

- Kaly UL and Jones GP (1998) Mangrove restoration: A potential tool for coastal management in tropical developing countries. *Ambio* 27: 656–661.
- Leatherman SP (1982) *Barrier Island Handbook*. College Park, MD: University of Maryland.
- Lewis RR (1982) *Creation and Restoration of Coastal Plant Communities*. Boca Raton, FL: CRC Press.
- Minello TJ and Webb JW, Jr. (1997) Use of natural and created *Spartina alterniflora* salt marshes by fishery species and other aquatic fauna in Galveston Bay, Texas, USA. *Marine Ecology – Progress Series* 151: 165–179.
- Mitsch WJ and Gosselink JG (2000) *Wetlands*. New York: Wiley.
- Roze F and Lemauviel S (2004) Sand dune restoration in North Brittany, France: A 10-year monitoring study. *Restoration Ecology* 12: 29–35.
- Thayer GW (ed.) (1992) *Restoring the Nation's Marine Environments*. College Park, MD: Maryland Sea Grant.
- Van der Muelen F, Junerius PD, and Visser JH (eds.) (1980) *Perspectives in Coastal Dune Management*. The Hague: SPB Academic Publishing.
- Weinstein MP and Kreeger DA (eds.) (2000) *Concepts and Controversies in Tidal Marsh Ecology*. Dordrecht: Kluwer Academic Publishers.
- Woodhouse WW, Jr. (1978) *Dune Building and Stabilization with Vegetation*. Special Report 3. Fort Belvoir, Virginia: US Army Corps of Engineers, Coastal Engineering Research Center.
- Zedler JB (ed.) (2001) *Handbook for Restoring Tidal Wetlands*. Boca Raton, FL: CRC Press.

Coevolution

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Introduction

The Basics of Coevolution

Coevolution Drives Diversification

Further Reading

Introduction

What Is Coevolution?

All organismal populations experience multiple selective pressures deriving from varied aspects of their environment. In addition to abiotic features (e.g., climate), this ‘environment’ is often comprised of many other organisms. Thus, most populations evolve in response to interactions with other species. While the abiotic components of the environment cannot evolve in response to organisms, the biotic components can – and this phenomenon has played an integral role in the evolution of phenotypic diversity. Coevolution is reciprocal evolutionary change between interacting species driven by natural selection. That is, each player in a coevolutionary relationship evolves adaptations in response to its interaction with the other player(s). Although this general concept has been around since Darwin, the term ‘coevolution’ was coined by Paul Ehrlich and Peter Raven in a classic article in 1964, “Butterflies and plants: A study in coevolution.” Since then, the field of research examining coevolution has blossomed into a large-scale research program.

The Broad Importance of Coevolution

Coevolution is undisputed as one of the most important processes shaping biodiversity. The importance of

coevolution goes far beyond the classic examples, such as predator–prey coevolutionary arms races, figs and fig wasps, yuccas and yucca moths, ants and acacias, and fungal farming by several taxa. Coevolution’s influence spans all subdisciplines within ecology and evolutionary biology. Indeed, a large extent of the historical and ongoing patterns of phenotypic evolution and species diversification is the product of coevolution. Coevolution can stem from numerous types of species interactions that are commonplace on this planet, such as interspecific competition for resources, predator–prey interactions, host–parasite interactions, plant–herbivore interactions, and flower–pollinator interactions. Even the eukaryotic cell originated from a symbiotic relationship where one of the species evolved into the organelles we now call mitochondria. A similar scenario is responsible for the formation of chloroplasts, and thus the origin of plants. Most vertebrate and invertebrate species rely heavily on coevolved symbionts residing within their digestive system or other special organs to allow proper digestion and growth. Coral reefs, and the communities they support, depend largely on coevolved symbioses between corals and zooanthellae, as well as interactions with other corals and algae-feeding fish. The symbiotic organisms, lichens, are critically important during primary succession in terrestrial ecosystems. Even the colonization of land by plants was facilitated by mutualistic interactions with

mycorrhizal fungi. Coevolution's influence is so far reaching that the history of life on Earth would be unrecognizable in the absence of it.

