

The Coevolving Web of Life

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ABSTRACT: Coevolution—reciprocal evolutionary change in interacting species—is one of the central biological processes organizing the web of life, and most species are involved in one or more coevolved interactions. We have learned in recent years that coevolution is a highly dynamic process that continually reshapes interactions among species across ecosystems, creating geographic mosaics over timescales sometimes as short as thousands or even hundreds of years. If we take that as our starting point, what should we now be asking about the coevolutionary process? Here I suggest five major questions that we need to answer if we are to understand how coevolution shapes the web of life. How evolutionarily dynamic is specialization to other species, and what is the role of coevolutionary alternation in driving those dynamics? Does the geographic mosaic of coevolution shape adaptation in fundamentally different ways in different forms of interaction? How does the geographic mosaic of coevolution shape speciation? How does the structure of reciprocal selection change during the assembly of large webs of interacting species? How important are genomic events such as whole-genome duplication (i.e., polyploidy) and whole-genome capture (i.e., hybridization) in generating novel webs of interacting species? I end by suggesting four points about coevolution that we should tell every new student or researcher in biology.

Keywords: multispecific coevolution, coevolutionary alternation, geographic mosaic, interaction networks, mutualism, specialization.

Introduction

Everything we have learned about the diversity of life over the 150 years since the publication of Darwin's *On the Origin of Species* suggests that populations continually evolve and interacting species continually coevolve. The problem to solve is not the question of what permits evolution and coevolution but rather what limits relentless directional evolution and coevolution. The failure to apply that perspective consistently to all major research ques-

tions about organisms, populations, and communities has prevented the full conceptual unification of the biological sciences. Here I explore one part of what we need to reach that unification. If we take as our starting point that natural selection continually reshapes the web of interacting species, how does that influence the questions we should be asking about the coevolutionary process?

The Ubiquitous Potential for Evolution and Coevolution

Consider what we know. When we have looked for heritable genetic variation within species for traits potentially important to Darwinian fitness, we have often found evidence for it (Visscher et al. 2008). When we have looked at multiple populations of the same species, we have found evidence for genetic differences among populations in molecular markers and in traits involved in local adaptation (e.g., Thrall et al. 2002; Laine 2005; Sotka 2005; Nash et al. 2008; Toju 2008). When we have looked for phenotypic selection acting on populations, we have often found evidence for it (Hoekstra et al. 2001; Kingsolver et al. 2001; Hereford et al. 2004; Carroll et al. 2007). When we have looked deeper for evidence of rapid evolution following phenotypic selection, we have often found it (Endler 1986; Grant 1986; Thompson 1998a; Hendry and Kinnison 1999; Grant and Grant 2008), even over timescales of just a few decades or hundreds of years (Phillips and Shine 2006; Singer et al. 2008; Zangerl et al. 2008). When we have carefully studied interactions among species from the perspective of all participants, we have often found evidence of reciprocal selection (Thompson 2005; Benkman et al. 2008; Hanifin et al. 2008; Toju 2008). Hence, even though we know that natural selection does not reshape every population of every species in every generation, we now know from the accumulating body of careful research over the past 150 years that the potential for ongoing evolutionary change is high in most populations. The genetic structure of most species is therefore likely altered every

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generation through evolutionary change, in at least some populations.

It is therefore no longer tenable to study population ecology and community ecology devoid of attention to ongoing, and sometimes rapid, evolution. That does not mean that every aspect of the dynamics of populations and communities is driven by ongoing evolution. But given what we now know, rapid evolution and coevolution must be one of our working hypotheses for explaining even short-term patterns and processes in the ever-changing web of life. There is no reason to think that the rapid evolutionary changes found in Darwin's finches, some invasive plants and insects, and microbes in laboratory microcosms are in any way exceptions. We do not lack for examples of rapid evolution in nature, and we would have many more examples if more research programs incorporated the analysis of potential rapid evolution in their observational and experimental designs.

Evolutionary studies are therefore not something that can be added on later once the molecular, physiological, and ecological mechanisms are well understood. Evolutionary processes contribute to the structure of variation at every temporal and spatial scale that is relevant to answering the major questions on the organization of biodiversity. Almost every widespread species that has been studied in detail shows a geographic pattern of genetic differentiation (Avice 2000). We therefore need to know much better than we do now how evolutionary processes contribute to the structure and dynamics of metapopulations and communities (Saccheri and Hanski 2006; Urban and Skelly 2006; Fussman et al. 2007; Kinnison and Hairston 2007; Loeuille and Leibold 2008) and how rapid evolution and coevolution continually reshape the web of life. Taken alone, ecological theory developed in the absence of evolutionary theory cannot explain why life is so ecologically diverse and why it is organized into complex, constantly changing, multitrophic webs of interaction.

Encouragingly, ecological theories of population and community dynamics are incorporating genetic structure and evolutionary change. Some approaches to island biogeographic theory have incorporated speciation as part of the process (Losos and Schluter 2000; Mayr and Diamond 2001). Hubbell's (2001, 2005) neutral theory incorporates variable selection and speciation as components of the evolution of functional equivalence among plant species. And studies of metapopulation dynamics are increasingly incorporating analysis of genetic variation and rapid evolution (Hanski and Gilpin 1997; Hanski and Saccheri 2006). Similarly, some approaches to community ecology, under designations such as community or landscape genetics, have begun to ask more explicitly how the genetic structure of populations shapes the structure of food webs within communities (Whitham et al. 2003; Bangert et al.

2006) and how landscapes shape population genetic structure (Holderegger and Wagner 2008). The geographic mosaic theory of coevolution provides a bridge among these various approaches, linking the dynamics of adaptation and coadaptation among interacting species within local communities to the diversification of those interactions across complex landscapes (Thompson 1994, 2005).

