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Rapid evolution as an ecological process

John N. Thompson

Rapid evolution of interspecific interactions (during a timespan of about 100 years) has the potential to be an important influence on the ecological dynamics of communities. However, despite the growing number of examples, rapid evolution is still not a standard working hypothesis for many ecological studies on the dynamics of population structure or the organization of communities. Analysis of rapid evolution as an ecological process has the potential to make evolutionary ecology one of the most central of applied biological sciences.

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Ecological and evolutionary processes are often thought to occupy different timescales, so much so that it is common to hear biologists talk about ecological time and evolutionary time. Indeed, there are processes that occur at very long timescales that are far beyond anything that any of us commonly calls ecological time. But several decades of study in evolutionary ecology and evolutionary genetics have indicated that the timescales of ecological and evolutionary processes overlap for many of the questions posed by physiological ecologists, population ecologists, community ecologists and ecosystem ecologists. Metapopulation structure can rapidly shape and reshape the genetic structure of species at different geographical scales, and interspecific interactions have now been shown to coevolve over the timescale of decades.

Nevertheless, much ecological research continues to be carried out without considering – as one of a group of working hypotheses – whether some of the observed patterns and ecological dynamics are the result of rapid evolutionary change within and among populations. The National Center for Ecological Analysis and Synthesis in Santa Barbara, California, USA, recently sponsored a workshop on rapid evolution and the organization of biodiversity. Eighteen participants working at the interface of evolution and ecology discussed what we know and what we do not know

about the links between the ecology and evolution of interspecific interactions over a timescale of about 100 years. This timespan was chosen because it is the timescale at which much ecological research on community dynamics is carried out and at which many conservation decisions are made.

What we know

When Endler[1] summarized and evaluated the known examples of natural selection in the wild, researchers responded in two ways, depending on their expectations: either there was an impressive list of known examples or there was a very small list of known examples. Since Endler's review, the list of examples has continued to grow and now includes increasingly precise evolutionary analyses of long-term field experiments[2,3] and observations of populations under changing conditions[4,5]. These studies of natural populations show that ecologically important evolutionary change can happen rapidly. In addition, artificial selection experiments continue to show the potential for fast rates of evolutionary change[6], and mathematical models linking genetics to population ecology indicate that rapid evolution and coevolution of interspecific interactions can have a major effect on the structure and dynamics of populations[7–9].

Among the studies showing rapid evolution are a growing number indicating

rapidly evolving interspecific interactions within natural communities. Because interspecific interactions are the basis of community organization, rapid evolution of these connections among species has the potential to have major ripple effects throughout communities. The observed results fall into four major groups (Table 1). The first consists of studies showing rapid evolution of the number or strength of interspecific connections maintained by species within food webs or broader interaction webs. These studies concern specialization of predators and parasites to particular prey and hosts, and of mutualists to one another. If rapid evolutionary changes in interspecific links are common, then questions about the short-term relationships between diversity, food web connectedness and stability will need to include more careful consideration of rapid evolution. The important question to answer is whether the persistence of interactions and the stability of communities truly rely upon ongoing rapid evolution that fine-tunes interactions over timescales of decades, or whether such rapid evolution is ecologically trivial.

The second group includes studies showing rapid evolution of defenses against enemies within communities (Table 1). These are, in effect, examples of selection for decreased interspecific connections, or adjustments to the connections resulting from conflicting evolutionary processes. Such studies include directional changes in defensive morphs in response to changes in local environments, selection favoring rare or novel phenotypes, and changes potentially driven by genetic correlations, linkage disequilibrium or gene flow. As in studies of the evolution of specialization in predators and parasites, these results suggest that the strength of connections among species might constantly be evolving within and among communities.

