Specific Hypotheses on the Geographic Mosaic of Coevolution

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ABSTRACT: Coevolution is one of the major processes organizing the earth's biodiversity. The need to understand coevolution as an ongoing process has grown as ecological concerns have risen over the dynamics of rapidly changing biological communities, the conservation of genetic diversity, and the population biology of diseases. The biggest current challenge is to understand how coevolution operates across broad geographic landscapes, linking local ecological processes with phylogeographic patterns. The geographic mosaic theory of coevolution provides a framework for asking how coevolution continually reshapes interactions across different spatial and temporal scales. It produces specific hypotheses on how geographically structured coevolution differs from coevolution at the local scale. It also provides a framework for understanding how local maladaptation can result from coevolution and why coevolved interactions may rarely produce long lists of coevolved traits that become fixed within species. Long-term field studies of the same interaction across multiple communities and spatially structured mathematical models are together beginning to show that coevolution may be a more important ongoing process than had been indicated by earlier empirical and theoretical studies lacking a geographic perspective.

Keywords: coevolution, geographic mosaic, local adaptation, maladaptation, metapopulation, mutualism.

As we learn more about the organization of the earth's biodiversity, the central role of the coevolutionary process is becoming more evident. It is now clear that some of the most important events in the history of life have resulted directly from coevolutionary events. Among the most obvious are the origin of the eukaryotic cell through coevolution with symbionts that became mitochondria, the origin of plants through the symbiosis that produced chloroplasts, and the development of the gut systems of many animal species through coevolved symbioses with microbial taxa. Coevolution also seems to play a crucial role in other fundamental processes such as the mainte-

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nance of sexual reproduction and the dynamics of some genetic polymorphisms. Examples of coevolution continue to proliferate (Thompson 1994; articles in this issue), and protocols are being developed for evaluating reciprocal selection within natural communities (Thompson and Pellmyr 1992; Iwao and Rausher 1997). At the same time, research in medical epidemiology, plant pathology, and biological control is beginning to highlight the clear practical need for understanding coevolution as an ongoing process (see, e.g., Anderson and May 1991; Crute et al. 1997; Hill et al. 1997; Holt and Hochberg 1997; Lederberg 1997).

We have three goals in this volume: to illustrate how ongoing coevolution can be studied across natural communities, to evaluate what we currently know about the dynamics of coevolution across landscapes, and to suggest specific hypotheses on the geographic mosaic of coevolution. We ask, using a variety of approaches, how the geographic structure of coevolution produces broad ecological patterns and how coevolution contributes to the ongoing organization of the earth's biodiversity.

If geographic structure is important to the coevolutionary process, it must be possible to show that it creates patterns and dynamics different from what we have observed simply through studies of local communities or the branching patterns of interacting lineages. Moreover, it must be possible to show that the geographic processes and patterns are testable. In this article, I introduce the problem and suggest how the framework of the geographic mosaic of coevolution provides specific hypotheses on the coevolutionary process and its ecological effects that can be tested in natural communities. The subsequent articles show the range of approaches being taken to evaluate the coevolutionary process within a broad geographic framework.

Background to the Problem

Studies of interspecific interactions have oscillated over the past several decades between expecting too much and expecting too little from coevolution. We have created caricatures of the process, sometimes expecting every local interaction to be highly coevolved and then becoming frus-

trated when reciprocal selection could not be demonstrated between a pair of species within a local community during a 3-yr study. At other times, coevolution has been dismissed as a rare event (e.g., origin of chloroplasts), generally unimportant in the day-to-day organization of communities because each species interacts with many other species. By this view, reciprocal selection is usually so multispecific and diffuse that it cannot be analyzed. The evolution of highly multispecific interactions requires careful study (Rausher 1996), but there is much more to the evolving web of life than the artificial dichotomy between local pairwise reciprocal selection and highly diffuse coevolution.

These continually shifting caricatures in perspective have developed because, until the past decade, there were few specific hypotheses to test about the coevolutionary process. Moreover, we lacked a view of coevolution that took into account the hierarchical structure of species interactions. Most coevolutionary studies have been designed to evaluate coevolution by looking for reciprocal selection among pairs or small groups of species within a single local community. Such short-term local studies have often produced little evidence for reciprocal selection, creating the impression that coevolution is uncommon. At the other extreme, studies of how traits are distributed among interacting phylogenetic lineages have often shown that taxa are phylogenetically constrained in their traits and in whom they interact with (Ehrlich and Raven 1964; Futuyma and Mitter 1996), and such results have sometimes reinforced the view that ongoing coevolution may be rare.

Although both of these kinds of analysis are crucial for understanding coevolution, they are only the extremes in the hierarchical process of coevolution. The local interactions are part of the raw material for coevolutionary change, sometimes producing reciprocal selection and sometimes not. And the phylogenetic conservatism of many interactions simply constrains the trajectories of the ongoing coevolutionary dynamics. Phylogenetic analyses are best used in coevolutionary research as crucial tools for guiding our understanding of which traits of interacting taxa are likely to be truly coevolved, how those traits originated, and how they may have shaped patterns of diversification (see, e.g., Pellmyr et al. 1996a, 1996b; Farrell 1998). But taken alone or even together, these extremes in the hierarchy of coevolution ignore the ecological dynamics that make up the middle level—the mesoevolutionary level—in the hierarchy of biological organization. They ignore the geographic structuring of species and their interactions.

