# The Population Biology of Coevolution

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**Abstract.** New populational approaches to the study of coevolution among species are confronting two major problems: the geographic scale at which coevolution proceeds, and the long-standing issue of how species may coevolve with more than one other species. By incorporating the ecological structure of life histories and populations into analyses of the coevolutionary process, these studies are indicating that coevolutionary change is much more ecologically dynamic than indicated by earlier work. Rather than simply a slow, stately process shaping species over long periods of time, parts of the coevolutionary process may proceed rapidly (sometimes observable in less than a decade), continually molding and remolding populations and communities locally and over broad geographic scales.

**Key words:** coevolution, gene-for-gene interaction, geographic structure, local adaptation, rapid evolution.

## Introduction

The process of coevolution—reciprocal evolution in interacting species—is one of the major organizing influences on the structure of biological communities and the worldwide organization of biodiversity. It creates evolutionary arms races between predators and prey, modifies levels of virulence in parasites and resistance in hosts, adjusts the similarity of traits among competing species, and molds mutualistic alliances among phylogenetically distant taxa. At the extreme, the coevolutionary process produces highly specialized and mutually interdependent species incapable of existing without one another. Figs and their pollinating fig wasps, and yuccas and yucca moths, are well known examples.

We know that coevolution occurs, but we are only now starting to understand just how ecologically dynamic the process can be. We often tend to think of coevolution as a slow process, gradually molding species over long periods of time. But by focusing on the structure and dynamics of populations rather than on long-term directional changes in species, recent studies are beginning to show that coevolution can be a rapid process, continually

remolding the ecological relationships of organisms. Many of the rapid coevolutionary changes among local populations will not eventually spread to become fixed traits of interacting species. But that does not make these changes any less important. As ecologists we are interested in the processes that shape the structure and dynamics of populations and communities, and ongoing rapid evolution (and sometimes coevolution) of interspecific interactions is turning out to be one of the important organizing processes. Here I evaluate how approaches from population biology—studies of life histories and population structure and dynamics—are beginning to unravel the ecological structure and dynamics of coevolutionary change.

## Background

Until recently, there had been two major overlapping periods of coevolutionary study following Darwin's introduction of the concept in the *Origin of Species*. These two periods differed in the kinds of questions they posed about reciprocal evolutionary change. In Darwin's day, coevolution between pollinators and flowers, and coevolution within mimicry complexes, became the major test cases for the theory of natural selection. The problem to be solved was how selection favored specialization and

reciprocal adaptation in these interactions. Biologists concerned themselves with specifying the ecological conditions favoring coevolution. A resurgence of interest in these questions occurred in the 1960s with the rise of evolutionary ecology and continues until today.

A second major period of coevolutionary studies blossomed following the appearance of Ehrlich and Raven's (1964) paper on coevolution between butterflies and plants. Using the tools of ecology, population genetics, and systematics, biologists searched for patterns of reciprocal change within local communities and evidence for long term coevolution in the fixed traits of interacting lineages of species (Janzen 1966, 1980; Thompson 1982; Futuyma and Slatkin 1983; Nitecki 1983).

For a while coevolution seemed everywhere, but then skepticism set in. Population ecologists and geneticists studying local populations of interacting species often found little evidence for reciprocal change between pairs of species, at least over the short periods of time at which most studies occurred. Field biologists uncovered relatively few convincing cases of repeated bouts of reciprocal change when analyzing local communities. Modelers found that long-term local stability of coevolving interactions often occurred only with restrictive assumptions (May and Anderson 1990; Frank 1993). Moreover, ecologists trying to understand interactions within a broader community context observed that the potential for local coevolution could sometimes be reduced by interactions with other species within the community.