These are all ways of exploring how ecological and evolutionary processes together shape the web of life. They are, though, just the beginning of what needs to be a renaissance in combining ecological and evolutionary theory. We need to go much further and deeper to answer the central questions about the diversity of life. Why are there millions of species rather than one? Why do species look so different from each other? And why are there so many ways of making a living? There are three possible answers to these questions. Physical environments are highly variable across space and time. Nature is relentlessly tooth-and-claw, continuing reshaping the evolution of antagonistic interactions within and among species. Or, species inherently form intraspecific and interspecific partnerships that are often commensalistic or mutualistic and allow diversification into new adaptive zones.

Undoubtedly, all three answers are correct, and so we need to understand how these selective forces interact to create diversity. We simply do not know. Ecophysicists and community ecologists in the early twentieth century were impressed with the role of the physical environment in shaping communities. Later ecologists became impressed with the role of competition, then predation, and, more recently, parasitism and mutualism. Yet other biologists have become equally impressed with the roles of sexual selection and mating structure in shaping the diversification of populations and interactions within and among species. But we still really do not know which of these components of life are the major drivers of diversification and the major shapers of the overall web of life.

Paleobiologists have increasingly provided us with a clearer view of the long-term context of the ecological interactions we observe today. What does local stability mean when the populations we study were located somewhere else 15,000 years ago? What does species sorting mean within ecological communities when we are combining and recombining species that have been around for millions of years with those that have been around for 20,000 years? Paleobiology has shown us that much of evolutionary change is a sloshing bucket, to use Niles Eldredge's (2003) analogy, moving species back and forth over time. Evolution is ongoing, with some taxa showing evidence of change at any moment in evolutionary history even as others show evidence of stasis for long periods of time. Jablonski (2008) has argued that there are mismatches in the patterns of interaction among species that

we observe at different spatial scales and taxonomic levels and in the processes that we invoke to explain those patterns, but we still do not truly understand the reasons for these mismatches.

In general, we need to get the temporal and spatial scaling of ecological and evolutionary processes sorted out properly. We need to understand why the web of life is so dynamic in some respects and so static in other respects, and why there are patterns in the organization of the web of life amid continual extinction, adaptation, and speciation.

Five Questions on Coevolution and the Web of Life

We now know that at least some of the ecological patterns found in the web of life are shaped by coevolution among species. Extrapolating from studies completed during the past several decades, I think that more of the organization of the web of life is shaped by coevolution than we currently realize. We need to know, however, much more precisely how ongoing coevolution contributes to the diversification and continual reassembly of the web of life.

I will consider five unanswered questions. Before I start, I want to say that these are big questions and they are hard questions, but we should not be afraid to ask them. Without deepening our understanding of how selection and reciprocal selection weave species together as they adapt and diversify, we cannot understand how the web of life itself has evolved and coevolved. The questions I raise here go beyond the evolution or coevolution of morphological or physiological traits. Much coevolutionary research focuses on trait evolution, and justifiably so. That approach, though, is only the beginning, if we are to develop a truly ecological theory of coevolution that helps us understand how natural selection organizes the web of life. The major unanswered questions involve problems in the evolution of specialization, geographic structure, and the assembly of webs of interacting species.

Question 1: How Evolutionarily Dynamic Is Specialization to Other Species, and What Is the Role of Coevolutionary Alternation in Driving Those Dynamics?

Many species interact with multiple other species. That observation held back coevolutionary biology for many years, as some researchers argued that coevolution between any two species would rarely occur because selection would be too “diffuse” among all the interacting species. Such views implicitly assume that species cannot evolve specialized adaptations to cope with multiple, and very different, selective pressures. Yet no evolutionary biologist would argue that a population cannot evolve specific adaptations to, say, temperature while evolving specific ad-

aptations to parasites or predators. Similarly, there is no biological reason why species cannot coevolve simultaneously with multiple other species.

We therefore need more sophisticated ways of understanding how reciprocal selection shapes webs of interaction. The first step is to understand better how coevolution shapes the relative degrees of specialization of species to one another. Although many species can behaviorally adjust their interactions with other species under different ecological conditions, we also now know that natural selection can alter the relative degree to which species are genetically specialized to interact with other species. For example, swallowtail butterflies in the *Papilio machaon* group differ in their relative preferences for plant species when laying their eggs. These differences occur not only among species but also among populations and among maternal families within populations (Wiklund 1981; Thompson 1988, 1998b). The major differences in host choice are governed by sex-linked genes, and the differences in larval performance on different hosts appear to be governed by autosomal genes (Thompson et al. 1990; Thompson 2008). The result is an almost continuous gradient within this clade of species in their relative preferences for potential host species (fig. 1).

This kind of genetically based variation in specialization within and among closely related species is probably not unusual. In fact, the degree of specialization in preference or defense is turning out to be much more dynamic than we previously thought. There are now well-studied examples of population differences in prey use by vertebrates (Arnold 1981; Ghedin et al. 2005; Smith and Benkman 2007), variation in prey choice by marine invertebrates (Sanford et al. 2003; Sotka et al. 2003), variation in specificity in interactions between plants and fungi (Shefferson et al. 2007), and variation in preference and specialization in insect and microbial species (Janz 2003; Nylin et al. 2005; Tanaka et al. 2007; Thrall et al. 2007; Abrahamson and Blair 2008; Feder and Forbes 2008; Scriber et al. 2008; Singer et al. 2008). Other studies have shown rapid evolution of specialized defenses (Cousyn et al. 2001; O’Steen et al. 2002; Duncan et al. 2006; Losos et al. 2006), in some cases in the same interactions in which rapid evolution of the predators or parasites has been studied (e.g., Berenbaum and Zangerl 1998; Lively and Dybdahl 2000; Jokela et al. 2003; Zangerl and Berenbaum 2005). Moreover, microcosm studies of coevolution have shown that some parasitoids or parasites are able to evolutionarily track changes in defenses of their hosts, and hosts can respond rapidly in their defenses, although most of these experiments so far have involved pairwise coevolution rather than multispecific coevolution (e.g., Forde et al. 2004; Brockhurst et al. 2005; Buckling et al. 2006; Koskella and Lively 2007; Poullain et al. 2007).