Geographic approaches to the study of coevolution have grown out of the developing hierarchical view of ecological and evolutionary processes. Central to this view is the spatial structure, and phylogeographic structure (Avise 1998), of populations. Using data from published studies of allozyme and DNA differences among populations, Hughes et al. (1997) estimated that species are divided on average into 220 genetically differentiated populations and that worldwide there are between 1.1 and 6.6 billion populations. It does not really matter whether these numbers are off even by an order of magnitude. What matters is that the past 30 yr of protein and DNA analyses—along with studies of phenotypic traits under selection—have demonstrated that the worldwide network of genetically differentiated populations is the core structure of biodiversity.

Ignoring population differentiation in developing a framework for coevolutionary theory creates an unjustifiable caricature of the ecological and genetic setting for evolving interactions. We now know that populations are commonly groups of genetically differentiated populations, that interspecific interactions commonly differ in outcomes among communities, and that interacting species and their component traits differ in their geographic ranges. Hence, there is a geographic structure to most interspecific interactions that must be part of any theory of the coevolutionary process and its effects on the organization of the earth's biodiversity.

Geographic Dynamics of Coevolution in Space and Time

Addressing the geographic dynamics of coevolution demands confronting the problem not only of space but also of time. Many ecologists still keep evolution—and coevolution—at a safe distance, giving nodding acknowledgment to its long-term effects on the history of life but devoting little research effort to its ongoing influence on the ecological dynamics of communities. It is as if the individual variation and population structure on which species are built were simply unmalleable random elements—part of the error term in analyses of current community and landscape dynamics. It is community ecology based on the assumption that the evolutionary process is so slow that it has little effect on community dynamics.

We are learning, however, that evolution-free community dynamics, even on short timescales, is not a safe assumption. There are now dozens of published examples in which species interactions, which are the basis of community organization, have been shown to have evolved over the course of just a few decades (Thompson 1997a, 1998a). The fluctuating and directional selection driving these changes has the potential to contribute substantially to the local and geographic dynamics of biodiversity. Coevolution over regional and broader geographic scales is part of that process.

The geographic mosaic theory of coevolution was developed as one way of unifying into a framework for future studies what we have learned about the geographic structure and dynamics of species interactions over the past 30 yr (Thompson 1994, 1997b). It is a tripartite general hypothesis that suggests how the raw material of coevolution is organized: there is a selection mosaic among populations, favoring different evolutionary trajectories to interactions in different populations; there are coevolutionary hot spots, which are the subset of communities in which reciprocal selection is actually occurring; and there is a continual geographic remixing of the range of coevolving traits, resulting from the selection mosaic, coevolutionary hot spots, gene flow, random genetic drift, and local extinction of populations (table 1). By this view, the central problem is to understand the coevolutionary dynamics created by different combinations of selection mosaics, coevolutionary hot spots, and geographic remixing of traits (fig. 1). For example, can the overall evolutionary trajectories of two interacting species be driven by a small number of coevolutionary hot spots distributed over the species' geographic ranges?

As interactions evolve, the distribution of coevolutionary hot spots in "coevolutionary fitness space" is likely to change. At any moment, coevolutionary hot spots may be few or many (fig. 1). Moreover, reciprocal selection intensity will differ geographically, producing a gradient of warm spots as well as hot spots and cold spots. A local interaction may show no reciprocal selection, or symmetrical but weak reciprocal selection, or asymmetrical (strong on one, weak on the other) reciprocal selection, or strong reciprocal selection on both. If coevolutionary hot spots occur in a minority of communities, then short-term studies of an interaction at a few sites will often show little evidence for ongoing coevolution.

The tripartite geographic mosaic hypothesis generates three ecological predictions: populations will differ in the traits shaped by an interaction; traits of interacting species will be well matched in some communities and mismatched in others, producing some cases of local maladaptation; and there will be few species-level coevolved traits (i.e., coevolved traits that are distributed across all populations of a set of interacting species), because few coevolved traits will be favored across all communities. When species-level coevolved traits occur, they may have at least two possible origins: selective sweeps in novel mutations that are favored across all communities and fixation of traits that get established at the time of speciation, when geographic ranges of species are very small.

Testing the Geographic Mosaic Theory of Coevolution

Evaluating the geographic mosaic of coevolution requires studying the same interspecific interaction across multiple communities. As with all landscape-level questions in the evolution and ecology of populations, the problem is to obtain adequate sampling. Studying several populations for a short period of time is unlikely to be sufficient. Moreover, the outcomes of interactions can vary not only among communities but also over time within a single

Table 1: Raw material for the coevolutionary process and the components of the geographic mosaic of coevolution

| General aspects of the geographic mosaic of coevolution	Specific components
Raw material for the coevolutionary process	Phylogenetic context
	Specialization on other species
	Genetic architecture of traits
	Variation in the outcome of interactions (distributed outcomes)
	Variable forms and rates of selection
	Geographic structure of interactions
Tripartite evolutionary hypothesis	Selection mosaics
	Coevolutionary hot spots
	Trait remixing
Ecological predictions	Populations differ in the traits shaped by an interaction
	Traits of interacting species are well matched in only some communities
	Few coevolved traits spread to all populations of interacting species

