



CHICAGO JOURNALS



The University of Chicago

A Critical Look at Reciprocity in Ecology and Evolution: Introduction to the Symposium.

Author(s): David N. Reznick

Source: *The American Naturalist*, Vol. 181, No. S1, A Critical Look at Reciprocity in Ecology and Evolution (May 2013), pp. S1-S8

Published by: [The University of Chicago Press](#) for [The American Society of Naturalists](#)

Stable URL: <http://www.jstor.org/stable/10.1086/670030>

Accessed: 19/04/2013 12:22

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



The University of Chicago Press, The American Society of Naturalists, The University of Chicago are collaborating with JSTOR to digitize, preserve and extend access to *The American Naturalist*.

<http://www.jstor.org>

A Critical Look at Reciprocity in Ecology and Evolution: Introduction to the Symposium*

David N. Reznick[†]

Department of Biology, University of California, Riverside, California 92521

G. E. Hutchinson's (1965) famous essay *The Ecological Theater and the Evolutionary Play* helped launch the new discipline of evolutionary ecology. Hutchinson envisioned ecology as governing evolution; the ecological theater presents a template or niche. The evolutionary play tailors the organism to fit the niche. In a recent perspective, Schoener (2011) argued that we should instead think of ecology and evolution as two actors in the same play dynamically interacting with one another. Schoener also argued that too much of what we have learned about such interactions is derived from laboratory experiments performed on model ecosystems. We need to move research out of the laboratory and into nature.

The 2011 Vice Presidential Symposium of the American Society of Naturalists took a critical look at this new perspective, which I will refer to as "eco-evo interactions," in four ways. First, it addressed whether there really is a difference between eco-evo interactions and the well-established discipline of evolutionary ecology. Second, it presented four examples of empirical studies that ask whether such interactions are seen in natural ecosystems and, if present, how important they are. Third, it showed how a coupling of theory and empirical studies can address the prevalence and importance of such interactions. Finally, it considered what latent evidence is available in the literature to argue for the prevalence of such interactions, either in contemporary ecosystems or in shaping the history of life.

Background

In the 1950s, the dominant question in ecology was, What determines the abundance and distribution of organisms? Opposing answers were encapsulated in the long-running

debate about density-dependent versus density-independent population regulation. This debate was more than 20 years old when it boiled over at the 1957 Cold Spring Harbor Symposium on Quantitative Biology, which was entitled "Animal Ecology and Demography." Those who favored density-independent population regulation argued that the answer to population regulation lay in the mapping of an organism's physiology on its physical environment. Those that favored density dependence argued that it was instead the biotic environment, or interactions with other organisms, that shaped abundance and distribution (Andrewartha 1957; Birch 1957; Nicholson 1957).

In the early 1960s, the debate about density-dependent versus density-independent population regulation was rebranded by Gordon Orians (1962) as two different types of ecology—evolutionary and functional ecology, respectively. Functional ecology follows Andrewartha and Birch's (1954) argument that we can explain distribution and abundance by studying the physiology of the organism in question, the nature of its physical habitat, and how the abundance of the organism maps onto these different habitats. The answers to questions concerning abundance and distribution are thus rooted in the proximate factors of the physical environment and the physiological tolerances of the organism. Orians proposed "evolutionary ecology" as a different perspective that attributes abundance and distribution to an ultimate factor—evolution. If we are to understand the abundance and distribution of an organism today, then we have to envision it as the product of a history of adaptation to the community in which it is found.

Evolutionary ecology emerged in two different forms. The first is characterized by Hutchinson's (1965) "ecological theater and evolutionary play," in which he argued that ecology shapes evolution. A peculiarity of most of the associated theory is that it models ecological interactions in a fashion that treats organisms as constants, which implicitly assumes that they do not evolve. The intent is not that evolution does not happen but rather that it happens on a different, much longer timescale than ecology. Evo-

* This issue originated as the 2011 Vice Presidential Symposium presented at the annual meetings of the American Society of Naturalists.

[†] E-mail: david.reznick@ucr.edu.

Am. Nat. 2013. Vol. 181, pp. S1–S8. © 2013 by The University of Chicago. 0003-0147/2013/181S1-5443\$15.00. All rights reserved.

