1996). These differential gene flow rates can create conditions under which one species becomes relatively more maladapted than the other across landscapes. These novel dynamics could develop even in the absence of selection mosaics and coevolutionary hotspots.

For example, recent models incorporating gene flow and extinction/recolonization dynamics have suggested that spatial patterns of maladaptation may frequently develop in host/parasite interactions (Gandon *et al.*, 1996, 1998). Furthermore, these models suggest that hosts may be less maladapted than parasites whenever host gene flow is higher than parasite gene flow and overall parasite gene flow is low. Maladaptation in this case means that parasites perform worse on their local host than on allopatric hosts, and host resistance to local parasites is relatively high. Shifting the relative and absolute gene flow rates between parasites and hosts shifts their degrees of local adaptation relative to one another. These results, however, have a complex structure, generating strong temporal patterns in the degrees of local maladaptation found in parasites and hosts.

Related spatial models using either a matching alleles or gene-for-gene structure have shown that metapopulation structure often allows for maintenance of genetic variation over longer periods of time in host/symbiont interactions than is possible through local

coevolutionary dynamics alone (*e.g.*, Frank, 1993a; Antonovics, 1994; Damgaard, 1999; Thrall and Burdon, 1999). Consequently, geographically structured coevolution provides ecological conditions under which coevolving populations could cycle through various states of adaptation and maladaptation over long periods of time as host and symbiont populations evolve through frequency-dependent selection, gene flow, and random genetic drift.

Selection mosaics

The current generation of metapopulation models assumes that the structure of selection is similar across space. Selection mosaics, however, are likely to be common in many interspecific interactions, depending upon the initial conditions under which the interaction arose, the genetic structure of local populations, the life histories of the local interacting populations, and the physical environments in which the interaction occurs. Even if the overall outcome (*e.g.*, mutualism) is the same across landscapes, coevolution may follow different trajectories in different populations. Parker's (1999) models of the evolution of symbiotic mutualisms suggest that geographic divergence may result from differences among populations in initial genetic conditions, which lead to subsequent fixation of different allelic combinations in different populations. More recently, the models of Switces and Moody (2001) have indicated that local coevolutionary dynamics involving diploid species (in particular, a diploid species interacting with a haploid species in their analysis) can show a wider range of dynamics and equilibria than found in haploid models. Their results suggest that selection mosaics are likely to be common in species interactions even in the absence of major environmental differences across landscapes, as a result of different initial conditions among populations and the complex genetic dynamics of coevolution.

In many interactions, however, the environments and ecological outcomes differ greatly across landscapes. An interaction may even be mutualistic in one environment, but antagonistic or commensalistic in another. If local mutualistic selection is stronger than antagonistic selection in neighboring communities, a local mutualism can be protected from invasion by other antagonistic genotypes (Nuismer *et al.*, 1999). Under other conditions, however, mutualisms may fluctuate in gene frequency over time, if they are linked by gene flow to communities in which the same interaction is strongly antagonistic. These local mutualistic populations will create coevolutionary dynamics similar to that observed in parasite/host interactions driven by frequency-dependent selection (Nuismer *et al.*, 1999). The coevolutionary trajectories of coevolving interactions will therefore depend not only upon the pattern of gene flow among populations but also upon the relative strengths of selection in different habitats and the overall strength of selection relative to gene flow.

Even if selection favors local fixation of traits in mutualistic interactions, it may take hundreds of gen-

erations for the mutualism to become genetically stabilized, when selection varies from antagonism to mutualism among communities (Nuismer *et al.*, 1999). How long it takes for an interaction to become genetically stabilized depends upon the relative strength of selection in the different communities and the amount of gene flow between communities. This stabilization itself assumes that the outcomes of interactions do not vary among the genetically connected communities over time. Hence, any biologist studying the structure of a local interaction within a natural community is often likely to be studying an interaction in nonequilibrium.

If the populations are connected clinally across landscapes, a broad range of maladaptive outcomes is possible. Recent models suggest that coevolutionary clines produced by antagonistic interactions are likely to be highly dynamic over time, producing geographically shifting patterns of adaptation and maladaptation (Nuismer *et al.*, 2000). In contrast, mutualistic clines tend toward a stable geographic equilibrium in allele frequencies.

In more geographically complicated interactions that vary from antagonism to mutualism among communities, maladaptation can occur not only at the boundaries of these different outcomes, but also well into neighboring areas across the geographic landscape (Fig. 1). Moreover, strong spikes of maladaptation (relative to local potential fitness peaks) can occur in host populations at the boundary between mutualistic and antagonistic sites. Those spikes can be especially pronounced whenever the strength of selection in the mutualistic sites is much stronger than the strength of selection in the antagonistic sites (Fig. 1a, b, c).