Universal hotspots

Complex mosaics
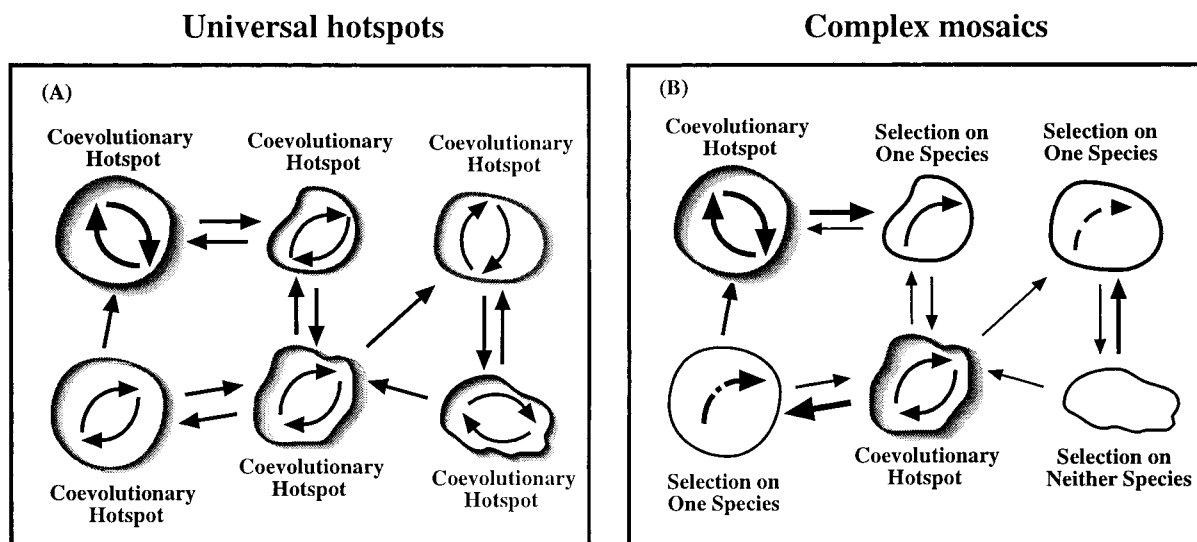
Figure 1: Hypothetical examples of a geographic mosaic of coevolution between a pair of species. Arrows within circles (biological communities) indicate selection on one or both species. Different arrow directions in different circles represent different (co)evolutionary trajectories. Arrows between communities indicate gene flow. *A,* Interaction coevolves in all populations in which it occurs; *B,* coevolutionary hot spots (i.e., communities in which reciprocal selection takes place) occur amid a matrix of coevolutionary cold spots.

community. Consequently, rigorous tests of the geographic scale at which interactions evolve and coevolve will require long-term analyses of a small set of model interactions such as those developed in the articles in this volume. Each component of the geographic mosaic framework is testable, but most of the tests fall outside the boundaries of what is practical on individual short-term grants. As our science scales up to broader landscape perspectives, we are learning that testing questions on the real scale of ecological processes requires approaches and collaborations beyond the resources of single individuals—as is the case for most of the large-scale questions now being addressed across many fields of science, ranging from molecular biology to physics.

Although long-term, collaborative studies of a few model interactions are crucial, we also require studies that can be used to corroborate or to falsify individual components of geographic coevolutionary theory in a wide range of cases. No single test can fully corroborate or falsify the argument, any more than a single short-term analysis of natural selection on one population can falsify the overall theory of natural selection. Like most biological theories, it is a probabilistic general hypothesis on the mechanisms by which the diversity of life is organized. It suggests that geographic structuring through selection mosaics, coevolutionary hot spots, and remixing of traits among populations are together often important in driving coevolutionary dynamics. It is the same kind of probabilistic argument that we use for the general role of natural

selection in evolution and similar general biological hypotheses on the organization of life. The importance of natural selection is demonstrated by the range of instances in which that mechanism can be shown to be driving evolutionary dynamics. Its general importance or lack of importance is not demonstrated by any single, short-term study of one species. Hence, a series of studies on the components of the geographic structure of coevolving interactions will help clarify if, where, and when the geographic mosaic is important in shaping the coevolutionary dynamics of interspecific interactions across broad landscapes.

Corroborating evidence for the overall theory takes the general form of showing that geographic structure is important to understanding the dynamics of coevolution. Falsifying evidence (i.e., evidence against the importance of geographic structuring in coevolutionary dynamics) takes the form of showing that selection mosaics, coevolutionary hot spots, and gene flow are not important in understanding coevolutionary dynamics. Specific forms of corroborating evidence include the following kinds of results.

First, the coevolved traits of an interaction differ among communities. (See Thompson 1994, 1997*b*, 1998*b*; Pellmyr et al. 1996*a*, 1996*b* for discussion of the use of phylogenetic and ecological approaches in the determination of coevolved traits.)