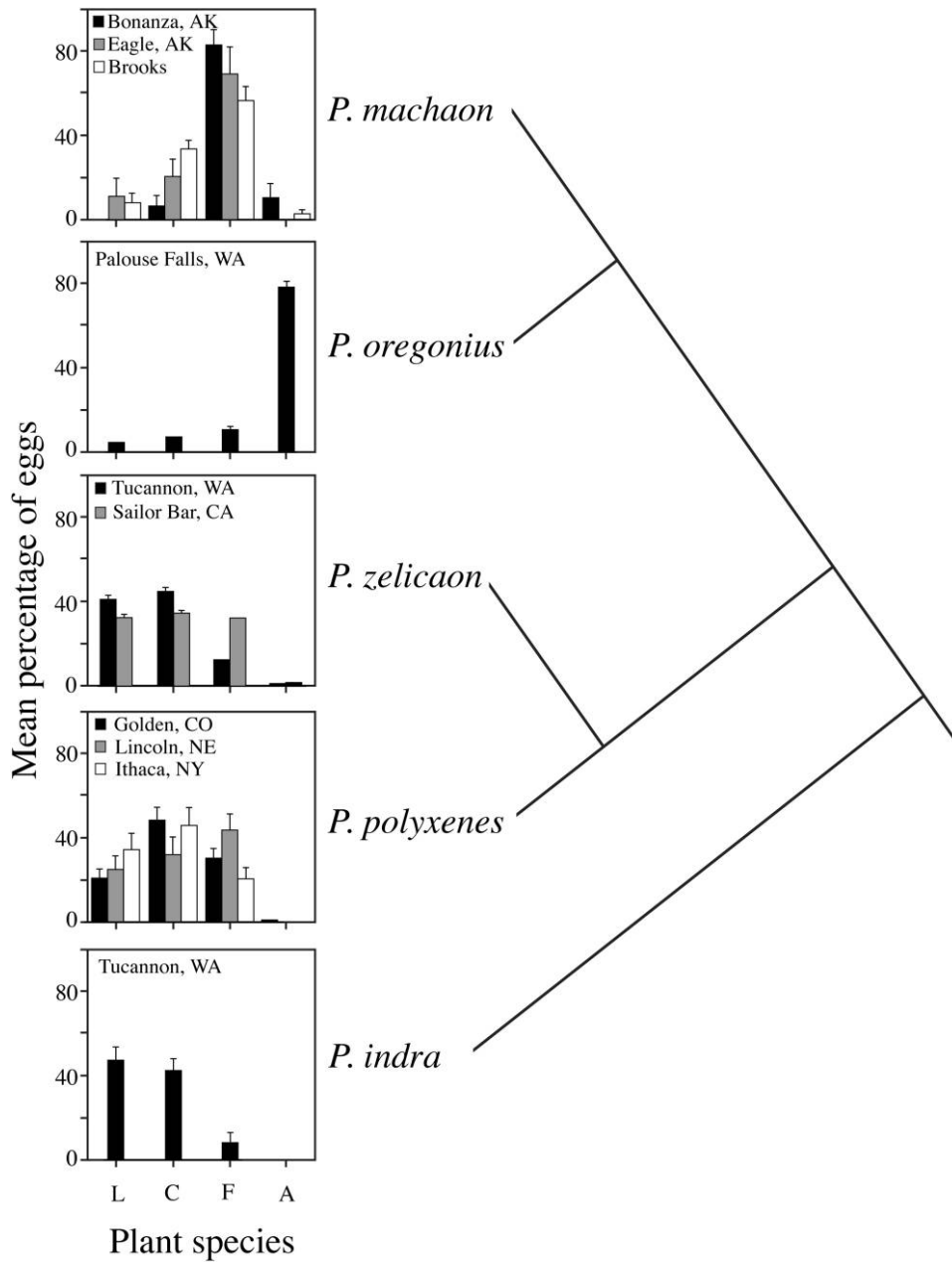


Figure 1: Variation in relative oviposition preference for four plant species within the *Papilio machaon* clade of swallowtail butterflies in North America. The plants include two native species within the Apiaceae (L = *Lomatium grayi* and C = *Cymopterus terebinthinus*), an introduced species within the Apiaceae (F = *Foeniculum vulgare*), and a native species within the Asteraceae (A = *Artemisia dracuncululus*). Populations differing significantly in preferences are shown for three species. Compiled from Thompson (1993, 1998b, 2008) and Wehling and Thompson (1997).

Ongoing natural selection on the relative preferences of predators and parasites and on defense levels in prey and hosts is therefore likely to be one of the keys to understanding how coevolution shapes webs, rather than just pairs, of interacting species. If specialization evolves through evolution of preference hierarchies, then webs of

interacting predators and prey, or parasites and hosts, may coevolve through the process of coevolutionary alternation (Davies and Brooke 1989; Thompson 1994; Nuismer and Thompson 2006). As natural selection favors escalation of defenses in the most commonly attacked prey species, selection will, in turn, favor predators that preferentially