DOI: 10.1086/670030

lution is thus seen as something that happened in the past but explains the present. The empirical work that dominated evolutionary ecology followed Hutchinson's lead in implicitly treating organisms as the product of past evolution. Evolution provides an ultimate explanation for what we see but is otherwise not a visible process.

Hutchinson's perspective was very much the same as Darwin's (1859) in chapter 3, "The Struggle for Existence," of *On the Origin of Species*. Darwin observed that all organisms have the capacity for exponential population growth but this capacity is almost never realized. We instead most often see species abundances remaining within some relatively narrow range of values that is constrained by biotic interactions. There was thus a natural connection to be made between density-dependent population regulation and evolution by natural selection; it was the ability of some phenotypes to be more successful in surviving and reproducing in the face of these biotic interactions that caused evolution. Darwin also held the conviction that evolution by natural selection was too slow a process to be directly observable.

David Pimentel (1961) presented a fundamentally different version of evolutionary ecology. He envisioned ecology and evolution as two actors interacting during the course of a play. He encapsulated this perspective in his "population regulation and genetic feedback" hypothesis: "Density influences selection; selection influences genetic make-up; and in turn, genetic make-up influences density. The actions and reactions of the interacting populations in the food chain cycling in this mechanism result in the evolution and regulation of animal populations" (p. 65).

Pimentel (1968) expanded the concept of population regulation and genetic feedback to characterize the ongoing interaction between organisms involved in a diversity of pairwise exploitative interactions (predator-prey, host-parasitoid, host-pathogen, competitors, plant-herbivore). He envisioned each species involved in such an interaction as evolving in a fashion that would result in the dampening of population cycles and hence cause an approach to the relative stability of organismal abundances. He argued for frequency-dependent selection and density-dependent selection as the mechanisms that underlie these interactions and the approach to population stability. The use of the word "reciprocity" in the title of this introduction to the symposium is rooted in this dynamic interaction between evolution and ecology. Organisms change their environment. Their impact on the environment feeds back on and changes the selection experienced by the organism.

Pimentel's definition might look superficially like Janzen's (1980) definition of coevolution—"Coevolution" may be usefully defined as an evolutionary change in a trait of the individuals in one population in response to

a trait of the individuals in a second population, followed by an evolutionary response by the second population to a change in the first" (p. 611)—but differs in critical ways. Pimentel envisioned a matching of the rate at which organisms can evolve with the dynamics of ecological interactions and focused on how evolution changes the dynamics of ecological interactions and then on how these changes feed back on and change evolution. Janzen just considered how two species evolve in response to each other without any regard to timing, population dynamics, or the intervening interactions with other components of the ecosystem.

Pimentel (1961) cited the priority of E. B. Ford (1930, 1931), D. Chitty (1957, 1960), and others in proposing variations on the genetic feedback mechanism, but Pimentel stands out by having formalized the proposal with models and testing them with experiments. He modeled the eco-evo interaction between a plant and herbivore and showed, with simulations, that genetic feedback causes a progressive dampening of the population oscillations. He then executed experiments to test this prediction with a host-parasitoid (housefly, *Musca domestica*, and wasp, *Nasonia vitripennis*, respectively) model system (Pimentel et al. 1963; Pimentel 1968). These experiments included an evolution treatment and a nonevolving control. In the evolution treatment, there were continuous, multigeneration interactions between the host and parasitoid and, hence, the opportunity for both to evolve. In the nonevolving control, each generation of wasps was provided with hosts derived from a housefly lab culture that had no prior contact with the wasps. The experiments revealed, as predicted, that the host and possibly the parasitoid evolved during the course of the interaction (Pimentel et al. 1963). Evolution dampened the oscillations in the abundance of hosts and parasitoids relative to what was seen in the nonevolving control (Pimentel 1968).

Hutchinson's and Pimentel's perspectives were each defined by emergent theory and the development of empirical approaches to test the theory. Hutchinson's perspective grew to dominate the field and blossomed into what we now refer to as evolutionary ecology. Pimentel's perspective was represented in subsequent studies (e.g., Antonovics 1976; Roughgarden 1976; Abrams and Matsuda 1997; see Travis et al. 2013 for more review and discussion) but otherwise remained in the background. It is now re-emerging in the form of new types of theory and empirical studies.