Second, coevolved traits show clines or mosaics across landscapes in the proportion of individuals harboring
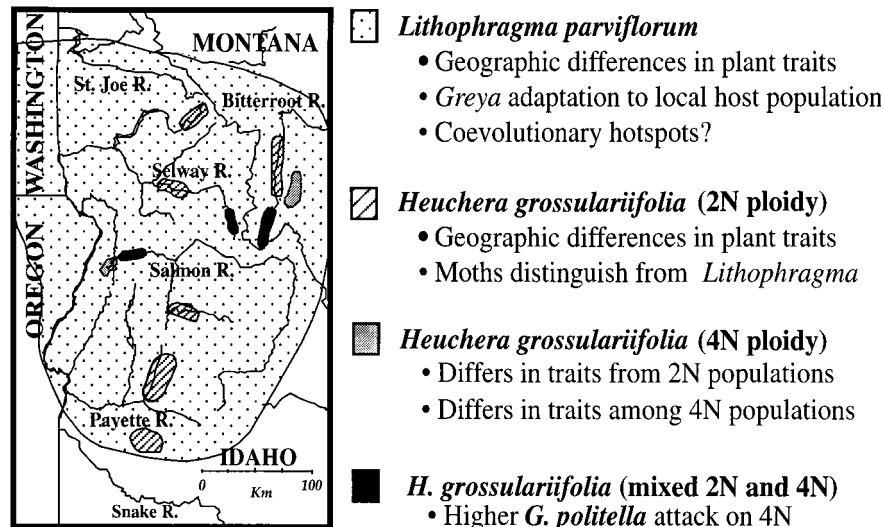
Figure 2: Part of the geographic mosaic of the interaction between *Greya politella* and its host plants in populations within and surrounding the wilderness core of Idaho. Studies documenting patterns shown in the figure are cited in the text.

them or in their phenotypic expression. See, for example, Kraaijeveld and Godfray (1999, in this issue) and Lively (1999, in this issue).

Third, some coevolved traits of an interaction are maintained only or primarily through connections among populations. See Burdon and Thrall (1999, in this issue).

Fourth, the coevolutionary trajectory of an interaction differs across the communities in which the interaction occurs. There are hot spots amid cold spots or differences among populations in the intensity of selection on coevolved traits. See Benkman (1999, in this issue).

Finally, gene flow among populations creates some local mismatches and maladaptation in a coevolved interaction; gene flow prevents (or swamps) local coevolution in some local communities. See Benkman (1999, in this issue), Burdon and Thrall (1999, in this issue), Lively (1999, in this issue), and Parker (1999, in this issue).

The Geographic Mosaic of *Greya/Lithophragma* Interactions

The interactions between the prodoxid moth *Greya politella* and its host plants show all the components of an interaction that appears to be governed by evolutionary dynamics across broad geographic landscapes. This moth is a close relative of yucca moths and, like some of the yucca moths, pollinates its host plant while ovipositing into the flowers (Thompson and Pellmyr 1992; Pellmyr and Thompson 1996). *Greya politella* has a geographic range that extends from southern British Columbia to southern California and east to the Rocky Mountains. It

has several host plants whose distributions are subsets of the range of *G. politella*. The interaction between *G. politella* and its hosts is being studied as part of a long-term project to analyze the relationships between prodoxid moths and their host plants as a model system for understanding the hierarchical structure and dynamics of coevolution (e.g., Thompson 1987, 1997b; Pellmyr and Thompson 1992; Pellmyr et al. 1996a, 1996b; Thompson et al. 1997). So far, we know that the interaction between *G. politella* and its host plants shows the following components of geographic structure.

First, *G. politella* is a set of genetically differentiated populations forming broad geographic groups, identified through mtDNA analyses: a northwestern group, a Siskiyous group, and a California group. These groups correspond partially, but not completely, to populations that oviposit into two species complexes of *Lithophragma* and a species complex of *Heuchera* (Brown et al. 1997; Thompson 1997b; Thompson et al. 1997). The northern and Siskiyous groups use the *Lithophragma parviflorum* species complex and, in the northern Rockies, some populations of the northern group use *Heuchera* (fig. 2). Within the California group, populations differ in their use of the *L. parviflorum* complex and the *Lithophragma bolanderi* complex.

Second, the two host genera are closely related members of the *Heuchera* group of Saxifragaceae and show considerable geographic differentiation among populations (Soltis et al. 1992; Segraves et al. 1999; R. Kuzoff, unpublished data). The complex geographic differentiation among these plant populations has resulted from multiple causes,

including autopolyploidy, hybridization/introgression, and restricted gene flow across populations at different elevations. This differentiation, in turn, shapes the pattern of host use by *G. politella*. Polyploid *Heuchera grossulariifolia* are more likely to be attacked than diploid plants in all geographic areas in which the interaction has been studied (Thompson et al. 1997). Genetic differentiation perceptible to *G. politella* also occurs in *L. parviflorum*. Moths from Turnbull National Wildlife Refuge in eastern Washington State show local adaptation, preferring their local *L. parviflorum* population to two Idaho populations offered in experimental trials (B. Cunningham and J. N. Thompson, unpublished data).

Third, *G. politella* is an effective pollinator of at least *L. parviflorum* sensu stricto, but its contribution to pollination depends on the local relative abundance of copollinators, especially bombyliid flies (Thompson and Pellmyr 1992; Pellmyr and Thompson 1996). Hence, the interaction has the potential to vary among communities from mutualism through commensalism to antagonism, depending on community context, which includes the presence of copollinators, presence of the alternative *Heuchera* host in some populations, and the matching and mismatching of *Greya* and *Lithophragma* traits that may result from gene flow among populations across communities. This geographically structured interaction is now being used for a long-term study on whether these kinds of relationships evolve as coevolutionary hot spots amid a matrix of coevolutionary cold spots (fig. 2).

Formal Models of the Geographic Mosaic of Coevolution

The relative importance of each of the three components of the geographic mosaic theory of coevolution undoubtedly varies among interactions. Recent mathematical models are beginning to unravel how the geographic dynamics and local outcomes of coevolution may depend on the relative importance and structure of each of these components. But no model yet incorporates all the components in a full analysis of coevolutionary dynamics. As metapopulation studies and models integrating population dynamics with populations genetics continue to develop (Hastings and Harrison 1994; Hanski and Gilpin 1997; Thrall and Burdon 1997), they are providing some of the conceptual background and modeling tools that are needed for these analyses.