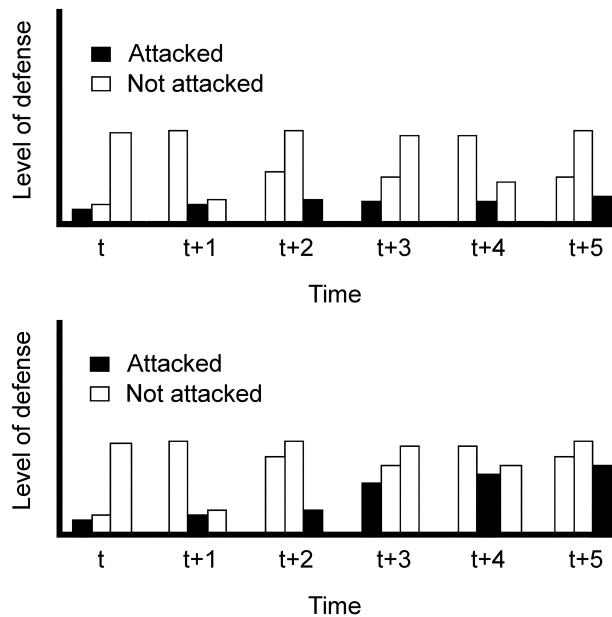


Figure 2: Representation of coevolutionary alternation in a predator-prey interaction or parasite-host interaction. The bars represent the relative levels of defense in each of three prey species at six points in time. Natural selection favors predators that attack relatively undefended prey species, and it favors prey that increase their defenses when they are heavily attacked and decrease their defenses when they are rarely attacked. The top panel shows coevolutionary alternation without escalation in defenses over time, because unattacked prey species evolve reduced levels of defense during periods when they are unattacked faster than predators evolve to preferentially attack relatively undefended prey species. The bottom panel shows coevolutionary alternation with an overall escalation in the defenses after the first two time periods, because selection on predators to change their relative preferences for prey species evolves faster than the rate of relaxation of prey defenses during periods when they are unattacked. Modified from Thompson (2005).

attack less-defended species. If defenses are costly, selection will favor decreased defenses in prey species that are no longer the major target of attack, thereby altering the relative defenses among prey species yet again.

Over time, then, predator populations will continue to evolve in their relative preferences among prey species, and prey populations will continue to evolve in their relative defenses. As the process continues, the degree to which a predator population is specialized to a particular prey species will vary over time. As prey species also continue to evolve in their defenses, the result will be coevolutionary alternation with or without overall escalation in prey defenses over time (fig. 2). Escalation will occur if preferences in the predator populations evolve faster than lowered defenses evolve in prey that currently are attacked rarely. Recent mathematical models suggest that coevolutionary alternation is possible under a wide range of

biologically realistic conditions, producing rapid and repeated shifts in patterns of specialization in a predator population that interacts with multiple prey species (Nuismer and Thompson 2006).

Coevolutionary alternation may therefore provide a specific mechanism by which reciprocal selection shapes the evolution of preferences and suites of defenses within webs of interacting antagonistic species, such as those involving the great diversity of thick-shelled marine invertebrates and their shell-crushing predators. Some empirical studies have, in fact, shown patterns of preferences and defenses that are consistent with the process of coevolutionary alternation. These include the geographically variable interactions between European cuckoos and their hosts (Davies and Brooke 1989; Soler et al. 1999; Martin-Gálvez et al. 2007) and the chemically and geographically complex interactions between European large blue butterflies and ants (Nash et al. 2008).

Coevolutionary alternation is just one specific way in which the evolution of relative degrees of specialization may shape the web of interacting species rather than just pairs of species. It shows, however, that it is possible to develop specific, testable hypotheses on multispecific coevolution.

Question 2: Does the Geographic Mosaic of Coevolution Shape Adaptation in Fundamentally Different Ways in Different Forms of Interaction?

If we take as given that species are often collections of genetically distinct populations and that selection often differs among populations in different environments, then interactions among species are bound to vary among environments. The geographic mosaic theory of coevolution was developed in an attempt to formalize the components of variation in evolving interactions and build a more ecologically realistic theory of the coevolutionary process (Thompson 1994, 2005). The goal has been to incorporate the minimum additional complexity beyond panmictic models needed to capture the ecological and genetic structure and dynamics of real interactions. More broadly, geographic mosaic theory attempts to explain why evolving interactions can be highly dynamic yet sometimes persist for millions of years.

Geographic mosaic theory hypothesizes that the evolution of interactions among real species is shaped by three components of coevolutionary variation: geographic variation in the structure of selection on an interaction, geographic variation in the strength of reciprocal selection, and geographic variation in the distribution of traits found within interacting species. Variation in the structure of selection takes the form of geographic selection mosaics in which the effect of a genotype in one species on the

genotype of another species differs among environments ($G \times G \times E$ interactions). Variation in the strength of reciprocal selection produces, at one extreme, coevolutionary hotspots that exhibit strong reciprocal selection on interacting species and, at the other extreme, coevolutionary coldspots that exhibit no reciprocal selection. Variation in the distribution of traits across landscapes is further shaped by gene flow, random genetic drift, and metapopulation dynamics, thereby creating an ongoing remixing of coevolving traits across ecosystems.

At its most fundamental level, geographic mosaic theory argues that long-term coevolution in real species is an inherently geographic process. It argues that studies of local (co)adaptation and panmictic models of coevolution cannot fully capture the causes of the structure, evolutionary dynamics, and persistence of real interactions. It is not just the traits of species that shape coevolution; it is also the varying community and ecosystem contexts in which those species occur across their ranges.

Although geographic mosaic theory was developed as a theory about the coevolutionary process and the spatial scales at which it operates, I initially made several general predictions about the patterns likely to result if species were to coevolve as a geographic mosaic (Thompson 1994, 1997, 1999). Those predictions included expectations that interacting species vary across environments in their coevolved traits, that those traits vary geographically in their degree of matching and mismatching, and that few coevolved traits become fixed at the species level. Those predictions were intended to provide a starting point for exploring the implications of the coevolutionary process envisioned by geographic mosaic theory across space and time.