There are important distinctions between these two brands of evolutionary ecology. The theory and a small body of empirical evidence associated with Pimentel's perspective bear out Pimentel's original claim—if evolution is indeed a part of ongoing ecological interactions, then the outcome of those interactions can be fundamentally

different from what is predicted from theory that does not formally incorporate evolution.

Yoshida and colleagues (2003) present a more recent, iconic example of the potential importance of such reciprocity between ecology and evolution in their experimental study of predator-prey population oscillations in a model ecosystem. The predator was a rotifer (*Brachionus calyciflorus*), and the prey was an algae (*Chlorella vulgaris*). Their ecosystems were replicate chemostats. Their study followed on an earlier study by Fussmann et al. (2000), who worked with the same experimental system, coupled with theory, to explore the conditions that resulted in stable predator-prey cycles. Some features of results by Fussmann and colleagues were not consistent with the associated theory, which prompted a later theoretical work by Shertzer et al. (2002) in which they explored possible explanations for the unexpected results. Shertzer and colleagues concluded that the results could be reconciled only with models that included algae populations that were evolving in concert with their population cycles. Yoshida et al. (2003) tested this hypothesis by initiating ecosystems with either a single clone or multiple clones of algae. The single-clone cultures were the equivalent of Pimentel's nonevolving control, while the multiple-clone cultures had the potential to evolve via changes in the relative abundance of different clones. This subtle difference in starting point resulted in huge differences in the resulting population cycles. The cycles in the evolution treatment had smaller amplitudes, longer periods, and a substantial shift in the peaks and troughs of the predator and prey cycles relative to one another from what was seen in the non-evolving control. Yoshida et al. (2004) confirmed that such evolution was indeed taking place and was driven by changes in the relative abundance of two classes of algal clones—those that were competitively superior but more susceptible to rotifer predation versus those that were competitively inferior but less susceptible to rotifer predation.

Experiments by Pimentel and Yoshida et al. and the associated theory demonstrate reciprocity because they formally contrast what happens with and without evolution. The differences between the two treatments document how contemporary evolution impacts ecological dynamics. They show that a potential consequence of an organism evolving during the course of an ecological interaction is that it can cause an outcome that is substantially different from what is predicted if such evolution is not accounted for. A second possible consequence of reciprocity is that organisms may evolve in a way that is different from what one would predict without taking the organism's impact on its environment into account. Such an interaction need not be linked to population cycles, as in Pimentel's and Yoshida et al.'s studies. For example, any form of density-dependent evolution can qualify as

the product of an eco-evo interaction to the extent that the organism has adapted to the impact its population has had on some abiotic or biotic feature of the local ecosystem.

Demonstration by Pimentel and Yoshida et al. of eco-evo interactions in model ecosystems creates the challenge of generalizing their results to the study of natural ecosystems. If we can, there is the promise that we can improve the predictive quality of ecology and evolution. Doing so first requires a more general framework for defining eco-evo interactions than Pimentel's "population regulation and genetic feedback." Ferrière et al. (2004) do so when they propose that reciprocity between ecology and evolution "arise(s) from the interaction of individuals with their local environment, which consists of abiotic factors as well as conspecifics, preys and predators, mutualists and parasites" (p. 5). Reciprocity occurs when an organism modifies some feature(s) of its environment and by doing so changes the kind of selection it experiences, causing it to evolve and, as a consequence, change its impact on the environment. "This two-way causal relationship—from the environment to the individuals, and back—defines the environment feedback loop that intimately links ecological and evolutionary processes" (p. 6). The difference between Pimentel's definition and that of Ferrière and colleagues is that the later authors expand the focus from pairwise, antagonistic interactions to a larger diversity of biotic interactions. They also include all of the other complexities of the ecosystem (e.g., nutrient cycling) that are involved with and can contribute to shaping such interactions.