The third group comprises studies that demonstrate the rapid evolution of the actual outcome of interactions between species. Such rapid evolution could be due to coevolutionary change or unidirectional change in one of the species. The most famous example is that of the coevolution

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Table 1. Representative examples of rapid evolution affecting the interaction structure of natural communities, drawn from work published since Endler's[1] summary of studies of natural selection in the wild

Interaction	Evolutionary change	Length of study or inferred timespan (years)	Refs
Evolution of trophic links through specialization			
Rhagoletis flies and host plants	Population divergence in preference for introduced host	<100	22
Euphydryas butterflies and host plants	Population divergence in preference for introduced host	<100	23
Papilio butterflies and host plants	Population divergence in preference for introduced host	100+	24
Apterothrips and host plants	Specialization to individual host plants	<100	25
Jadera bugs and host plants	Specialization in beak morphology and performance on introduced hosts	40	26
Acyrthosiphon aphids and host plants	Change over season in traits associated with staying on host	<1	27
Vestiaria honeycreepers and flowers	Change in beak morphology following change availability of plant species	<100	28
Geospiza finches and seeds	Change in beak morphology following change in seed availability	<10	5
Melampsora rust and *Linum* plants	Change in frequency of virulence morphs within populations	<10	29
Evolution of defense			
Biston moths and predators	Change in frequency of defensive morphs	30 (continuous)	4
Littorina snails and predators	Change in shell shape and thickness following predator range expansion	<100	30
Bulinus snails and trematode parasites	Parasite-maintained differences among populations in frequency of outcrossing morphs	ongoing?[a]	31
Potamopyrgus snails and trematodes	Parasite-maintained differences within and among lakes in frequency of sexual individuals	ongoing?[a]	32
Diaptomus copepods and fish predators	Change to earlier spring diapause in years following high predation	<1	33
Human influenza virus A and humans	Change in hemagglutinin molecule (which is used by immune system in making its humoral response)	13	34
HIV virus and humans	Change in virus at molecular sites used by host in immune response	2–7	35
Amphicarpaea plants and pathogen	Decrease in frequency of resistant biotype, despite pathogen presence	2	36
Linum plants and rust pathogens	Change in frequency of resistance morphs in host	<10	11
Rapid loss of traits in absence of interaction			
Ploceus weaver birds and brood parasites	Loss of egg rejection behavior in population lacking parasites	<200	37
Spartina plants and insect herbivores	Divergence among populations in resistance because of founder effects and perhaps subsequent genetic drift or selection	<100	38
Poecilia guppies and predators	Loss of defensive antipredator behaviors in population without predation	34	39
Overall change in outcome of interaction			
Oryctolagus rabbits and myxoma virus	Change in outcome through change in virulence and defense	<10	10
Drosophila buzzattii and *D. aldrichi*	Evolution of competitive ability	60	40

[a]Ongoing? = potentially rapid evolution inferred from comparisons among communities but rapid evolution not actually demonstrated within a community.

of defense in rabbits (*Oryctolagus cuniculus*) and virulence in myxoma virus in Australia[10], but rapid evolution of outcomes within communities might be common in the dynamics of interactions between parasites and hosts. For example, the local frequencies and combinations of genes for resistance against flax rust (*Melampsora lini*) have fluctuated broadly in Australian wild flax (*Linum marginale*) populations over just the past decade[11].

The final group includes studies indicating loss of traits involved in interspecific interactions (Table 1). Rapid loss of traits, such as genes for resistance against parasites, have important consequences for community dynamics and conservation. As communities are made more depauperate, combinations of resistance genes maintained by the diversity of interspecific interactions could rapidly disappear. However, the problem is not that simple, and work on bacteria and bacteriophages illustrate that some interactions can show asymmetries in the rates at which resistance traits are gained and lost. Some bacteria can rapidly evolve resistance to a particular bacteriophage, but those resistance genes are sometimes associated with a fitness cost in the absence of the phage. The expectation should therefore be that such resistance should be lost in the absence of phage. Lenski[12], however, found that the evolution of modifier genes can gradually lessen the fitness costs of harboring resistance genes. Consequently, when the phage are removed, natural selection would not necessarily favor the susceptible strains over the resistant ones. Different kinds of asymmetry in the rate of gain and loss of traits associated with interspecific interactions could occur for a variety of traits within natural communities, and they merit study as we try to understand how rapid evolution continually reshapes the dynamics of communities.