In recent years, our expectations about these patterns have been refined and expanded as mathematical models, laboratory experiments, and field studies have increased our understanding of the coevolutionary process as envisioned by geographic mosaic theory. For example, some recent studies have explored the structure of selection mosaics in cases in which a limited set of genotypes of two species is allowed to interact in different environments (e.g., Nuismer 2006; Gomulkiewicz et al. 2007; Hoeksema and Thompson 2007; Piculell et al. 2008). These analyses have indicated that selection mosaics could shape geographic divergence in evolving interactions even when populations of the interacting species have the same initial distribution of genotypes throughout their geographic ranges. The biology of species in nature, of course, is much richer than that, and no two populations of the same species are ever exactly identical in genetic structure. Hence, studies of selection mosaics in nature will always involve populations that have already diverged to some extent for a variety of reasons. The problem, then, is to

understand the extent to which geographic differences in the structure of selection on interactions alter patterns of divergence across environments, and some new models are beginning to confront that problem (Nuismer and Gandon 2008). Some suggested ways of testing geographic mosaic theory have focused on contemporary selection (Gomulkiewicz et al. 2007), but inferences gained from phylogeographic and phylogenetic analyses and other approaches are equally important (Thompson 2005).

Field studies have suggested that selection mosaics, intermingling of coevolutionary hotspots and coldspots, and trait remixing do indeed create dynamics that differ from the patterns found in earlier panmictic models of coevolution and local studies of coevolution. Those earlier non-geographic studies showed us that there are about seven potential kinds of local coevolutionary change involving pairs or small groups of species: coevolutionary escalation, coevolving polymorphisms, attenuated antagonism, coevolutionary alternation, coevolutionary displacement, coevolutionary complementarity, and coevolutionary convergence (Thompson 2005). Some of these outcomes are specific to particular forms of interaction. Predators and prey can coevolve through various combinations of coevolutionary escalation, coevolving polymorphisms, and coevolutionary alternation. Competitors coevolve through coevolutionary displacement. Mutualisms coevolve through a combination of coevolutionary complementarity and coevolutionary convergence. These local coevolutionary changes, though, are often just the raw materials for the broader coevolutionary dynamics that occur among the interacting species across ecosystems.

Studies of the geographic mosaic of coevolution have shown that these local coevolutionary dynamics become altered in the broader geographic context in which most interacting species coevolve, as suggested by the following eight results:

1. Species interacting in a geographic mosaic may coevolve faster and toward different equilibrium states than under panmictic conditions, at least under some conditions (Brockhurst et al. 2003; Forde et al. 2004, 2007; Lopez-Pascua and Buckling 2008).
2. Species interacting in a geographic mosaic may maintain polymorphisms over a longer term than species interacting only locally (Burdon and Thrall 2000; Kniskern and Rausher 2007).
3. Differences in productivity among communities can create selection mosaics that lead to geographic differences in the levels or dynamics of host resistance, parasite infectivity, or ecological outcomes (Hochberg and van Baalen 1998; Hochberg et al. 2000; Forde et al. 2004, 2007; Lopez-Pascua and Buckling 2008).
4. Geographic differences in the web of interacting species can create selection mosaics (e.g., Benkman 1999;

Thompson and Cunningham 2002; Zangerl and Berenbaum 2003; Piculell et al. 2008). That is, the “environment” in genotype \times genotype \times environment interactions is often the “biotic environment” in which any pairwise interaction occurs.

5. Selection mosaics may occur at even small geographic scales (Laine 2006; Toju 2008).

6. Coevolutionary hotspots may be widely separated geographically and may vary in the degree of asymmetry in the strength of reciprocal selection (Brodie et al. 2002; Hanifin et al. 2008).

7. Local maladaptation may be less likely to occur in geographically structured antagonistic interactions governed by quantitative traits than in interactions governed by major genes (Ridenhour and Nuismer 2007).

8. Differences among populations in the magnitude and sign of local adaptation in interactions coevolving as a geographic mosaic may be determined to a large extent by selection mosaics and intermingled coevolutionary hotspots and coldspots rather than by the balance between gene flow and selection alone (Nuismer 2006).

We need to evaluate the generality of these results on the geographic mosaic of coevolution for multiple forms of interaction: predators and prey as compared with parasites and hosts, symbiotic mutualisms as compared with mutualisms among free-living species, competition as compared with facilitation. We currently do not know if selection mosaics, coevolutionary hotspots and coldspots, and trait remixing produce similar or different dynamics and patterns among all these forms of interaction.

Question 3: How Does the Geographic Mosaic of Coevolution Shape Speciation?

The geographic mosaic of coevolution may fuel not only the ongoing coadaptation of species but also speciation itself. For example, diversifying coevolution has molded the radiation of crossbills in North America and Eurasia as they have adapted to different conifer species and populations (Benkman 2003; Edelaar and Benkman 2006; Smith and Benkman 2007), and multiple taxa have diverged and possibly speciated through coevolutionary displacement, either directly through coevolution with competitors or indirectly through coevolution with other enemies (Schluter 2000). Recent studies of the well-known interactions between figs and fig wasps and between yuccas and yucca moths have shown much more speciation in these interactions than previously suspected (Molbo et al. 2003; Pellmyr et al. 2008), and the complex interactions between these species appear to be responsible for at least part of these remarkable radiations of species. Even larger-scale patterns of diversification, as initially envisioned by Ehrlich and Raven (1964), seem possible now that pale-

ontological data on the age and relative timing of diversification of plants, herbivores, and pollinators has suggested that these interactions have been going on for very long periods of time (Hu et al. 2008; Iannuzzi and Labandeira 2008). In addition, the early stages of speciation driven by diversifying coevolution are being identified in laboratory microcosm studies (Rainey and Travisano 1998; Buckling and Rainey 2002; Brockhurst et al. 2005).

Nevertheless, few models of speciation directly assess the role of coevolution as a driver of speciation, and few major reviews of the speciation process even mention the potential role of coevolution as a major agent of speciation. I think the reason is that many analyses of ecological speciation consider only the focal group (e.g., a genus of plants, insects, or birds) and treat other species as resources that drive divergence but do not undergo reciprocal evolutionary response. Studies of the geographic mosaic of coevolution, however, are beginning to provide the kinds of data needed to assess the role of coevolution as an agent of speciation as well as adaptation.