The Symposium

Schoener (2011) identified experimental studies of eco-evo interactions in nature as the prevailing deficiency in the development of this field. The first goal of this symposium, represented by the first five articles, is to address this deficiency. Experiments like the rotifer-algae interaction plus associated theory tell us that eco-evo interactions have potential importance, but it remains fair game to ask whether such processes are evident in nature or whether they are just an artifact of the simplicity of a laboratory ecosystem. The reciprocity that is so clear in pairwise interactions in a model ecosystem may be dissipated by the diversity of interactions that prevail in a more complex, natural community. If such processes are there to be found, how do we characterize them if we do not have the luxury of a lab setting with evolving and nonevolving treatments? Where (e.g., in what types of species interactions) are they most likely to be seen? How important are they in explaining patterns in nature versus all of the other deterministic and stochastic forces traditionally thought to be most important?

The second goal of this symposium is to fulfill the Society of American Naturalists' ideal of expanding on the conceptual unification of the life sciences. The last two articles do so by addressing the potential role of eco-evo interactions in a wider array of circumstances.

The opening article of this collection by Travis et al. (2013) begins by looking back in time to expand on prior historical reviews of the interaction between ecology and evolution. The authors show that this perspective was well established before Pimentel in earlier treatments of density-dependent selection. They then look forward in time by reviewing their own work on density-dependent selection in the least killifish (*Heterandria formosa*). Their combination of past and current research on this system shows that natural populations are systematically different in their exposure to density regulation and have correlated differences in life-history traits. They then show that documenting adaptation to density is not a straightforward venture. They compared killifish from the high- versus low-density populations in two contexts. In the first, each was cultured separately at either high or low densities. In the second, they were competed against one another at high and low densities. Differences among populations in density-dependent fitness were visible only in the design that pitted the two populations against one another across a range of densities.

The next three works present experimental studies of eco-evo interactions and support the argument for reciprocity to varying degrees. Turley et al. (2013) build on the long-term rabbit exclusion experiments initiated by M. J. Crawley at Silwood Park. They focus on the evolution of the perennial herb *Rumex acetosa* by comparing individuals derived from seeds collected from rabbit-exclusion enclosures that range in age from 4 months to 26 years. Their study includes an evaluation of one possible component of eco-evo feedback, which is the evolution of competitive ability. The height and density of plants is far greater when rabbits are excluded, so it is reasonable to assume that interspecific competition is intensified as well. They find no evidence for such an interaction.

Agrawal et al. (2013) fulfill half of the required reciprocity by showing that evolution changes ecology. They report on a field experiment in which they observe rapid evolution of shorter life span and later flowering date of evening primrose (*Oenothera biennis*), which in turn reduces the abundance of a specialist seed predator moth (*Mompha brevivittella*). They initiated their experiment with replicate communities that each contained an equal abundance of the same genotypes and then documented evolution as a change in genotype frequencies over three seasons. Future research will address whether the second half of the reciprocity cycle is fulfilled. Doing so requires that Agrawal and colleagues show that the ecological

change in turn changes the selection experienced by the moth or primrose and alters their direction of evolution.

Turcotte et al. (2013) report on a study in which they document a complete eco-evo cycle by showing that evolution changes population dynamics, as done by Yoshida et al. (2003). They report on experiments on eco-evo feedbacks within populations of the green pea aphid (*Myzus persicae*) feeding on wild mustard (*Hirschfeldia incana*). The results reported here are part of a family of experiments conducted either in a greenhouse or in the field (Turcotte et al. 2011a, 2011b) in which eco-evo feedbacks are tested by quantifying population dynamics (ecology) in evolving and nonevolving experimental populations. Nonevolving controls were initiated with a single clone of aphids, while evolving treatments were initiated with multiple clones. This new study shows that aphid density alters the rate and direction of evolution and that these different evolutionary dynamics in turn alter population growth. While the experiment reported here was done in a greenhouse, the collection of experiments documents a complete feedback between ecology and evolution, including experimental evolution studies in nature.

All three groups of investigators witnessed evolution in the context of replicated experiments performed in nature. Turcotte et al. documented evolution within 16 days (two to three generations) and Agrawal et al. within three to four generations. Turley et al. report linear evolution of decreased growth rate over 26 years, or up to 26 generations. Such rapid evolution facilitates the study of eco-evo interactions, but only one of the three studies thus far yields evidence for a complete cycle of interaction between ecology and evolution. In that one case, it was possible to show why the interaction matters—it resulted in an acceleration in the rate of population growth relative to what one would predict if evolution had not occurred.