Systematists, too, often found little evidence for coevolution (Stone and Hawksworth 1986). But here the problem was complicated by interpretation. The hypothesis of Ehrlich and Raven (1964), now formalized as escape-and-radiate coevolution, was commonly misinterpreted to mean that there should be close parallel speciation in coevolving species. Researchers commonly expected that the descendent species should show a lock-step escalation of traits and matching counter-traits. In fact, Ehrlich and Raven's hypothesis predicts something quite different: starbursts of speciation in one taxon followed by starbursts of speciation in the other taxon (Thompson 1998). By their hypothesis, a host with a new mutation becomes free of its enemies. It then diversifies through speciation, in the absence of the interaction, as it colonizes a new adaptive zone. Subsequently, a mutant form of the enemy taxon (not necessarily the most derived species within that taxon) overcomes these new defenses, and this enemy lineage then diversifies into new species as populations become specialized to attack one or another of the new hosts.

During these starbursts of speciation, there is nothing in the hypothesis to suggest that the new enemy lineage will colonize first the most ancestral species within the new host lineage, and then radiate step by step through the more derived species. There would be no reason for such a constraint on colonization. After all, the host lineage had radiated in species in the absence of the enemy and not as a result of a species-by-species escalation of defense and counter-defense. Nevertheless, this misinterpretation of the Ehrlich and Raven view of the relationship between coevolution and speciation, coupled with the common failure to find such relationships, contributed to a growing view that coevolution may be uncommon.

## Dismantling diffuse coevolution and revealing the dynamics of coevolution

These problems encountered in studies of local pairwise interactions and in patterns of speciation produced two general views that, until recently, stifled coevolutionary research. The two views are different ways of saying the same thing. Phrased one way, the view is that pairwise coevolution is uncommon among interacting species because species interact with many other species. Phrased the other way, the view is that coevolution occurs among taxa but it is often highly diffuse and difficult to study. The catch-all phrase "diffuse coevolution" has therefore become one way of lumping together a wide range of complex interactions that are highly dynamic and often involve more than a pair of species. The result has been an artificial dichotomy—specific coevolution and diffuse coevolution—as if there were only two "kinds" of coevolution.

This artificial dichotomy masks a wide array of ecological, genetic, and evolutionary processes that shape coevolution at the population level. Certainly, some evolving interactions are so highly complex—involving many species over large geographic areas—that they are at the limits of what we can evaluate experimentally about the coevolutionary process. The most obvious examples are the intercontinental relationships between migrating birds and the thousands of plants that exploit these migrants on their breeding grounds, migratory routes, and wintering grounds. But between this transcontinental extreme on the one hand and local coadaptation between pairs of species on the other hand is a wide range of coevolving interactions among groups of species.

The past few years have produced new approaches to the study of coevolution designed to dismantle diffuse coevolution into testable analyses of coevolutionary processes and the ecological patterns they produce. The key to revealing the ongoing dynamics of coevolution has been to evaluate the population biology of coevolution based upon the local and geographic structure of populations and life histories of organisms. These more ecological approaches have the potential to generate a third wave of coevolutionary studies. They can contribute directly to our un-

derstanding of community organization, the scale of ecological and evolutionary processes, and the conservation of biodiversity.

I will highlight three of these approaches here. The approaches differ in the kinds of questions they can answer about the coevolutionary process. They also differ in how they link population biology with other subdisciplines of biology. But they all show the importance of focusing on populations—and differences among populations—rather than on species if we are to understand the dynamics of the coevolutionary process.

# The geographic mosaic of evolving interactions

## The argument

Recent ecological approaches to coevolutionary studies have begun to take the complex spatial structure of populations into account. There are three common ecological observations which together suggest that the dynamics of coevolution cannot be fully understood either through ecological and genetic analyses of single, local populations or through phylogenetic analyses of the fixed traits of species: species are groups of genetically-differentiated populations; outcomes of interspecific interactions differ among communities and with the demographic structure of populations; and interacting species differ in their geographic ranges (Thompson 1994). As a result, natural selection may shape interactions in different ways in different populations or even in different subpopulations (e.g. Komatsu and Akimoto 1995; Ritland 1995; Mallett and Gilbert 1995).