The links between the geographic mosaic of coevolution and ecological speciation are becoming greater as some studies provide evidence for cryptic speciation in interactions that previously appeared to show simply geographic differences in adaptation. For example, studies of the prodoxid moth species *Greya politella* and its host plants in western North America have indicated that speciation or incipient speciation is occurring at the geographic boundaries of these interactions, where the moths have colonized novel host plants (Thompson et al. 1997; Janz and Thompson 2002). These moths and their host plants are distributed across a wide range of habitats in western North America, and they show more divergence in local specialization and ecological outcomes than we initially expected (Thompson and Pellmyr 1992; Thompson and Cunningham 2002; Thompson et al. 2004). Some of these differences appear to be due to historical factors that have separated populations for long periods of time. Recent phylogeographic studies of these species have shown up to 4% sequence divergence between populations at the edges of the geographic range of the interaction and some other populations (Rich et al. 2008). In addition, some populations at these geographic edges have evolved with novel hosts in ways suggesting that selection during differential coevolution may be driving at least some of the divergence (Thompson et al. 1997; Nuismer and Cunningham 2005; Thompson and Merg 2008).

Specialized cryptic species, or at least highly differentiated populations, are increasingly being discovered within taxa previously considered single species that interact with many other species (Hebert et al. 2004; Nosil and Crespi 2006; Smith et al. 2006; Thompson 2008). The task now is to understand the extent to which species

interactions and the coevolutionary process are driving that divergence through specialization. Such situations must surely be common, because the constantly changing geographic ranges of interacting species provide not only opportunities for new adaptations but also multiple opportunities for restricted gene flow from other populations of the same species (Janz and Nylin 2008). It is therefore likely that we are underestimating how commonly cryptic speciation occurs as species evolve and coevolve across their continually changing geographic ranges. Most of these cryptic species will probably not persist for long, but they are part of the dynamics of evolving interactions and, occasionally, one of them becomes the basis of a new adaptive radiation.

Question 4: How Does the Structure of Reciprocal Selection Change during the Assembly of Large Webs of Interacting Species?

This question follows from questions 1, 2, and 3. If we look at the patterns of specialization between any set of interacting lineages, we often find a distribution ranging from extreme specialists that interact with only one or a few other species to generalists that interact with multiple other species (Jordano et al. 2003; Fenster et al. 2004; Mueller et al. 2005; Bronstein et al. 2006; Waser and Ollerton 2006). This variation in specialization has multiple potential causes: specialization is evolutionarily more dynamic than we have often supposed (see question 1), the geographic mosaic of coevolution creates populations that differ in their degrees of specialization to other species (see question 2), and the geographic mosaic may continually generate new species that differ right from the start in the degree to which they are specific to one or more other species (see question 3).

Consequently, as evolving interactions diversify they are bound to create multispecific networks that vary across ecosystems in the number of interacting species and in the pattern of links among the species. Our current challenge is to develop specific hypotheses on the evolution of multispecific interactions. Coevolutionary alternation in antagonistic interactions (see question 1) is one such hypothesis. Similarly, studies of coevolving mutualisms have begun to focus on the process by which reciprocal evolutionary change may directly favor networks of interacting species (Thompson 1994, 2005; Bascompte and Jordano 2007). In addition, several approaches have begun to provide ways of assessing whether a local pairwise interaction is likely to be shaped primarily by reciprocal selection on that pair or by other species as well (Iwao and Rausher 1997; Gómez and Zamora 2000; Stinchcombe and Rausher 2002; Strauss et al. 2005). That is very different from describing coevolution as diffuse in the sense

of selection being so broadly distributed among the interacting species that the patterns of reciprocal selection cannot be studied and understood. Yet other studies have focused directly on selection mosaics in which a focal pair of species occurs together in different community contexts (Thompson and Cunningham 2002; Siepielski and Benkman 2004; Berenbaum and Zangerl 2006; Parchman and Benkman 2008).

Our goal, then, must be to understand how coevolution shapes the structure of multispecific interactions and how the structure of multispecific webs shapes coevolution. Just as we have been able to identify seven major ways in which pairs or small groups of species coevolve locally and then become altered by the geographic mosaic, we should be able to do the same eventually for coevolution within larger networks of interacting species. To do that, we need answers to some basic questions.

Does the number of species involved in a coevolving interaction vary predictably with the form of interaction? There are “typical” sizes to multiple aspects of intraspecific and interspecific interactions: two sexes (but sometimes with multiple strategies within sexes), trios of morphs in rock-paper-scissors evolutionary games (Sinervo and Calsbeek 2006), and potentially, an optimal number of alleles favored within local populations in response to pathogen attack (Nowak et al. 1992; Thompson 2005). The number of species typically shaping a locally coevolving interaction or structuring the geographic mosaic of a coevolving interaction could vary with the form of interaction, between tropical and temperate environments, or among oceanic and terrestrial environments. We simply do not know because we have not parsed the structure of selection in that way in our studies.

Are keystone predators or mutualists, however defined, the foci of coevolutionary selection within communities, and do coevolving interaction webs exhibit predictable structure while assembling or disassembling? It is clear that some species have disproportionate ecological effects on interaction webs (Brown et al. 2001), but we have little understanding of how some species have evolved to become so. Species such as honeybees and resplendent quetzals, which rely upon the local presence of multiple other mutualistic species, are not even possible as evolutionary products until mutualisms have diversified into multispecific networks. They are, in a sense, “network specialists” in that they have a lifestyle that has evolved to exploit multispecific networks. What, then, are honeybees, quetzals, and figs in a coevolutionary sense?

We therefore need a broader view of how reciprocal selection acts within large webs of interacting species. We must ask how selection on one species affects the evolution of links among species and the traits of species throughout the web and, in turn, how changes in the overall structure

of a web (e.g., through extinction of taxa) affect individual species. This is not a return to diffuse coevolution. It is the opposite. It is a focus on how reciprocal selection acts not only on individual species but also on the larger structure (i.e., topology) of webs of interacting species.