Recent molecular studies further highlight the potential for ongoing rapid evolution of some interspecific interactions. Mutator alleles have now been found repeatedly in bacterial populations, and their incidence can be surprisingly high[13]. Hypermutable clones can be composed of more than 1% of pathogenic isolates of *Escherichia coli* and *Salmonella enterica*[14]. Although mutations are generally deleterious, theoretical models and empirical studies have shown that mutator alleles can rise to high frequencies in populations if they are associated with an adaptive mutation[13,15]. Once established, these mutator clones can remain within bacterial populations for a long time. In the longest experiment conducted so far, Sniegowski *et al.*[13] showed that as soon as naturally occurring mutators appeared within *E. coli* populations in the laboratory, they remained within those populations through the remaining 10 000 generations of the experiment.

Rapid evolution of community structure within an historical context

This broad range of results indicates that rapid evolution could contribute significantly to the short-term dynamics of the interaction structure of communities. Hence, models of community dynamics cannot assume that the structure of interspecific links remains unchanged even over short periods. But there are limits to this rapid change; the interactions among species are not completely plastic. Most aspects of community structure are bounded by the phylogenetic histories of the component species. Shifts in specialization in

predators, grazers, parasites and various forms of mutualists generally occur within only a small subset of the prey or hosts available. Studies designed specifically to address how rapid evolution proceeds within the constraints imposed by phylogenetic history, therefore, have the potential to contribute to a more predictive view of the dynamics of communities. Achieving that goal will demand more input from the insights of systematics, phylogenetic trait maps, and biogeography into our understanding of evolutionary community ecology.

Such studies are likely to increase in importance as the rate at which we change the composition of communities worldwide continues to accelerate. There has probably never been a period in the earth's history when the historical associations of species have been so rapidly remixed. Many of the best documented examples of rapid directional evolution of interspecific interactions have involved introduced species (Table 1), and there are few communities where the number of introduced species is not growing each decade. As the historical mix of species changes, so does the potential for formation of new interspecific hybrids and polyploids, both of which have the potential to affect a wide range of interspecific interactions[16,17].

These wholesale changes in ecological communities increase the importance of understanding how introduced species shape rapid evolution of community dynamics. For example, perhaps one of the reasons that rapid evolution is more readily perceived in introduced species is that these species are more likely to undergo rapid directional selection rather than rapid fluctuating selection. We would then expect the trajectory of natural selection to change over time for introduced taxa – as the number of links between introduced species and the surrounding community increases (e.g. through colonization by parasites and mutualists, and coevolution with competitors), directional selection would come to be replaced by fluctuating selection.

In all communities, ecological succession adds an additional historical component. We currently know very little about the rapid dynamics of natural selection within communities during ecological succession as community context changes. Few studies have even begun to evaluate the role played by rapid natural selection in driving differences in successional cycles across landscapes[18,19]. The possibility of coevolutionary cycles of succession[20] is not one of the standard working hypotheses tested during studies of community dynamics, but it deserves more attention now that it is known that interactions can sometimes evolve rapidly within communities.

Fluctuating selection and community dynamics

Persistence of the view that ecological and evolutionary time are somehow fundamentally different could be the result of a perceptual problem, arising from implicit biases in what constitutes important rather than trivial evolution. Directional selection, speciation and macroevolutionary patterns have been the mainstays of evolutionary biology. Rapid and fluctuating selection that does not produce long-term evolutionary trajectories is deemed evolutionary noise. By this view, important evolutionary change is change that can be measured in darwins over long periods of time.