Finally, the demographic structure of interacting hosts and symbionts has the potential to further reshape selection mosaics in symbiotic interactions. In a recent model, Hochberg *et al.* (2000) assumed that host populations varied geographically from demographic sources to sinks in the absence of symbionts, and then explored competition between virulent and relatively avirulent symbionts. Their models indicated that the interactions were more likely to evolve toward increased antagonism in environments that are demographic sources for the host and toward mutualism in environments that are weak demographic sinks. In these models, weak demographic sinks become the likely sources for symbiotic mutualisms.

Coevolutionary hotspots

In addition to the effects of gene flow and selection mosaics, recent models have suggested that coevolution need not be ubiquitous to shape the evolution of species interactions. Coevolutionary hotspots, whether antagonistic or mutualistic, can shape the overall trajectories of species interactions, even when the hotspots are uncommon relative to the coldspots (Gomulkiewicz *et al.*, 2000). In the process, hotspots can generate either increased or decreased maladaptation in species interactions, and they may do so either lo-

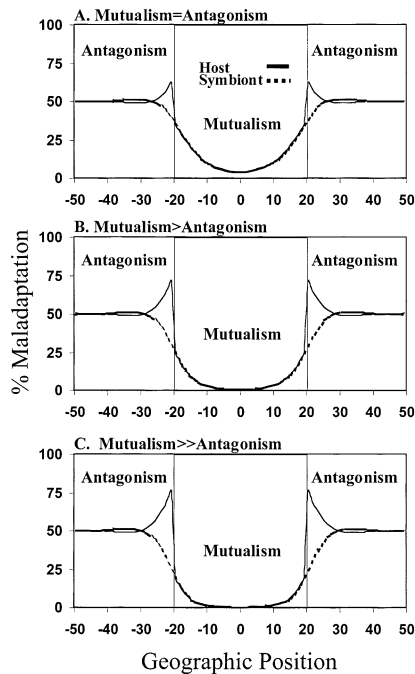


FIG. 1. The spatial structure of maladaptation in a host and symbiont for an interaction that varies between mutualism and antagonism. Maladaptation is scaled relative to the local adaptive peak for each population. The interaction is composed of a central core of mutualistic communities (between -20 to $+20$), surrounded on either side by antagonistic communities. Gene flow for both species follows a Gaussian distribution with migration variance $\sigma^2 = 2$ for both species. As the strength of mutualistic selection increases from panels A through C, the level of maladaptation experienced within the mutualistic habitat decreases. This decrease in maladaptation within the mutualism leads to a corresponding increase in maladaptation at the interface between mutualistic and antagonistic habitats. In all figure panels the rate of gene flow remains constant, demonstrating that observed patterns of maladaptation depend fundamentally on the strength of local selection. Relative maladaptation (here displayed as a percentage) is defined as $(w_{\max} - w_{\text{mean}})/(w_{\max} - w_{\min})$, where w_{\max} and w_{\min} are the maximum and minimum local fitnesses, respectively, for a species and w_{mean} is its local mean fitness. These figures were generated by numerical simulation of the model described in Nuismer *et al.* (2000).

cally or globally. Depending upon the geographic structure of selection and the extent of gene flow, populations of coevolving species can experience higher fitness either in the hotspots or the coldspots. Hence, patterns of local adaptation will depend upon the geographic mix of genetically connected coevolutionary hotspots and coldspots, and local populations may commonly cycle in maladaptation over time.

For example, consider two interactions between a symbiont and a host, with a geographic structure similar to that used in Figure 1. In one community, the interaction is in a coevolutionary hotspot in which frequency-dependent selection drives the interaction as a parasite/host relationship; in the other, the interaction is in a coldspot in which the interaction is commensalistic and acts only on the parasite (Fig. 2). In the absence of gene flow between the hotspot and coldspot, the relative maladaptation of the species in the hotspot cycles with increasing oscillations, whereas in