Luo and Koelle (2013) present a theoretical perspective on the study of reciprocal evolutionary and ecological interactions between hosts and pathogens. They cite Pimentel's descriptor of the effects of eco-evo interactions as often being "devious" in the sense that such dynamics often cause quantitative rather than qualitative differences in the outcome and may be similar in effect to other types of ecological interactions. In this role, eco-evo interactions remain important contributors to shaping the outcome yet may be harder to recognize because their impact does not generate the same sort of qualitative effects as seen in the work of Yoshida et al. (2003). Luo and Koelle show that one can demonstrate the importance of such interactions by coupling experiments with mechanistic models that define the differences in outcome expected with and without such interactions.

What do these articles add to the current state of the art? Turcotte et al. subscribe to the rigor of having an

evolution treatment and a nonevolving control and demonstrate an eco-evo interaction. An important distinction between Turcotte et al. and the prior work of Yoshida et al. is that Yoshida and colleagues worked with an abstracted ecosystem (two species in a chemostat). Turcotte et al. show that this work can also be done in a natural ecosystem, do so with an organism of great economic importance, and show that evolution can cause a 10% increase in the rate of population growth. In related experiments, Turcotte et al. (2011a, 2011b) found that evolution caused differences of up to 42% in exponential growth rate.

All of the remaining works depart from this rigorous design because the alternative of a nonevolving control either is not possible or was not an included treatment. The question is whether eco-evo interactions can still be demonstrated without a nonevolving control. Travis et al. do so in the context of a wedding of comparative studies of natural populations and mesocosm experiments to reveal density-dependent evolution. Nash et al. and Agrawal et al. do so with experimental studies of evolution combined with assessments of key species interactions. While neither group demonstrates a full eco-evo cycle thus far, they at least point the way toward how a case can be built for such interactions with a combination of comparative and experimental studies. Luo and Koelle argue instead for a close coupling of mechanistic theory with empirical studies and show that it is possible to make inferences about such interactions even when they might otherwise be missed because they mimic more conventional interactions.

The final two articles contribute to the American Society of Naturalists' goal of seeking a conceptual unification of the life sciences. Both seek broader venues for addressing the possible interactions between ecology and evolution, first in contemporary ecosystems (Estes et al. 2013) and then in the geological record and the history of life (Kennedy 2013).

A prerequisite for there to be an interaction between ecology and evolution is that organisms must be able to change their ecosystem in a way that affects the selection that they and other organisms experience. Estes et al. (2013) present a summary of a large body of ecological work that demonstrates strong impacts of individual organisms on their ecosystems. While this work lies outside of the formal study of the interaction between ecology and evolution, it shows how often we see circumstances that lend themselves to such interactions. Every time we see reference to a keystone species, trophic cascade, or ecosystem engineer, we are talking about how individual organisms affect the structure of their ecosystem. The study of such interactions is a common feature of the discipline of ecology, and they have been described in hundreds of

ecosystems. In a related work, Estes et al. (2011) summarize the ecological consequences of the anthropogenic trophic downgrading of natural ecosystems via the elimination of the apex predators. They illustrate the profound changes in the ecosystem that results, often because when predators are eliminated, herbivores proliferate and cause changes in the plant community, which in turn cause cascading effects on the entire ecosystem.

What has rarely been done in the context of such studies is to ask how these ecological changes feed back on evolutionary processes. Each of the many studies cited by Estes et al. (2013) represents a potential model for studying such interactions, because the presence of such strong ecosystem effects caused by individual species enhances our ability to find and characterize eco-evo interactions. The key to converting such prior knowledge into future studies of eco-evo interactions is to consider those species that are present with and without the key species that had a strong impact on the ecosystem. For example, when an apex predator is removed, causing herbivores to proliferate and in turn change the plant community, we would want to know how herbivores evolve in response to their impact on the community. Estes et al. (2013) illustrate this potential with their reinterpretation of the interactions among macroalgae and herbivores in marine environments and how those interactions have been shaped by the presence of otters in the Northern Hemisphere versus their absence in the Southern Hemisphere. The hundreds of examples of such strong ecological interaction in the literature thus present us with hundreds of venues for studying the potential importance of reciprocal interactions between ecology and evolution. Anyone who wishes to initiate such a research program can find in this article a diversity of ecosystems for which the literature provides a promising point of entry.