Hence, we should expect that the coevolutionary process will commonly exhibit three properties that follow from the population structure of species (Thompson 1997). First, there should commonly be a selection mosaic among populations. That is, natural selection on an interspecific interaction will differ among communities. Second, there should be coevolutionary hotspots, which are communities in which much of the coevolutionary change occurs, intermixed with coevolutionary coldspots, which are communities in which the interaction is commensalistic or does not occur at all. Finally, there should be a continual mixing of coevolved traits among populations, resulting from the selection mosaic, coevolutionary hotspots, gene flow, random genetic drift, and local extinction of populations.

This three-part coevolutionary process takes into account what we have learned about the population biology of species in recent decades. The process should result in three ecological patterns. 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. And there will be few species-level coevolved traits (i.e. coevolved traits that become fixed traits for a species), because few traits will be globally favored (i.e. favored across all populations). If the process often works in this way and produces the patterns I have predicted, then coevolutionary studies will demand a thorough understanding of the population structure of the species being studied.

## The evidence

Published studies during the past several years have provided evidence for some components of the geographic mosaic view of coevolution and for the importance of understanding the population biology of coevolution. For example, studies of the metapopulation dynamics of gene-for-gene coevolution between plants and pathogens have provided important insights into the geographic scale at which these interactions may be maintained. Gene-for-gene coevolution is a special form of reciprocal evolutionary change in which each gene for resistance in a plant population is overcome by a specific gene in the pathogen population. This specific genetic form of coevolution has been important, because it is the paradigm under which much research on breeding for resistance is carried out, it is known to occur in some natural populations, and it has been the basis of much mathematical modelling of coevolution (Thompson and Burdon 1992). The classic theoretical problem in gene-for-gene coevolution has generally been to understand how populations can maintain polymorphisms for resistance in hosts and virulence in pathogens at the level of local populations. For several decades, the general expectation has been that genetic polymorphisms are maintained in these interactions within local communities solely through frequency-dependent, and sometimes density-dependent, natural selection.

That expectation, however, is becoming less likely. As genetic models of gene-for-gene coevolution have added ecological parameters, the local dynamics they exhibit have become more chaotic and the conditions for maintaining a stable polymorphism more restrictive (Anderson and May 1991; Frank 1992, 1993). Moreover, long-term monitoring of local populations of wild flax (*Linum marginale* A. Cunn. ex. Planch) and flax rust (*Melampsora lini* (Ehrenb.) Lev.) in Australia has shown that the local numbers of interacting individuals and their allele frequencies can fluctuate wildly over a time scale of a decade (Burdon and Jarosz 1991; Jarosz and Burdon 1991; Burdon 1994; Burdon and Thompson 1995). As theoretical and empirical studies have progressed, it has therefore become increasingly evident that gene-for-gene coevolution is probably maintained not at the local level but instead at the metapopulation level or over even broader geographic scales (Thompson and Burdon 1992; Burdon

1994).

It is the added perspective of population ecology that has allowed this change in view on how these interactions may be maintained. What are needed now are a series of comparative long-term studies that carefully monitor the local and regional population dynamics of plants and pathogens. These studies are needed to allow us to evaluate how the process of coevolution varies with (1) the demographic structure of local populations, (2) the metapopulation structure and broader geographic structure of interacting species, and (3) the life histories of species.

Other antagonistic interactions appear to be coevolving through even more complex geographic structuring of populations. Throughout Europe populations of *Drosophila melanogaster* Meigen differ greatly in their ability to defend themselves against the parasitoids *Asobara tabida* Nees and *Leptopilina boulardi* Barbotin, Carton & Kelner-Pillault (Kraaijeveld and van Alphen 1994, 1995a, b). Defense occurs through encapsulation of the parasitoid's eggs, and encapsulation ability differs among populations throughout the continent. The ability of *D. melanogaster* populations to encapsulate the eggs of either parasitoid species is independent of the ability to encapsulate the other species. This independence of defenses further increases the geographic differences among *D. melanogaster* populations. Moreover, the parasitoid populations differ in their abilities to resist encapsulation (Kraaijeveld and van Alphen 1994). These combined results on defense and counter-defenses show that there is a highly complex geographic structure to coevolution between *D. melanogaster* and its parasitoids. The problem now is to evaluate how this geographic structuring of populations shapes the overall dynamics of the coevolutionary process among these species, beyond what occurs solely within local populations.