The simplest models of coevolution are those involving gene-for-gene or matching-gene interactions within single, local communities. These models have a long tradition, and their emphasis has been on the conditions that create local genetic equilibria in host and parasite polymorphisms. For example, Leonard's (1997) population genetic models of gene-for-gene coevolution suggest that balanced polymorphisms in host resistance and pathogen virulence can be maintained within local populations under some conditions. Creating separate populations linked by gene flow can increase the rate at which these polymorphisms approach genetic equilibrium, but the equilibrium itself does not rely on spatial structuring. Taken alone, such models would suggest that balanced polymorphisms maintained by frequency-dependent selection within local populations would be sufficient to explain long-term coevolution in gene-for-gene relationships. But Gandon et al.'s (1996) matching-gene model suggests that coevolving interactions with spatial structure have different dynamics and may be more stable over the long term than interactions lacking spatial structure.

Adding ecological population dynamics and some spatial structure to these models can further change the evolutionary outcome. Frank's (1991, 1993, 1997) models have suggested that an understanding of the maintenance of polymorphisms in interactions with spatial structure requires an integrated approach using both population genetics and population dynamics. As we are learning more about the genetic structure of species and the geographic mosaic of interactions, complex geographic structuring is turning out to be more the norm than a special case. Even spatial structuring at very local scales can have important effects on evolutionary and ecological dynamics of coevolving interactions (Hartvigsen and Levin 1997).

Real geographic mosaics may take the shape of anything from a blotchy mix of highly differentiated and juxtaposed populations to smooth gradients of traits and outcomes over geographic ranges. The problem of how the shape and scale of the geographic mosaic affect the dynamics of coevolution will be one of the most important questions to answer in coming years. In some cases, the geographic dynamics may rely heavily on the colonization and extinction dynamics of metapopulations as suggested by several recent models of parasite-host interactions (Antonovics et al. 1997) and coevolving competitors (Roughgarden 1995). In other cases, the dynamics may be built on large-scale geographic gradients. Hochberg and van Baalen (1998) have recently shown that the intensity of coevolution between predators and prey can differ along environmental gradients of prey productivity (i.e., prey birth rate). These gradients of coevolutionary intensity can be further modified by the pattern of gene flow, sometimes creating coevolutionary patterns that vary from the centers to the edges of the geographic ranges of interacting species. Their models predict that the intensity of coevolution (as measured by investment in the interaction) will be greatest in communities of highest prey productivity.

Future models of the geographic mosaic of coevolution will need to incorporate the effects of different configu-

rations of coevolutionary hot spots and cold spots, co-evolution for different traits in different communities, and geographic restructuring of the distribution of traits through gene flow, random genetic drift, founder effects, and local population extinctions and recolonizations.

Specific Forms of the Geographic Mosaic of Coevolution

There are now a number of specific hypotheses about the dynamics of the coevolutionary process (table 2), and we are beginning to learn that different genetic and ecological conditions may result in different coevolutionary dynamics over broad geographic scales. I will highlight here several of these hypotheses to suggest how consideration of the geographic mosaic of coevolution modifies expectations about the coevolutionary process as compared with expectations based solely on local coevolution. In addition, the other articles in this volume address these and some of the other current coevolutionary hypotheses from a geographic mosaic perspective (e.g., Benkman's [1999] analysis of interactions that may involve diversifying coevolution in crossbills and pines, in this issue). For each of the current coevolutionary hypotheses, it will eventually be necessary to evaluate how selection mosaics, coevolutionary hot spots, and geographic remixing of traits act together to shape coevolutionary dynamics.

Gene-for-Gene Coevolution and Polymorphisms

Gene-for-gene coevolution appears to be an important part of the evolution of interactions between plants and pathogens, and it is a major paradigm for research in plant pathology (Thompson and Burdon 1992). Whether gene-for-gene interactions occur between other taxa remains untested, except for a few examples between plants and insects or nematodes under agricultural conditions (e.g., Zantoko and Shukle 1997). Gene-for-gene coevolution is likely to occur in natural populations when interactions between a host and a parasite are governed by major genes for resistance in the host and avirulence in the parasite, when those genes interact in a matching gene-for-gene fashion, and when the parasite population does not have the option of switching to alternative hosts within local communities (see "Coevolutionary Alternation").

Geographic Hypothesis. Gene-for-gene polymorphisms for resistance in the host and avirulence in the parasite are locally transient and are maintained primarily through a combination of local selection, gene flow, and colonization-extinction dynamics among populations.

Local Hypothesis. Polymorphisms for resistance in the host and avirulence in the parasite are locally stable and are maintained through frequency-dependent selection and/or density-dependent selection.