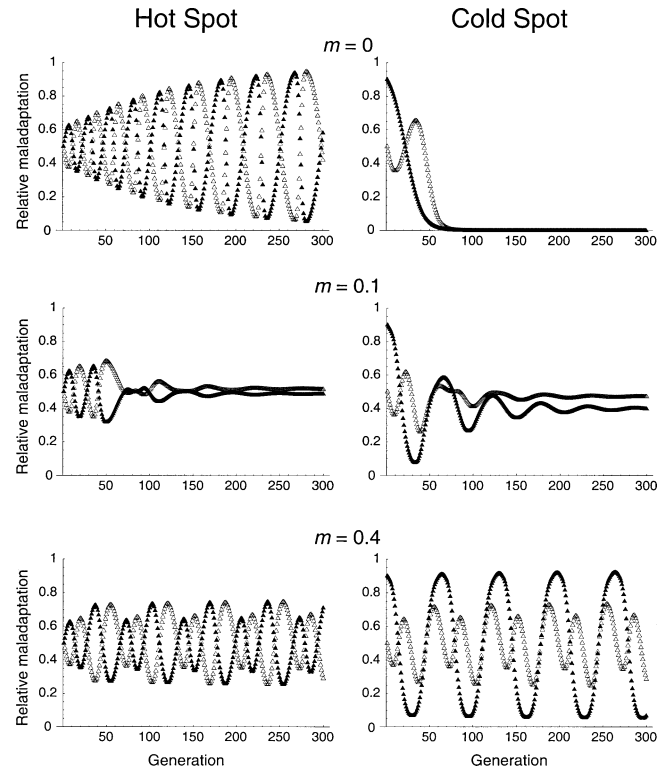


FIG. 2. The spatial structure of maladaptation in host and parasite for an interspecific interaction that spans coevolutionary hotspots and coldspots. Maladaptation is scaled relative to the local adaptive peak for each population. Panels show the dynamics of relative maladaptation in hot spots (left panels) and cold spots (right panels) for a parasite (open symbols) and its host (closed symbols) over 300 generations of coevolution for three levels of gene flow (m). See Figure 1 for the definition of relative maladaptation used here. Simulations are based on the model described in the legend of figure 6 of Gomulkiewicz *et al.* (2000).

the coldspot the interaction rapidly approaches an adaptive peak. With moderate gene flow between the hotspot and coldspot ($m = 0.1$), the interacting species become permanently moderately maladapted in both communities, despite the local differences in the structure of selection. With even higher levels of gene flow ($m = 0.4$), the populations of both species oscillate over time in relative maladaptation in the hotspot and in the coldspot. It is evident from this simple simulation that a geographic mix of hotspots and coldspots could maintain complex patterns of adaptation and maladaptation across landscapes.

DISCUSSION

The study of coevolving symbioses has often been plagued by inexplicable patterns of local outcome that require ad hoc explanations. As we continue to develop a full theory of coevolution based upon the actual genetic, ecological, and historical structure of interactions, we will become better at interpreting the patterns of adaptation, apparent maladaptation, and real maladaptation that we find in local studies of interacting populations. We are already beginning to understand that local maladaptation is not always necessarily

a result of the failure of coevolutionary selection to adapt species to each other. Instead, local maladaptation—sometimes transient; sometimes more permanent—is an inevitable and important part of the coevolutionary process for species interactions distributed across complex landscapes.

The maladaptation found in interactions is the origin of future evolution. The deviation from adaptation drives further selection. In that respect, coevolution is likely a central force in most populations and species, driving ongoing selection and new evolutionary solutions. One way of thinking of antagonistic coevolution between parasites and hosts is as a process favoring traits that make the other species more maladapted. The formation of mutualistic interactions changes the structure of selection, but it does not eliminate the role of maladaptation as a major component of coevolutionary selection. Cheaters are inevitable within mutualisms, either as cheater genotypes within the mutualistic species or as yet other species that exploit the mutualism. The result is that most mutualisms can erode over time in the absence of ongoing selection to mitigate what could otherwise become a ratchet of maladaptation.

All the current mathematical models of the geographic mosaic of coevolution produce complex spatial patterns and dynamics. Spikes of maladaptation, for instance, can occur near the boundaries of coevolutionary hotspots and selection mosaics. These spikes may reflect what can actually happen at boundaries, or they may reflect the simplifying genetic assumptions of the models and the simplifying ecological assumptions about the structure of hotspot boundaries. No models of selection mosaics and coevolutionary hotspots have incorporated metapopulation dynamics, with either extinction/recolonization or source/sink structures. More complex models with linked genetics and epistasis and more complex demography will likely show even more complex patchworks of maladaptation across landscapes. These dynamics will likely depend upon the distribution of selection mosaics, coevolutionary patterns, relative rates of gene flow, and metapopulation dynamics. Even so, the current results already suggest that most geographically structured interactions will generate a mix of highly adapted, moderately well adapted, and maladapted populations.

Darwin understood that the most convincing evidence for evolution was in the imperfection of nature and the jury-rigged structure of adaptation. Subsequent evolutionary biologists have understood this fact as well. Nonetheless, it has taken longer to realize that coevolution, which produces some of the best examples of exquisite adaptation, relies upon a constant interplay of adaptation and maladaptation to drive much of the ongoing adaptation and diversification of life.

Understanding the geographic structure and dynamics of maladaptation is becoming increasingly important as we continue to alter communities worldwide. Ecological conditions creating maladaptation in interactions through introduction of new taxa and geno-

types may be increasing as anthropogenic alteration of communities worldwide rapidly remixes traits among populations that have been traditionally widely separated (Harvell *et al.*, 1999). Managing the ecological dynamics of interspecific interactions, whether parasitic or mutualistic, will rely upon understanding and managing coevolutionary dynamics. The current models and empirical studies on the geographic mosaic of coevolution are beginning to move our understanding in that direction.

ACKNOWLEDGMENTS

We thank Mary Beth Saffo for organizing the symposium, and Rebecca Hufft and two anonymous reviewers for very helpful comments on the manuscript. This work was supported by NSF grant DEB-0073911 and DEB-0083548.

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