Recent studies are also showing that the coevolutionary dynamics of antagonism and mutualism may vary over broad geographic scales as the community context of an interaction changes. *Greya politella* (Walsingham), a close relative of yucca moths (Brown et al. 1994), consists of a group of geographically-differentiated populations. Most of these populations attack a group of geographically-differentiated populations of *Lithophragma* (Saxifragaceae). *Greya politella* is a very effective pollinator of the *L. parviflorum* (Huok.) Torr. & Gray complex (a group of closely-related populations or species), which it accomplishes passively while ovipositing through the floral corolla (Pellmyr and Thompson 1992; Thompson and Pellmyr 1992). Phylogenetic analyses and ecological studies of the mutualism between *G. politella* and the *L. parviflorum* complex have shown that several unique plant and moth traits are involved in this interaction (Thompson 1997), suggesting that the mutualism may possibly be coevolved. The floral and moth traits, however, vary geographically, and the mutualism is swamped in some local populations by abundant co-pollinators (Thompson and Pellmyr 1992). Adding to the geographic complexity, some moth populations use other *Lithophragma* species and another saxifrage genus (*Heuchera*) at the edges of the species' geographic range (Thompson et al. 1997).

The current working hypothesis, then, is that this is a geographically-differentiated interaction, possibly coevolved between *G. politella* and *L. parviflorum*, but now further differentiating and diversifying as the moths and plants have colonized different environments and communities (Thompson 1997; Thompson et al 1997). Ignoring the complex geographic structure of these interactions would terribly underestimate the current, ongoing evolutionary dynamics of these relationships.

Other recent studies of local adaptation of parasite populations and the local responses of hosts reinforce the importance of the ongoing geographic dynamics of the coevolutionary process (Antonovics 1994; Ebert 1994; Kelley 1994; Lively and Jokela 1996; Mopper 1996). The general hypothesis that attack by parasites favors the evolution of sexual reproduction in hosts (Hamilton et al. 1990; Ebert and Hamilton 1996) has been reformulated in more populational terms in some recent field studies. These analyses have tested the specific hypothesis that structuring of parasites into locally-adapted demes maintains sexual reproduction in hosts as the local coevolutionary response. The most detailed field studies so far within natural populations are those using the digenean parasite *Microphallus* sp. and its snail host *Potamopyrgus antipodarum* (Gray) in New Zealand (Dybdahl and Lively 1996; Lively and Jokela 1996). These analyses have shown that the parasites can become highly adapted to local host populations. In turn, natural selection favors sexual reproduction in host populations that are currently subjected to high levels of parasite attack. The adaptations and counter-adaptations found in these interactions, and their distribution among populations, began to make sense only once the population structure of the interacting species was taken into account.

Other ways in which the structure and ecology of populations shape the coevolutionary process are continuing to be proposed. We now have hypotheses for coevolutionary turnover among competitors on archipelagos (Roughgarden 1995), coevolutionary alternation of parasites among groups of host species (Davies and Brooke 1989), and the maintenance of competitive or mutualistic polymorphisms in species during successional cycles of coevolution over broad landscapes (Thompson 1994, 1998). These are all hypotheses about the ways in which the spatial and demographic structure of populations shapes the geographic mosaic of coevolution.

# Correlated and coordinated changes in interactions

Another recent approach in coevolutionary studies has been to study multiple populations in order to understand how the same suites of traits are recycled to confront different combinations of enemies and mutualists in different populations. It is an approach that uses the divergence of populations to evaluate how species deal with the problem of coevolving with more than one species. Particularly powerful are approaches that place the divergence of traits among populations in a phylogenetic context. The phylogenetic framework provides a template for evaluating the observed differences among populations.