Recent studies of mutualism, for example, have indicated that webs of interaction between free-living mutualists show asymmetries in specialization among interacting species greater than that found in many predator-prey food webs (Bascompte et al. 2003; Jordano et al. 2003; Guimarães et al. 2006; Bascompte and Jordano 2007; Olesen et al. 2007). There is currently considerable debate over the causes and degree of those differences (Vásquez et al. 2007; Okuyama and Holland 2008), but the structure of large mutualistic webs follows from what we know about the structure of coevolutionary selection on mutualisms among free-living species such as those between pollinators or frugivores and plants. In the absence of the coevolutionary chases that are common to predator-prey interactions, a combination of coevolutionary complementarity and convergence often appears to draw other species into the interaction over time, creating a coevolutionary vortex (Thompson 2005, 2006). Hence, mutualisms among free-living species may often inherently coevolve toward formation of multispecific webs, and those webs appear to develop structures that are repeated across ecosystems.

In addition, the structure of mutualistic webs also differs between intimate, symbiotic interactions and those involving free-living species. Symbiotic interactions show, as expected, more evidence of reciprocal specialization (Blüthgen et al. 2007; Guimarães et al. 2007). Some recent models have suggested that these different network structures may have important ramifications for the coevolutionary process (Guimarães et al. 2007). The models predict that coevolution in symbiotic interactions should exhibit frequent reciprocal changes involving few partners, whereas coevolution within networks of free-living mutualists should show rare bursts of change in which many species show a reciprocal response to evolutionary changes in a single species.

These empirical and mathematical results indicate that we should be able to develop a deeper understanding of the role of coevolution in shaping the overall structure of complex networks. Recent approaches to the modular structure of multispecific networks (Olesen et al. 2007) and the phylogenetic structure of assemblages (Webb et al. 2002; Price 2003; Ives and Godfray 2006; Rezende et al. 2007; Kraft et al. 2008) are providing the tools needed to undertake these analyses.

Question 5: How Important Are Genomic Events Such as Whole-Genome Duplication (i.e., Polyploidy) and Whole-Genome Capture (i.e., Hybridization) in Generating Novel Webs of Interacting Species?

Almost all genetic models of coevolution have been devoted to exploring dynamics governed by mutation and selection at a single locus or within a set of loci exhibiting various combinations of additivity, dominance, and epistasis. It is becoming evident, though, that coevolution is probably also driven by genomic processes: polyploidization, hybridization among species, and sometimes both (i.e., allopolyploidy). In addition, parts of the genomes of some coevolving symbiotic species are now known to have come from their partner species (Moran 2007). We need mathematical theory and empirical studies that explore just how important these processes are in shaping coevolution and the overall structure of the web of life.

We already know that interspecific hybridization alters the ecological web of interacting species (Whitham et al. 1994; Bangert et al. 2006; Aldridge and Campbell 2007; Craig et al. 2007) and that it can alter coevolving interactions (Barrett et al. 2007). Hybridization produces direct effects and indirect effects on the assembly of species associated with hybrid populations as compared with their parental populations. At longer timescales, interspecific hybridization may shape the diversification of coevolving taxa. Recent studies of figs and fig wasps have suggested that part of the diversification of these coevolving interactions may have resulted from host shifts by fig wasps among frequently hybridizing fig species (Machado et al. 2005). We lack, however, a comprehensive understanding of the importance of hybridization in shaping coevolution within interaction webs.

More recently, we have learned that genome duplication without hybridization (i.e., autopolyploidy) can also affect the structure of interaction webs. Polyploidization is common in some taxa, such as angiosperms, and much of modern agriculture is based on the selective cultivation of polyploid forms of wild species. Over 70% of angiosperm species have an increase in ploidal level in their evolutionary past (Levin 2002), and at least 2%–4% of the rate of speciation in plants may be due to the rate of polyploidization (Otto and Whitton 2000). Within lineages, polyploidy may act as a ratchet such that the proportion of polyploid species increases over time (Meyers and Levin 2006). In fact, recent studies have suggested that estimates of the number of autopolyploid plant species may be grossly underestimated (Soltis et al. 2007), because taxonomic treatments have often grouped polyploid populations with their diploid ancestors.

During the past decade, we have learned that plant poly-

Four Central Points

Every new student and researcher in biology should be told the following points about coevolution and its importance in the organization of biodiversity:

1. Multicellular organisms require one or more coevolved interactions to survive and reproduce.
2. Species-rich ecosystems are built upon a base of coevolved interactions.
3. Coevolution generates a diversity of outcomes beyond escalating arms races or obligate mutualisms.
4. Interactions often coevolve as geographic mosaics that are continually reshaped across ecosystems.

ploidy can have large effects on interspecific interactions. The saxifrage herb *Heuchera grossulariifolia* has repeatedly produced autotetraploid populations from diploid parents in the northern U.S. Rocky Mountains, and sympatric populations of diploids and tetraploids differ in both their patterns of attack by insect herbivores and visitation by insect pollinators (Thompson et al. 1997; Seagraves and Thompson 1999; Nuismer and Thompson 2001; Janz and Thompson 2002; Nuismer and Cunningham 2005; Thompson and Merg 2008). Some of these autopolyploid populations are morphologically cryptic, and the patterns of specificity within this interaction web would be completely missed by ecological studies that did not take ploidy level into account. Similar effects of polyploidy on interaction webs are being discovered in other plant-insect interactions (Husband and Sabara 2004; Arvanitis et al. 2007; Münzbergová 2007; Halverson et al. 2008), and in other kinds of interaction (Osnas and Lively 2006), as more studies take genome duplication into account. Some mathematical models have begun to suggest how polyploidy can affect the evolutionary dynamics of species interactions (Nuismer and Otto 2004).