Empirical Evidence for Coevolution

Despite the widespread importance of coevolutionary interactions, empirical demonstration of coevolution is a difficult task. This derives from the inherent difficulties of demonstrating adaptation – much less reciprocal adaptation – that has plagued evolutionary biology for many decades (see Adaptation). Nevertheless, a great deal of supportive evidence has been gathered for coevolution, coming from an assortment of tests for an array of hypotheses stemming from coevolutionary theory. As is discussed below, coevolution comes in many forms, and thus there are different manners in which researchers approach the question of coevolutionary association. As a general approach, researchers often examine phenotypic, ecological, and genetic evidence to test the hypothesis that organisms are evolving (or have evolved) in response to one another.

The Basics of Coevolution

Types of Coevolution

A few different categories of coevolution are often discussed by scientists in ecology and evolutionary biology: pairwise coevolution, diffuse coevolution, and gene-for-gene coevolution. Pairwise coevolution (or 'specific' coevolution) describes tight coevolutionary relationships between two species. Diffuse coevolution (or 'guild' coevolution) refers to reciprocal evolutionary responses between suites of species. This type of coevolution emphasizes that most species experience a complex suite of selective pressures derived from numerous other species, and their evolutionary responses change the selective environment for other species. Gene-for-gene coevolution (or 'matching gene' coevolution) describes the specific case where coevolution involves gene-for-gene correspondence among species, such as when hosts and parasites have complementary genes for resistance and virulence.

Symbiosis and the Nature of Coevolutionary Interactions

Some of the classic, and most obvious, examples of coevolutionary interactions involve two species that live in continuing, intimate associations, termed symbiosis. With such tight ecological associations, strong and repeated coevolutionary responses are easy to envision. Symbiosis is commonly used to refer to all relationships between different species, and thus an association need not be extremely close to qualify as symbiotic. There are five

Table 1 The five types of relationships between species. Effects of interaction are negative (–), positive (+), or indifferent (0)

Type of interaction	Effects of interaction on	
	Species 1	Species 2
Antagonism	–	–
Parasitism	–	+
Amensalism	–	0
Commensalism	+	0
Mutualism	+	+

major types of interspecific relationships: antagonism, parasitism, amensalism, commensalism, and mutualism (Table 1). Antagonism describes the scenario where both members of the interaction are harmed, such as interspecific competition. In parasitic coevolution, one member benefits (parasite), while the other is harmed (host). Parasitism is an extremely common form of coevolution (see Parasites and Abiotic and Biotic Diversity in the Biosphere). Parasitic interactions do not only include associations where one organism lives in or on a second organism, but also encompass some other very common interactions such as herbivory and predation. Sometimes the benefiting member kills the harmed member (e.g., parasitoid–host, predator–prey), whereas other times the harmed member is merely injured (e.g., parasite–host, herbivore–plant). Amensalism is where one member is harmed, while the other member is neither positively nor negatively affected (see Amensalism). A common example of amensalism is the production of a chemical compound by one member as part of its normal metabolism which is detrimental to another organism (e.g., allelopathy in plants, toxic skin secretions in animals). Commensalism describes a symbiotic relationship where one member benefits, while the other member is neither helped nor harmed (see Commensalisms). It is possible for some interactions to be parasitic under some circumstances (e.g., low host nutrition), but commensal during others (e.g., high host nutrition). Mutualism is a coevolutionary relationship where both members benefit (see Mutualism). For instance, clownfish gain protection from sea anemones, and anemones gain food from clownfish. Many relationships may change in nature over time, space, or ecological context, and the distribution of these types of outcomes for a given interaction (e.g., percentage of outcomes that are antagonistic vs. mutualistic) can be important in determining the coevolutionary responses that will be elicited.

The Red Queen Hypothesis

The Red Queen hypothesis was first proposed by Leigh Van Valen in 1973, and is a coevolutionary hypothesis describing how reciprocal evolutionary effects among

species can lead to some particularly interesting outcomes. While Van Valen specifically addressed macroevolutionary extinction probabilities, the hypothesis has since become much more general, providing an evolutionary explanation for numerous characters (e.g., sex, mating systems, pathogen virulence, maintenance of genetic diversity), and coevolutionary arms races in general. The conceptual basis of the Red Queen hypothesis is that species (or populations) must continually evolve new adaptations in response to evolutionary changes in other organisms to avoid extinction. The term is derived from Lewis Carroll's *Through the Looking Glass*, where the Red Queen informs Alice that "here, you see, it takes all the running you can do to keep in the same place." Thus, with organisms, it may require multitudes of evolutionary adjustments just to keep from going extinct.