Comments. It is likely that, even if a gene-for-gene interaction is maintained primarily through metapopulation or broader geographic dynamics, local frequency-dependent selection will occur. The question is whether frequency-dependent selection—perhaps together with

Table 2: Current specific hypotheses on the coevolutionary process

Form of interaction	Current specific hypotheses
Antagonistic trophic interactions	Coevolutionary arms races (more is better)
	Gene-for-gene polymorphisms (rare genotype advantage)
	Parasite-maintained sexual reproduction (rare genotype advantage)
	Coevolutionary alternation (exploitation of undefended diversity)
Competition and coevolutionary divergence	Competitive character displacement
	Coevolutionary turnover
Mutualism and coevolutionary convergence	Müllerian mimicry
	Mutualistic spread to include new taxa
Coevolution and speciation	Diversifying coevolution (antagonistic and mutualistic)[a]
	Escape-and-radiate coevolution

Note: Updated from Thompson (1994). See text for details on interpretation of the hypotheses from a geographic perspective.

[a] Several versions in which populations of a species evolve to specialize (often on different species) as a result of reciprocal local adaptation, and hybrids among the specialist populations are at a selective disadvantage, thereby favoring reproductive isolating mechanism (i.e., reinforcement).

density-dependent selection—is sufficient to maintain locally coevolved gene-for-gene polymorphisms.

Recent studies of the molecular biology of gene-for-gene relationships have further helped to clarify how these interactions work biochemically (Scofield et al. 1996; Baker et al. 1997), thereby lessening past criticisms that such simple genetic coevolutionary relationships are unlikely within natural populations. Nevertheless, gene-for-gene relationships are likely to be only one component of coevolution between plants and pathogens. The "resistance" and "avirulence" genes of gene-for-gene interactions appear to be mostly involved in recognition of attack (plants) and escape from recognition (pathogen). Once a plant has recognized the presence of a particular pathogen through its gene-for-gene system, then it can enlist its polygenic arsenal of other defense genes.

Among the still unanswered questions are the conditions under which coevolution through major genes rather than polygenes is favored and how the genetics of coevolution affect the ecological dynamics of coevolving species (Thompson 1994). Burdon et al. (1996) have argued that gene-for-gene interactions (or at least race-specific resistance genes against pathogens) should be favored especially where substantial reduction in pathogen populations commonly occur and local extinctions of the pathogen are frequent.

Field Evidence. The best current evidence comes from Burdon's long-term study of the dynamics of allelic frequencies of resistance and avirulence within and among natural populations of Australian wild flax, *Linum marginale,* and flax rust, *Melampsora lini* (Burdon 1997; Burdon and Thrall 1999, in this issue). The results suggest that a metapopulation or broader geographic structure may be essential for maintaining these coevolving polymorphisms in the plants and in the rust. Related studies (see Burdon and Thrall 1999, in this issue) providing evidence for the importance of geographic structuring in plant-pathogen interactions in natural communities include analyses of *Avena* and *Puccinia* species (Burdon et al. 1983; Oates et al. 1983), *Silene vulgaris* and *Erysiphe fischeri* in Britain (Clarke 1997), *S. vulgaris* and *Ustilago violacea* in North America (Antonovics et al. 1994, 1997; Thrall and Antonovics 1995), and *Filipendula ulmaria* and *Triphragmium ulmariae* (Burdon et al. 1995).

In addition to gene-for-gene coevolution, evidence is increasing that geographic differences in other polymorphisms are maintained by the geographic mosaic of coevolution. Potential examples include the geographic structure of major histocompatibility complex polymorphisms in humans, including the geographic dynamics of coevolution between humans and malaria-causing *Plasmodium* (Gilbert et al. 1998).

Coevolutionary Alternation

If parasites can alternate among a range of potential hosts, then the coevolutionary options widen. Using the interactions between avian brood parasites and their hosts, Davies and Brooke (1989a, 1989b) were the first to suggest that the proportion of brood parasites preferring a particular host may oscillate over time as the most commonly used avian hosts evolve increased defenses and uncommonly used hosts evolve decreased defenses. Generalizing from their hypothesis, we may find that coevolutionary alternation is a potentially powerful hypothesis for understanding how parasites (and possibly some predators and grazers) coevolve with a number of hosts or prey over long periods of evolutionary time and over broad spatial scales (Thompson 1994).

Assumptions. Parasite populations are specialized to particular host species and are able to evolve preferences for new host taxa through frequency-dependent selection as the defenses of their current host(s) increase.

Geographic Hypothesis. Predators, grazers, and parasites alternate locally and geographically among victim species, as natural selection favors individuals that preferentially attack the least well-defended species among the array of potential victims. Reciprocal evolution between one parasite (or grazer or predator) species and a group of victim species proceeds as the parasite population alternates among host species over evolutionary time. Alternation results because populations of the currently attacked victim species evolve greater defenses, while populations of the currently unattacked victim species lose these defenses. The process proceeds through local alternation among hosts and changes in the geographic range of the parasite species as it fares better on poorly defended populations of its various host species.

Local Hypothesis. This hypothesis is like the geographic one, but the process occurs through alternation driven only by frequency-dependent selection at the local level.

An Additional Twist: Coevolutionary Alternation Coupled to Escalating Defenses and Counterdefenses. Coevolutionary alternation may sometimes also lead to escalating levels of defense and counterdefense. Coevolutionary alternation involves evolutionary time lags in defense and enemy switching. Recently abandoned hosts will exhibit high defenses because selection has not yet shifted the population mean to low levels of defense. Recently acquired hosts will have low defenses, because selection has not yet had the time to act. If the enemy alternates among hosts/prey at a rate slower than the time lag, then coevolution may proceed simply as coevolutionary alternation. But if the enemy switches quickly as the current host defenses rise above the mean of other hosts but before old hosts have fully relaxed their defenses, then the whole process may

escalate. Defenses in all the hosts will ratchet up over time to higher levels of defense, pulling the enemy in turn to higher levels of counterdefense.