Martin Kennedy (2013) addresses the possible importance of interactions between ecology and evolution in deep time. Characterizing such interactions hundreds of millions to billions of years ago demands a paleobiogeochemist's perspective. There is little to be learned from the fossil record prior to the proliferation of the metazoans, but clues can be found in the chemistry of sediments formed in deeper time. Kennedy's interest is in the relationship between the concentration of oxygen in the atmosphere and the explosion of metazoan life. We all know that the oxygen in the atmosphere is the product of photosynthetic life and that free oxygen helped shape subsequent evolution, but it turns out that there is a peculiar lag between the advent of photosynthesis and the accumulation of oxygen in the atmosphere. Photosynthesis evolved at least 2.5 billion years ago, but it was not until 600 million years ago that oxygen concentration began to increase toward present levels. The appearance and pro-

liferation of the *Metazoa* soon followed. Kennedy argues that this increase in atmospheric oxygen was associated with the proliferation of photosynthetic life on land, even though we currently have no direct evidence of such life. He also argues that the spike in atmospheric oxygen could not be a simple, direct consequence of the production of oxygen by these terrestrial photosynthesizers, since photosynthesis began billions of years earlier. It was instead caused by an indirect consequence of life on land that can be read in the accumulation of clay sediments from coastal marine deposits. Our contemplation of the importance of such reciprocity on a macroevolutionary scale begs the question that always applies to macroevolutionary phenomena: are the mechanisms that underlie macroevolution the same as those that operate on a microevolutionary scale? At the very least, Kennedy's essay suggests that eco-evo interactions have been of fundamental importance in shaping the history of life and that the scope of these interactions has yet to be fully characterized.

Where to Go from Here?

The goal of the symposium is to advocate moving the study of eco-evo interactions out of the laboratory and into nature. The question is whether there are any general lessons to be inferred from this collection of articles about how to do so. A good starting point is to ask how well the empirical studies included here conform to Fussmann et al.'s (2007) criteria for demonstrating eco-evo interactions. These criteria include (1) the characterization of multispecies dynamics over multiple generations, accompanied by evidence of evolution in at least some of them; (2) the characterization of a mechanistic link between ecological and evolutionary dynamics; and (3) the presence of a "control" that characterizes what the joint population dynamics are when evolution does not occur (Fussmann et al. 2007, p. 6). I would add to criterion 2 the explicit statement that the link between ecology and evolution be shown to be reciprocal, following Pimentel (1961) and Ferrière et al. (2004). All criteria save the last are characterized in studies such as those by Turley et al. (2013) and Agrawal et al. (2013). The last criterion will be the most difficult to address with experiments performed in natural communities, unless we restrict ourselves to working on organisms capable of clonal propagation, as did Turcotte et al. (2013), or perhaps manipulate the capacity of populations to evolve by creating treatments with substantially different levels of genetic variation. If we are to make progress in studying eco-evo interactions in a broader array of organisms, then we need to find ways around the necessity of a nonevolving control. One approach is the coupling of experiments with models, as proposed by Luo and Koelle (2013) or as done by Duffy

and coauthors (Duffy and Sivars-Becker 2007; Duffy and Hall 2008; Duffy et al. 2009) in their studies of host-pathogen interactions in natural communities.

A second possible approach is the combination of experiments deployed in the other four empirical studies included in this collection and in associated works by the same authors. In a companion article to the one in this collection, Agrawal et al. (2012) excluded herbivores from half of their experimental plots. This manipulation represents an ecological equivalent of Rice's (1996) separation of male and female evolution in *Drosophila* to reveal intergenomic conflict. Such conflict was all but invisible without manipulation because of the constant "rapprochement" of male-female coevolution. It took experimental manipulation to reveal that not only was conflict present but also it was likely to be constant and intense. Likewise, it was only through the removal of herbivores that it became apparent that the natural plant community represented a balance of interspecific competition among plant species and the relative susceptibility of each species to herbivores. Both competitive ability and resistance to herbivores evolved rapidly enough to affect the balance of these ecological interactions and the ultimate composition of the communities, but neither form of evolution would be visible without the experiment. The rapidity of the observed evolution (three to four generations) demonstrates the potential importance of eco-evo interactions in structuring natural communities.