The Red Queen hypothesis serves as a primary explanation for the evolution of sexual reproduction. As parasites (or other selective agents) become specialized on common host genotypes, frequency-dependent selection favors sexual reproduction (i.e., recombination) in host populations (which produces novel genotypes, increasing the rate of adaptation). The Red Queen hypothesis also describes how coevolution can produce extinction probabilities that are relatively constant over millions of years, which is consistent with much of the fossil record. Thus, extinction resistance of lineages does not improve over time, but rather remains fairly constant because the probability of evolutionary change in one species leading to extinction in another species should be independent of species age (they are constantly evolving with their changing environments, not constantly improving with respect to a static background environment).

The Geographic Mosaic Theory of Coevolution

Owing to relatively recent developments in ecological, evolutionary, genetic, mathematical, and phylogenetic studies, coevolution is viewed today as an ongoing, highly dynamic process where populations interact across geographical landscapes. This contrasts with the historical view dating back to Darwin where coevolution was largely visualized as a slow, directional molding of species' traits through long periods of evolutionary time. Recent and ongoing research in coevolution is revealing that ecological and evolutionary timescales are often one and the same, where effects of selection can be very rapid (strong intragenerational shifts), and evolutionary responses and counter-responses can be observable in only a few generations. This conceptualization of coevolution places a strong emphasis on the geographic context of coevolution and the continual reshaping of species' traits across geographic landscapes.

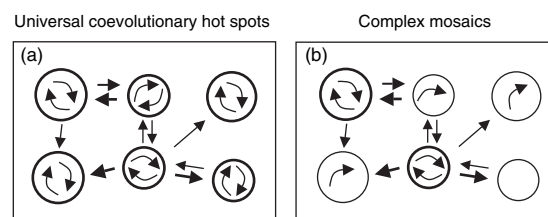


Figure 1 Hypothetical illustration of the geographic mosaic of coevolution. The example depicts interactions between two species within local communities (arrows within circles). Interaction arrows represent different types of selection acting on different species. Arrows between communities reflect the magnitude of gene flow. Thick circles represent coevolutionary hot spots, while thin circles are cold spots. (a) Coevolution occurs in all communities, although the interaction coevolves in different ways among communities. (b) Coevolutionary hot spots occur within a matrix of cold spots. Adapted from *The Geographic Mosaic of Coevolution* by John Thompson (see Further Reading).

John Thompson has championed this new framework for studying coevolution, the geographic mosaic theory of coevolution (Figure 1). This theory posits that coevolutionary interactions have three components driving evolutionary change:

- *Geographic selection mosaics.* Natural selection arising from interspecific interactions varies among populations.
- *Coevolutionary hot spots.* Interactions are subject to reciprocal selection only within some local communities (coevolutionary hot spots), embedded within a broader matrix of communities where selection is nonreciprocal or where only one of the participants occurs (coevolutionary cold spots).
- *Trait remixing.* Spatial distributions of potentially coevolving genes and traits are continually being altered due to new mutations, gene flow, genetic drift, and extinction of local populations.

Thus, with this theory, populations are placed within a context of geographic selection mosaics, providing a more complicated, but more realistic view, than previous perspectives. A couple of examples from nature help illustrate how this framework facilitates the understanding of how coevolution shapes species traits and interactions across landscapes: (1) garter snakes and newts, and (2) conifers and crossbills. These examples demonstrate how coevolutionary hot spots can result in geographic patterns in coevolved traits. First, *Taricha granulosa* newts and *Thamnophis sirtalis* garter snakes inhabit western North America, and show strong evidence of coevolving traits across this region. The newts possess a potent neurotoxin, which paralyzes and often kills a predator that has ingested a newt. However, the garter snake has evolved varying amounts of resistance to the neurotoxin (this resistance is physiologically costly). Newt toxicity levels and snake resistance levels are tightly matched across the geographic