Field Evidence. Davies and Brooke (1989*b*) provided convincing evidence that cuckoos, *Cuculus canorus,* in England may be coevolving with a group of host species through coevolutionary alternation. Moreover, host species of common cuckoos and great spotted cuckoos show evidence of geographic differences in their defenses against cuckoo attack, which suggests that geographic structuring may be important in the coevolutionary dynamics of these interactions (Davies and Brooke 1989*a*; Soler and Møller1990). There is debate over the rate at which some of these geographic differences can evolve (Lotem and Rothstein 1995), and similar interactions between cowbirds and hosts do not show much evidence of geographic structuring (Rothstein 1975). However, the overall results for cuckoos and their hosts suggest that geographic coevolutionary alternation may be an important part of the dynamics of these relationships.

Many other interactions between parasites and hosts show strong geographic differences in parasite preference for particular host species and host defense (Price 1980; Jaenike 1990; Thompson 1994, 1998*b*; Kraaijeveld and van Alphen 1995; Singer and Thomas 1996). There are many potential reasons for these differences besides coevolutionary alternation, including geographic differences in availability of hosts, competitive displacement, and enemy-free space. Analysis of coevolutionary alternation as one of the working hypotheses for these geographic differences will require, as a first step, evaluation of differences among communities in the relative levels of defense among potential host species.

Coevolution and Sex

Evidence is increasing that sexual reproduction in some species is maintained at least to some degree through coevolution with parasites (Ebert and Hamilton 1996; Lively 1996). One of the major unresolved problems is how geographic structuring affects selection for sexual reproduction. Is selection for sex greatest when there is complete geographic panmixia in the interacting species, very tight local coadaptation of parasites and hosts, or a geographic mosaic of local adaptation coupled with gene flow?

The basic argument of the Red Queen hypothesis is that parasites rapidly evolve to exploit common host genotypes and that sexual reproduction is a means for a host female to produce offspring with rare genotypes that are less likely to be parasitized (Hamilton et al. 1990; Clay and Kover 1996; Lively 1996). But locally coevolving interactions may not always fuel ongoing Red Queen coevolutionary dynamics. Purely local coadaptation of parasites and hosts may exhaust the genetic variation within parasite populations, if selection is time lagged. Parasite alleles maintained by frequency dependence may become fixed or lost during these time lags (Hamilton et al. 1990; May and Anderson 1990; Dybdahl and Lively 1996). Extreme local parasite adaptation, in which parasites become adapted to host individuals and are vertically transmitted to the host's offspring, may even favor parasites that prevent host sexual reproduction in favor of asexual reproduction. Clay and Kover (1996) dubbed this possibility the Red Queen–captured hypothesis. In addition, purely local coadaptation of parasites and hosts may select for the evolution of tolerance in hosts rather then sexual reproduction, especially if high levels of inbreeding in hosts and low local clonal diversity in parasites together lessen the potential range of local genetic diversity. Hence, it is not clear that extreme local coadaptation of parasites and hosts routinely creates the conditions most likely to favor ongoing Red Queen dynamics.

Geographic structuring of parasite and host populations coupled with moderate gene flow among communities may enhance or otherwise alter Red Queen dynamics over what would occur within isolated local populations. The problem is to understand the interplay between the effects of local parasite adaptation at different spatial scales, the mode of parasite transmission and host density—which affects selection on virulence (May and Anderson 1990)—and relative gene flow of parasite and host populations.

Geographic Hypothesis. Local adaptation of parasites to their host populations coupled with moderate gene flow enhances selection for sexual reproduction in hosts over that observed in interactions in which parasites are either not locally adapted or tightly coadapted.

Local Hypothesis. The coevolutionary dynamics of parasite adaptation and sexual reproduction in hosts do not rely on the geographic structure of interactions.

Field Evidence. Evidence for adaptation of parasites to their local host populations continues to accumulate (Ebert 1994; Lively and Jokela 1996), as does evidence of adaptation of parasite demes even to single long-lived hosts (Mopper 1996). Lively's (1999, in this issue) work on interactions between *Potamopyrgus* snails and trematodes in New Zealand is currently the best evidence from natural communities showing coevolution involving local adaptation in parasites and selection for sexual reproduction in hosts. Those studies have not addressed whether locally adapted parasites place stronger selection on hosts than more panmictic parasites, but the complex geographic structuring of these interactions offers the potential for addressing these questions.

Competitive Character Displacement and Coevolutionary Turnover

Character displacement is an inherently geographic hypothesis, because it involves differences in traits found in allopatric and sympatric populations of the interacting species. After several decades of debate, there is now a clear set of criteria by which to evaluate whether local competitive character displacement has occurred in a particular interaction (Grant 1994; Schluter 1994). Specific hypotheses on character displacement, however, differ in the extent to which the ongoing dynamics of coevolution rely on gene flow among populations.

Competitive Character Displacement. Sympatric populations of two or more species that compete for the same resources differ phenotypically from allopatric populations as a result of selection driven by interspecific competition.

Coevolutionary Turnover. Asymmetrical competition among groups of species on archipelagoes creates repeated cycles of invasion, local coevolution and competitive exclusion of the resident population, subsequent evolution of the invader in the absence of competitors, and reinvasion by other populations of these species (Roughgarden and Pacala 1989; Roughgarden 1995).