In my own research program, my colleagues and I are coupling comparative studies and experiments in our characterization of eco-evo interactions in stream communities in Trinidad. Our study is built around how guppies adapt to life with and without predators. Guppy populations respond to a low risk of predation in the same way herbivore communities do to the extirpation of apex predators (Estes et al. 2011), which is that they increase in population density. Because we have many natural populations for which we have already documented convergent evolution in response to life with and without predators (Reznick and Bryga 1996; Reznick et al. 1996), it is possible to look at eco-evo interactions in a retrospective fashion by comparing guppies adapted to these alternative environments. Our work includes experimental assessments of density regulation (Bassar et al. 2013; Reznick et al. 2012), density-dependent evolution (Bassar et al. 2013), the impact of guppies on their ecosystem, and how this impact changes as guppies adapt to different communities (Bassar et al. 2010, 2012). This combination of approaches has shown that guppies have diverse and easily quantified impacts on their ecosystem and that the way they have adapted to life without predators is in part a consequence of their impact on the ecosystem. Because it is possible to conduct experimental studies of evolution in natural populations

(Reznick and Bryga 1987; Reznick et al. 1990, 1997), it is also possible to study evolution prospectively. We are doing so by quantifying the simultaneous dynamics of evolution and ecology in natural streams by pairing sites where guppies are introduced with controls from which guppies are excluded.

While it remains to be seen how general and how important eco-evo interactions are, this collection of articles shows that they are amenable to study in natural ecosystems and that their effects can be substantial. My hope is that the collection will help set the stage for making progress in the study of eco-evo dynamics by providing access to ecosystems that are amenable to such studies and examples of methods for doing them.