landscape (i.e., where newts are more toxic, snakes have greater resistance). In addition, snake populations, where newts do not co-occur, exhibit very low levels of resistance. Research has revealed two coevolutionary hot spots, and a number of intermediate and cold spots. Second, both red crossbills (*Loxia* spp.) and red squirrels (*Tamiasciurus hudsonicus*) prey upon pine cones. Where squirrels are the primary seed predator, conifers have evolved heavier pine cones with fewer seeds and thinner scales, which defends against squirrels. Where crossbills are the major seed predator, pine cones are lighter with more seeds and thicker scales, which defends against crossbills. Crossbills in turn have evolved counter adaptations to consume the seeds, exhibiting deeper, less curved bills where pine cones have thick scales compared to areas where pine cones have thin scales. Thus, trees are evolving in response to crossbills and squirrels in different populations, and crossbills are evolving in response to these evolutionary changes in the trees.

Coevolution Drives Diversification

Cospeciation and Phylogenies

Farenholz's Rule (originally proposed in 1913) posits that parasites and their hosts speciate in synchrony. This process, the joint speciation of two or more lineages that are ecologically associated (coevolving), has since been termed cospeciation (or parallel cladogenesis). While most research to date has examined parasite–host interactions, other coevolutionary relationships may also exhibit cospeciation; however, we will focus on parasites and hosts for this discussion.

If the process of cospeciation were the only one operating, then phylogenetic trees of parasites and their hosts should be topologically identical (i.e., exact mirror images of each other; **Figure 2**). However, virtually all such phylogenies are not perfectly concordant. This implies that other processes must also be at work, such as host switching, speciating independently of their host, members going extinct, failure to colonize all descendants of a speciating

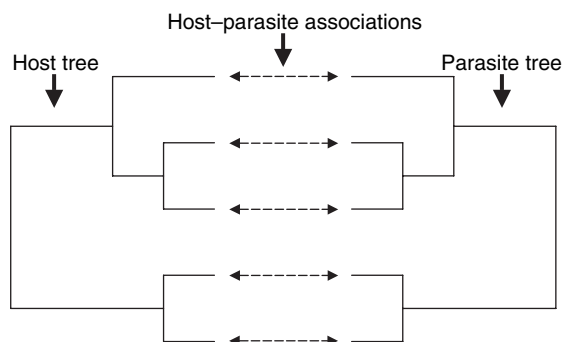


Figure 2 Hypothetical phylogenies for host and parasite clades illustrating evidence for cospeciation.

host lineage, or failure to speciate when its host does. Further, even when concordant, it is possible that one of the groups (often the parasite) has colonized the other (the host) – host shifts might correspond to the host phylogeny because closely related hosts are more liable to colonization by closely related parasites. Comparisons of species' phylogenies can produce insight (with limitations) into the coevolutionary history of interacting organisms. Thus, as phylogenetic data, and more sophisticated tree-building methods, have become widely available, phylogenies have become very useful in the study of coevolution. A number of empirical studies now, at least partially, support the general notion of cospeciation occurring with some regularity in some parasite–host interactions.

Coevolution, Divergence, and Adaptive Radiation

Coevolutionary interactions can lead to phenotypic divergence among populations, speciation, and adaptive radiation. In addition to the process of cospeciation described earlier, diversifying coevolution across landscapes, which has now been demonstrated in several empirical systems, can (and apparently does) contribute to the formation of new species, as well as phenotypic differentiation within species. One hypothesis of coevolutionary diversification has its roots in the original article that first coined the term coevolution (Ehrlich and Raven article mentioned above), and proposes that reciprocal diversification among members of a coevolutionary association (often parasite–host) results from reciprocal adaptation, geographic differentiation, speciation, and periods of noninteraction in the diversifying lineages. This process is called escape-and-radiate coevolution (**Figure 3**). In this process, one member evolves a defense (or some other innovation greatly reducing impact of interaction with other member), which enables a radiation due to the expansion of ecological opportunity. During the

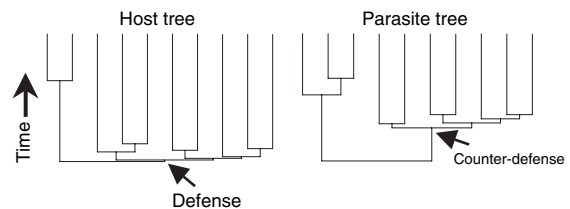


Figure 3 Hypothetical illustration of escape-and-radiate coevolution. In this example, a host lineage has undergone an adaptive radiation after evolving an effective defense against the parasite clade. During this time, interaction with the parasites does not occur. Then, the parasite lineage evolved a counter-defense and also radiated. Because the parasite clade did not cospeciate or colonize each new host in a systematic manner, the parasite–host associations are not anticipated to exhibit one-for-one matching as in **Figure 2**.

radiation, interaction among the members is minimal or nonexistent. Then, the other member evolves a counter-defense to overcome the innovation and radiates as well, producing reciprocal radiation events among the members. It is believed that diffuse coevolution among plants and herbivores may often follow such a coevolutionary diversification process.