Collectively, these studies suggest that whole-genome alterations through hybridization and polyploidy may have had important effects on the diversification of interspecific interactions among some taxa. The task now is to understand in a systematic way just how important these, and other kinds of genomic events, have been on the coevolutionary process and the overall structure of the web of life.

Toward a Fuller Integration of Coevolution into Evolutionary Biology

We cannot make progress in addressing these large questions unless we start teaching the next generation of researchers about coevolution as a central process in evolution, community ecology, and the overall organization of biodiversity. Despite all we have learned about the pervasiveness of coevolution, it is still often treated as a special topic in evolutionary biology. Some evolutionary biology

texts do not even include a major discussion of coevolution, despite the many advances in coevolutionary theory and the many careful laboratory and field studies of recent decades. I suggest that, at the very least, we should tell every student and researcher entering biology the following four central points about coevolution and its importance in the organization of biodiversity (see “Four Central Points”).

Multicellular Organisms Require One or More Coevolved Interactions to Survive and Reproduce

Mitochondria and chloroplasts are the most obvious coevolved partners, but multicellular organisms generally require multiple coevolved interactions to survive and reproduce in real populations. Coevolved gut symbionts are pervasive in animals. In some biological communities, reproduction for the vast majority of plants would stop immediately if pollinators became extinct. These interactions are not filigree at the edges of the evolution of nuclear genes. They are a major part of how life on earth has evolved through species “capturing” whole genomes (i.e., other species) and using those other genomes for their own ends. Multicellular species have a nuclear genome that is incomplete for survival and reproduction, because natural selection over billions of years has favored individuals that use the genomes of other species for many functions.

Species-Rich Ecosystems Are Built upon a Base of Coevolved Interactions

If you took away the lichens and mycorrhizae from terrestrial communities, the reef-building corals and their zooanthellae from the oceans, and the sulfur-converting symbioses from deep-sea vents, those ecosystems would collapse. Even the base of deep-sea planktonic communities now seems to involve complex coevolved interactions. *Prochlorococcus*, which is one of the major photosynthetic organisms in oceanic environments, is a complex of clades whose genes for photosynthesis show evidence

of repeated transfer back and forth between host and viral genomes (Lindell et al. 2004, 2007). The mainstays of discussions in community ecology—whether competition or predation is more important, or whether top-down or bottom-up processes are more important—are possible only because the coevolved interactions at the base of communities have made it possible for those complex webs of interaction to form.

Coevolution Generates a Diversity of Outcomes beyond Escalating Arms Races or Obligate Mutualisms

There are at least seven classes of coevolutionary dynamics. We need to emphasize that coevolution has identifiable classes of dynamics, only some of which lead to extreme outcomes between pairs of species through sustained directional selection. Coevolution between predators and prey, parasites and hosts, and competitors often favors individuals that simply differ from others in the same populations, rather than individuals that have yet higher levels of defense and counterdefense. The result is the continuing evolution of polymorphisms driven by frequency-dependent selection. The evolution of sexual reproduction is likely a result of this common aspect of coevolutionary selection, at least in part. A process analogous to coevolving polymorphisms may also occur at the multispecific level through coevolutionary alternation.

In addition, the coevolutionary process among free-living mutualists often favors the formation of mutualistic networks through coevolutionary complementarity and convergence rather than the formation of obligate pairwise mutualisms. Moreover, as networks grow in size, the number of ways in which evolution can act also increases, favoring everything from extreme specialists (“species-level specialists”) to generalists (“network specialists”) that depend on the very existence of the network itself (e.g., honeybees). The result is a coevolutionary vortex that continues to draw more species and lifestyles into the interaction web.

Interactions Coevolve as Geographic Mosaics That Are Continually Reshaped across Ecosystems

Coevolution is not just about long-ago events such as the evolution of mitochondria, chloroplasts, or the origin of sexual reproduction. It is a relentless ecological process that creates geographic mosaics in coevolving interactions from a myriad of minievolutionary and coevolutionary experiments across environments. Through the geographic mosaic of coevolution, interaction webs are continually remolded across landscapes, generating a wide range of novel adaptations, some of which lead to new species.

Just explaining these four points to biology students and

to researchers in other fields would go a long way toward helping the next generation of scientists understand the importance of coevolution in the structure and diversification of life.

Broader Implications for a Science of Applied Coevolutionary Biology

A deep understanding of the coevolutionary process is becoming increasingly important at a time when we are increasingly taking evolution into our own hands by altering webs of interacting species. We are continually adding or eliminating species to ecosystems and manipulating interactions by imposing direct or indirect genetic changes on populations. The spread of invasive species is changing natural selection on the web of life in all major ecosystems and may be altering the web of coevolved relationships among native species (Callaway et al. 2005). The introduction of species even from nearby ecosystems has already been demonstrated to have had major effects on coevolved interactions (Benkman et al. 2008). Invasive species themselves are coevolving with each other, creating their own geographic mosaics as they spread (Zangerl et al. 2008), even as we lose the geographic mosaic structure of some native species through habitat loss.

Even more directly, the development of new vaccines against pathogens, genetic engineering programs in agriculture, and genetically modified biological control agents are moving forward as focused efforts in surrogate coevolution (Thompson 2005). These techniques are based upon assumptions about how pests will or will not counter-evolve as we introduce novel genotypes into complex landscapes. As evolutionarily based genetic pest management strategies continue to develop (Gould 2008; Tabashnik et al. 2008), they will require scientific answers, or at least informed guesses, to how such strategies are likely to domino in their effects throughout the rest of a community and neighboring communities. These are, in effect, questions about how our biotechnological efforts generate reciprocal evolutionary change in the surrounding web of life.

These massive changes will continue but, as Ehrlich (2001) has argued, we need to learn how best to avoid foreclosing the evolutionary options of species faced with such rapid change. With better theory on multispecific coevolution, we should be able at least to outline the range of realistic potential outcomes rather than just produce a long list of unweighted possibilities. That process will lead us to a science of applied coevolutionary biology.

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