The darwin is a measure of proportional change over time defined as a change by a factor of e per million years, where e is the base of natural logarithms. Evolutionary rates measured in darwins over short timescales have provided very different estimates from those measured over long timescales. Because of the nature of the fossil record, most of the comparative estimates across different timescales have used rates of change based on morphological characters. These show an inverse relationship between the measured rate and the timescale on which the rate is based – fast evolution over short timescales and slow evolution over long timescales. As Gingerich[21] showed, at least part of this inverse relationship is an artefact of the following biases in the data: time averaging over different timescales; comparison of a narrow range of morphological variables over a wide range of timescales; and because rapid evolution over thousands of years is invisible in the fossil record. Organisms that evolved this rapidly would probably not be recognized as the same species in different geologic strata.

Rates in darwins that are measured over the long term are likely to underestimate significantly the role of evolution in shaping ecological processes within populations and communities. Values for long-term rates are for sustained directional selection. Estimates of short-term rates also evaluate directional selection, but the observed changes might often be part of a longer term pattern of fluctuating natural selection. It is these short-term rates that are the ecologically important ones, because it is these rates that tell us something about the speed at which populations can adapt to fluctuating environmental conditions and the speed at which evolution could continually reshape community structure.

Nevertheless, these high short-term rates are often viewed as transient phenomena that cannot be sustained. That view is based upon the idea that the observed changes are the first steps in long-term directional selection for new fixed traits in a species, forming the foundations of speciation or macroevolutionary patterns. Instead, most of these changes are part of the normal process of evolution, constantly reshaping populations and interspecific interactions through frequency-dependent selection, density-dependent selection, seasonal fluctuations in allele frequencies, selective death of genotypes within and among cohorts, and the constantly shifting genetic configuration of populations and interspecific interactions across broad geographical landscapes. To dismiss or ignore these rapid, fluctuating evolutionary processes as trivial evolutionary meanderings – or to view them simply as ways in which genetic variation is maintained within populations – is to miss the real interface of evolution and ecology in community dynamics.

At a time when ecological studies are moving towards broader landscape perspectives, an understanding of how rapid evolution may continually reshape the local and geographical organization of communities is becoming ever more important. We need a clear focus on rapid evolution as an ecological process if we are to develop a truly mechanistic, rather than a simply phenomenological, understanding of how communities respond to fragmentation, how diseases evolve and reshape communities, how introduced species spread across landscapes and how links among species change even amid normal environmental fluctuations.

Box 1. Hypotheses on the role of rapid evolution of interspecific interactions in the organization of biodiversity and the dynamics of communities

Fluctuating selection hypothesis of community dynamics: much of community dynamics observed over the timescales of decades and centuries is produced by rapid fluctuating selection on the links among species.

Fluctuating selection hypothesis of community stability: long-term stability of communities relies significantly upon rapid fluctuating selection on the links among species.

Rapidly evolving links hypothesis of altered community structure: persistent changes in community structure following introduction of novel species or major environmental change are partially the result of rapid directional selection on the links among species.

Coevolutionary cycles of succession: successional dynamics across landscapes are partially the result of rapid evolution and coevolution of interspecific interactions.

PERSPECTIVES

Prospects

There are four major hypotheses that require evaluation if we are to use the combined results of the past 30 years of evolutionary ecology to help understand the organization and dynamics of communities (Box 1). These hypotheses are all based upon the idea that rapid evolution often involves fluctuating selection that is ecologically important in populations and communities, even when it does not result in long-term macroevolutionary patterns. Because community dynamics is inherently multivariate, the problem is to sort out the extent to which rapid evolution is a major cause of community dynamics rather than its result. Testing these hypotheses has the potential to make the science of evolutionary ecology one of the most central of applied sciences.

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Erratum

***Trends Ecol. Evol.* July 1998 Vol. 13, No. 7**

On the cover of the July issue of *TREE* the issue number should have been [145] and not [144].