Coevolutionary interactions may also often produce character displacement (exaggerated phenotypic divergence in sympatry) within local hot spots. This coevolutionary displacement is typically embedded within the broader geographic mosaic of coevolution among species, but may also result in fixation or speciation. A number of potential outcomes may result from coevolutionary displacement: character displacement among competitors in coevolutionary hot spots, displacement via apparent competition in hot spots, replicated community structure in hot spots, and trait overdispersion in competitive networks. Such displacement has been demonstrated in numerous systems in nature.

See also: Adaptation; Amensalism; Coevolutionary Research; Commensalisms; Parasites; Parasitism; Units of Selection.

Further Reading

- Combes C (2001) *Parasitism: The Ecology and Evolution of Intimate Interactions*. Chicago: University of Chicago Press.
- Dawkins R and Krebs JR (1979) Arms races between and within species. *Proceedings of the Royal Society of London B, Biological Sciences* 205: 489–511.
- Ehrlich PR and Raven PH (1964) Butterflies and plants: A study in coevolution. *Evolution* 18: 586–608.
- Farrell BD and Mitter C (1998) The timing of insect/plant diversification: Might *Tetraopes* (Coleoptera: Cerambycidae) and *Asclepias* (Asclepiadaceae) have co-evolved? *Biological Journal of the Linnean Society* 63: 553–577.
- Norton DA and Carpenter MA (1998) Mistletoes as parasites: Host specificity and speciation. *Trends in Ecology and Evolution* 13: 101–105.
- Page RDM (ed.) (2003) *Tangled Trees: Phylogeny, Cospeciation, and Coevolution*. Chicago: University of Chicago Press.
- Paracer S and Ahmadjian V (2000) *Symbiosis: An Introduction to Biological Associations*. Oxford: Oxford University Press.
- Pellmyr O and Herrera CM (eds.) (2002) *Plant-Animal Interactions: An Evolutionary Approach*. Malden, MA: Blackwell Science.
- Silliman BR and Newell SY (2003) Fungal farming in a snail. *Proceedings of the National Academy of Sciences of the United States of America* 26: 15643–15648.
- Thompson JN (1999) The evolution of species interactions. *Science* 284: 2116–2118.
- Thompson JN (2005) *The Geographic Mosaic of Coevolution*. Chicago: University of Chicago Press.
- Van Valen L (1973) A new evolutionary law. *Evolutionary Theory* 1: 1–30.
- Waser NM and Ollerton J (eds.) (2006) *Plant-Pollinator Interactions: From Specialization to Generalization*. Chicago: University of Chicago Press.

Coevolution of the Biosphere and Climate

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Introduction

What Is a Biogeochemical Cycle, the Biosphere, Climate?

History of the Concept of Coevolution of Biosphere and Climate

The Carbon Biogeochemical Cycle

What Regulates the Long-Term Climate?

Sources and Sinks: Equal at Steady State

The Biotic Enhancement of Weathering and the Long-Term Carbon Cycle

Biogeochemical Cycles of Oxygen, Phosphorus, and Sulfur and Their Influences on the Coevolution of Life and Climate

The Habitability of Earth

The Faint Young Sun Paradox and Its Solution

The Temperature Constraint on Biologic Evolution

From 'Hothouse' to 'Icehouse': The Increase in Diversity of Habitats for Life

Summary

Further Reading

Introduction

This article summarizes the current state of knowledge of global biogeochemical cycles that are especially relevant to climate and its coevolution with life. Following

basic definitions is a short history of the essential concepts, including Gaia theory, followed by a survey of the carbon biogeochemical cycle operating on different timescales, concluding with a discussion of those aspects of the cycles of oxygen, phosphorus, and sulfur