The questions to be answered by this approach are longer-term than those addressed in the previous section on the geographic mosaic of coevolution. With the help of a phylogenetic template, it is possible to begin to ask whether particular life histories or particular demographic structures of populations tend to favor particular ways of handling the problem of coping with particular suites of enemies or mutualists. Or, turning it around, we can ask whether differences among taxa in life histories and demographic structure have tended to produce different phylogenetic patterns in coevolution.

Studies of the evolution of interactions between the plant genus *Dalechampia* and its herbivores and pollinators exemplify this approach (Armbruster 1990, 1993; Armbruster et al. 1997). The studies have been designed to evaluate how traits are shaped and reshaped through interactions with different combinations of antagonists and mutualists. The analyses have mostly used closely-related species rather than populations within species, but the same approach can be applied to populations of a species that differ in demographic structure and other features.

*Dalechampia* is a group of tropical euphorbiaceous plants that rely upon specialized resin-collecting, fragrance-collecting, or pollen-collecting bees for pollination. In a series of studies Armbruster has evaluated how different chemical and morphological traits in this genus influence both herbivore attack and visitation by pollinators. At the same time, he has analyzed when each of these traits arose during the phylogeny of the genus and how each has been subsequently modified in descendent populations and species.

These combined studies have suggested that the same traits have been used repeatedly in coping both with antagonistic interactions and mutualistic interactions. Triterpene resins used by some *Dalechampia* species as a floral reward to attract resin-collected female bees appear to have originated as defenses against florivores, and then secondarily became floral rewards. Subsequently, these same resins became co-opted again as defenses in some of the species, but now for use in the leaves. These triter-

pene-producing taxa have also given rise at least three times to descendent populations and species that use monoterpenes to attract fragrance-collecting male euglossine bees (Armbruster 1993; Armbruster et al. 1997).

Similar use and modification of old traits for new functions has occurred in morphological characters in *Dalechampia*. Large involucral bracts appear to have arisen primarily as floral advertisements and secondarily became used as defenses against folivores and seed predators. Attraction of different taxa of resin-collecting female bees has occurred through shifts in the amount of resin produced, the size of the resin gland, and the relative positions within the involucral bracts of this gland, the anther, and the stigmas. Only certain combinations of the relative placement of these morphological traits have arisen in *Dalechampia*. These combinations, mapped on an adaptive landscape, correspond to floral configurations that maximize pollination by different specialized pollinator taxa (Armbruster 1990).

These studies indicate that the evolution of interactions between *Dalechampia* and its herbivores and pollinators has been linked through the repeated recycling of old plant traits for new functions. Moreover, the process is evolutionarily highly dynamic, producing different combinations of traits in different populations and species. Hence, there appears to be a high potential in these plants for coevolving simultaneously with locally specialized herbivores and pollinators, and doing so in an integrated way.

Studies placing interactions in a phylogenetic context are also showing that current coevolution between species may involve only a small, but important, subset of traits shaping an interaction. Such studies can help us to understand which traits are most likely under selection in a coevolving interaction, when we study that interaction across multiple populations. Recent work on the evolution of interactions between prodoxid moths (the family that includes the yucca moths) and their host plants (in the families Rosaceae, Saxifragaceae, Apiaceae, and Agavaceae) has indicated that pollination by these moths has arisen several times from antagonistic interactions, and the traits involved in these relationships vary among populations and species (Pellmyr and Thompson 1992; Thompson and Pellmyr 1992; Pellmyr et al. 1996b). Most of the relatives of yucca moths and their ecological relationships with plant species have been described only within the past decade (Thompson 1987, 1997; Davis et al. 1992; Pellmyr et al. 1996a). By studying the ecological relationships of these species in natural populations, and placing them within a phylogenetic framework, it is now known that most of the traits involved in the mutualism between yuccas and yucca moths—such as local host specificity in the moths and oviposition in floral parts—were present in ancestral species (Pellmyr et al. 1996b). Moreover, these studies have helped to show how different

combinations of traits are clustered together among different populations within species (Brown et al. 1997; Thompson 1997).