Field Evidence. Examples of character displacement are proliferating (see, e.g., Armbruster et al. 1994; Dayan and Simberloff 1994; Schluter 1996; Radtkey et al. 1997; and references therein). But it remains difficult in cases involving sister species to determine the extent to which displacement of traits is due to competitive rather than reproductive character displacement. In contrast to local character displacement, the hypothesis of coevolutionary turnover has been evaluated in depth for only one set of interactions—*Anolis* lizards in the Lesser Antilles—and the interpretation of the processes producing the geographic patterns is still under debate (Losos 1994; Roughgarden 1995; Miles and Dunham 1996).

Mutualistic versus Antagonistic Interactions

How—and whether—the geographic mosaic of coevolution differs between mutualistic and antagonistic interactions still requires careful formulation, modeling, experimentation, and analyses of natural populations. Some mutualisms tend to spread within and among communities as they collect new species into the interaction, leading to coevolutionary dynamics that can differ from antagonistic relationships (Thompson 1982, 1994). The studies of Parker and his colleagues (e.g., Wilkinson et al. 1996; Parker 1999, in this issue) on the geographically structured symbiotic mutualisms between the legume *Amphicarpea bracteata* and its nitrogen-fixing root bacteria *Bradyrhizobium* species suggest that some of these kinds

of mutualism evolve toward less population-level and species-level specialization than commonly occurs in antagonistic relationships. Hence, one potential hypothesis is that antagonistic interactions are more likely than mutualisms to show a strong geographic mosaic in traits and outcomes, because at least one of the species is always evolving to minimize the interaction. Natural selection on antagonistic interactions may more commonly act to cause populations to diverge from one another than in mutualistic interactions. Nevertheless, selection on mutualisms may at least sometimes produce geographic mosaics. Parker's (1999, in this issue) models suggest that symbiotic mutualisms can favor geographic structuring through positive frequency dependence. Different populations become fixed for different traits through historical artifact as differences in initial gene frequencies among communities are followed by positive frequency-dependent selection for the most common local genotypes.

Field Evidence. One way of approaching the problem of how the geographic dynamics of coevolution may differ between antagonistic and mutualistic interactions is through two kinds of analysis. One is the analysis of the geographic structure of coevolution in relationships that vary among communities from antagonism to mutualism. The interactions between the pollinating floral parasite *Greya politella* and its host plants are currently being analyzed toward that end by studying the structure and outcome of the relationship across multiple communities (Thompson 1997b; Thompson et al. 1997). The other is analysis of interactions in which related species differ in the outcomes of an interaction. The interactions between yuccas and cheater yucca moths as compared with true yucca moths (Pellmyr et al. 1996b) hold promise for comparing the geographic mosaic of these antagonistic and mutualistic relationships.

Coevolution, Local Adaptation, and Maladaptation

Three of the most important outcomes of the geographic mosaic of coevolution are that it may allow the evolutionary persistence of interactions that would otherwise become extinct, it may fuel the diversification of taxa, and it may routinely produce local, transient mismatches of traits or maladaptation. It all depends on how the three components of the process—selection mosaics, coevolutionary hot spots, and trait remixing among populations—interact with one another. Gene flow between coevolutionary hot spots and cold spots, or between communities in which different coevolved traits are favored, could swamp local selection. Similarly, differences in the geographic structure of the interacting species could create a local mosaic of communities in which interacting

species are well matched or mismatched in their coevolving traits.

Several of the articles in this volume suggest examples in which such local, sometimes transient, maladaptation may occur. Other recently studied interactions offer potential for similar kinds of analysis. The nematode *Howardula aoronymphium,* which is parasitic on several *Drosophila* species, exhibits suboptimal levels of virulence on some hosts as a result of its population structure (Jaenike 1996). The nematode populations on the different hosts are not genetically isolated from one another at the local scale, and gene flow appears to be responsible for maintaining these suboptimal levels of virulence. The structure of virulence over the geographic range of *H. aoronymphium* and the reciprocal effects on adaptation in the *Drosophila* species have not yet been studied, but this interaction offers good potential for a detailed analysis of the relationship between the geographic mosaic of coevolution and local maladaptation in interacting species.

Conclusions

The developing focus on the geographic mosaic of coevolution is part of an overall sea change in ecology, evolutionary biology, conservation biology, and epidemiology that has been developing in recent decades. Although space and time have always been central variables, questions of hierarchy and scale are now coming to dominate discussions about ecological and evolutionary processes. Which processes dominate at which scales? How do the different levels in the hierarchy of life interact to shape and reshape the organization and dynamics of biodiversity? Biogeographic questions in ecology are coming back into their own again, this time with more powerful approaches than 20 yr ago (e.g., Ricklefs and Schluter 1993; Brown 1995; Rosenzweig 1995). Moreover, evolutionary biology is increasingly concerned with the interrelationship of processes at different hierarchical scales: molecular through organismal evolution, coordination of the genetics of interacting species through coevolution, and links between microevolutionary and macroevolutionary processes (e.g., Maynard Smith and Szathmary 1995). All these major ecological and evolutionary concerns come together in the study of the ongoing geographic dynamics of coevolution and its effects on the organization of biodiversity. In addition, because many geographic aspects of coevolution have major implications for human epidemiology, biological control, agriculture, and conservation, these studies are likely to lead evolutionary ecology into a period in which it becomes one of the most central of applied biological sciences (Thompson 1996, 1997*a*, 1998*a*).

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