These studies have therefore made it possible to focus on the small number of traits that are truly coevolved in these interactions and to begin to ask how the traits have been reshaped among populations. The fact that there is only a small number of coevolved traits does not mean that coevolution has been unimportant in these relationships. Rather, it suggests that the dynamics of coevolution may commonly involve a small number of traits that become the focus of intense natural selection. Changes in these few traits may drive much of the subsequent evolution of these interactions within and among populations.

## Life histories and the ontogenetic partitioning of coevolution

A third way of bringing more population biology into studies of coevolution is through analyses of the interplay between life histories and the coevolutionary process. We know that life histories are under intense natural selection, shaped by patterns of survivorship at different life history stages and by the spatial distribution of individuals (e.g. Yoshimura and Jansen 1996). And we know that life history differences among populations can evolve quickly (e.g. Ohgushi and Sawada 1997; Reznick et al. 1997). Hence, there is tremendous scope for studies linking the demographic structure of populations, the evolution of life histories, and the ways in which natural selection shapes coevolutionary interactions.

Populations are composed of groups of individuals of different size, developmental stage, and age. As individuals develop, they interact with other species in different ways. As a result, there is an ontogeny to the interactions of organisms, which has been called the ontogenetic niche (Werner and Gilliam 1984). That is, interactions with other species are compartmentalized throughout an individual's lifetime. In some species, this compartmentalization follows simply from growth in size. As it grows, an individual may become less vulnerable to attack from some enemies, and it may itself attack different prey species. The benefit it receives from mutualisms with other species may also be restricted to certain sizes, ages, or developmental stages. In species undergoing complete metamorphosis, developmental compartmentalization of interactions is often even more pronounced.

The importance for coevolution of these ontogenetic changes in interspecific interactions is that they provide the opportunity for individuals to specialize sequentially throughout their lives on their interactions with other species. These sequential life history events provide a template for natural selection to partition a species' inter-

actions with other species in a coordinated way (Thompson 1994). Natural selection can favor genes that turn on and off at different times during a lifetime. A leaf-chewing caterpillar coevolving with its larval host plant and its gut symbionts becomes a nectar-sucking butterfly coevolving with the flowers of a different plant species. Studies of developmental polymorphism (Meyer 1990; Snorrason et al. 1994), host alternation (Kundu and Dixon 1995), and metamorphosis therefore all have the potential to show how populations can coevolve simultaneously with more than one species by partitioning interactions into different stages of life histories.

## Future directions

There are two pressing challenges facing coevolutionary studies over the next decade. Both require that we take into account the actual demographic, life history, and spatial structure of populations. One is to understand the specific ways in which a species can coevolve simultaneously with a number of other species. Studies of life history evolution and differentiation among populations are the most important ecological tools for understanding how the composite of a species' adaptations to many other species is built up and maintained. Dismantling diffuse coevolution into more testable hypotheses will continue to require the posing of specific questions about how individuals organize their interspecific interactions over the course of their lifetimes. And it will require careful analyses of how evolutionary changes within single populations become linked among metapopulations and over broad geographic scales to create the genetic composite that we call a species.

The other challenge is the overall problem of scale. What is the geographic scale at which most of the dynamics of reciprocal evolutionary change occur? The challenge is not just to characterize differences in coevolution among populations or species but rather to understand how those differences shape the geographic mosaic of coevolution among populations. By studying the geographic structuring of interactions, it is becoming evident that some features of relationships previously considered "troublesome"—lack of local stability, differences in outcomes among populations, little evidence of coevolution within a local group of interacting populations—are not evidence against coevolution but rather part of the coevolutionary process itself.

These studies of the population biology of coevolution have implications not only for evolutionary theory but also for the conservation of biodiversity. Nature reserves are increasingly becoming blocks of isolated habitat. If maintenance of the coevolutionary process commonly relies upon interactions among diversified populations over

broader geographic regions, then the dynamics of reciprocal change among species may be drastically disrupted with the loss of that geographic mosaic.

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