Literature Cited

- Abrams, P. A., and H. Matsuda. 1997. Fitness minimization and dynamic instability as a consequence of predator-prey coevolution. *Evolutionary Ecology* 11:1–20.
- Agrawal, A. A., A. P. Hastings, M. T. J. Johnson, J. L. Maron, and J. P. Salminen. 2012. Insect herbivores drive real-time ecological and evolutionary change in plant populations. *Science* 338:113–116.
- Agrawal, A. A., M. T. J. Johnson, A. P. Hastings, and J. L. Maron. 2012. A field experiment demonstrating plant life-history evolution and its eco-evolutionary feedback to seed predator populations. *American Naturalist* 181(suppl.):S35–S45, doi:10.1086/666727.
- Andrewartha, H. G. 1957. The use of conceptual models in population ecology. *Cold Spring Harbor Symposia in Quantitative Biology* 22:219–236.
- Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago.
- Antonovics, J. 1976. The new ecological genetics. *Systematic Botany* 1:233–245.
- Bassar, R. D., R. Ferrière, A. Lopez-Sepulcre, M. C. Marshall, J. Travis, C. M. Pringle, and D. N. Reznick. 2012. Direct and indirect ecosystem effects of evolutionary adaptation in the Trinidadian guppy (*Poecilia reticulata*). *American Naturalist* 180:167–185.
- Bassar, R. D., A. Lopez-Sepulcre, J. Travis, and D. N. Reznick. 2013. Experimental evidence for density-dependent regulation and selection on Trinidadian guppy life histories. *American Naturalist* 181:25–38.
- Bassar, R. D., M. C. Marshall, A. Lopez-Sepulcre, E. Zandonata, S. K. Auer, J. Travis, C. M. Pringle, et al. 2010. Local adaptation in Trinidadian guppies alters ecosystem processes. *Proceedings of the National Academy of Sciences of the USA* 107:3616–3621.
- Birch, L. C. 1957. The role of weather in determining the distribution and abundance of animals. *Cold Spring Harbor Symposia in Quantitative Biology* 22:203–218.
- Darwin, C. 1859. On the origin of species by means of natural selection. J. Murray, London.
- Duffy, M. A., and S. R. Hall. 2008. Selective predation and rapid evolution can jointly dampen effects of virulent parasites on *Daphnia* populations. *American Naturalist* 171:499–510.
- Duffy, M. A., S. R. Hall, C. E. Caceres, and A. R. Ives. 2009. Rapid evolution, seasonality, and the termination of parasite epidemics. *Ecology* 90:1441–1448.
- Duffy, M. A., and L. Sivars-Becker. 2007. Rapid evolution and ecological host-parasite dynamics. *Ecology Letters* 10:44–53.
- Estes, J. A., J. S. Brashares, and M. E. Power. 2013. Predicting and detecting reciprocity between indirect ecological interactions and evolution. *American Naturalist* 181(suppl.):S76–S99, doi:10.1086/668120.
- Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, et al. 2011. Trophic downgrading of planet earth. *Science* 333:301–306.
- Ferrière, R., U. Dieckmann, and D. Couvet. 2004. Introduction. Pages 1–14 in R. Ferrière, U. Dieckmann, and D. Couvet, eds. *Evolutionary conservation biology*. Cambridge University Press, Cambridge.
- Fussmann, G. F., S. P. Ellner, K. W. Shertzer, and N. G. Hairston. 2000. Crossing the Hopf bifurcation in a live predator-prey system. *Science* 290:1358–1360.
- Fussmann, G. F., M. Loreau, and P. A. Abrams. 2007. Eco-evolutionary dynamics of communities and ecosystems. *Functional Ecology* 21:465–477.
- Hutchinson, G. E. 1965. The ecological theater and the evolutionary play. Yale University Press, New Haven, CT.
- Janzen, D. H. 1980. When is it coevolution? *Evolution* 34:611–612.
- Kennedy, M. 2013. The nonlinear effects of evolutionary innovation biospheric feedbacks on qualitative environmental change: from the microbial to metazoan world. *American Naturalist* 181(suppl.):S100–S111, doi:10.1086/670023.
- Luo, S., and K. Koelle. 2013. Navigating the devious course of evolution: the importance of mechanistic models for identifying eco-evolutionary dynamics in nature. *American Naturalist* 181(suppl.):S58–S75, doi:10.1086/669952.
- Nicholson, A. J. 1957. The self-adjustment of populations to change. *Cold Spring Harbor Symposia in Quantitative Biology* 22:153–173.
- Orians, G. H. 1962. Natural selection and ecological theory. *American Naturalist* 96:257–263.
- Pimentel, D. 1961. Animal population regulation by the genetic feedback mechanism. *American Naturalist* 95:65–79.
- . 1968. Population regulation and genetic feedback. *Science* 159:1432–1437.
- Pimentel, D., W. P. Nagel, and J. L. Madden. 1963. Space-time structure of the environment and the survival of parasite-host systems. *American Naturalist* 97:141–167.
- Reznick, D. A., H. Bryga, and J. A. Endler. 1990. Experimentally induced life-history evolution in a natural population. *Nature* 346:357–359.
- Reznick, D. N., R. D. Bassar, J. Travis, and F. H. Rodd. 2012. Life-history evolution in guppies. VIII. The demographics of density regulation in guppies (*Poecilia reticulata*). *Evolution* 66:2903–2915.
- Reznick, D. N., and H. Bryga. 1987. Life-history evolution in guppies. 1. Phenotypic and genotypic changes in an introduction experiment. *Evolution* 41:1370–1385.
- . 1996. Life-history evolution in guppies (*Poecilia reticulata*: Poeciliidae). V. Genetic basis of parallelism in life histories. *American Naturalist* 147:339–359.
- Reznick, D. N., F. H. Rodd, and M. Cardenas. 1996. Life-history evolution in guppies (*Poecilia reticulata*: Poeciliidae). IV. Parallelism in life-history phenotypes. *American Naturalist* 147:319–338.
- Reznick, D. N., F. H. Shaw, F. H. Rodd, and R. G. Shaw. 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science* 275:1934–1937.

- Rice, W. R. 1996. Sexually antagonistic male adaptation triggered by experimental arrest of female evolution. *Nature* 381:232–234.
- Roughgarden, J. 1976. Resource partitioning among competing species: a coevolutionary approach. *Theoretical Population Biology* 9:388–424.
- Schoener, T. W. 2011. The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. *Science* 331:426–429.
- Shertzer, K. W., S. P. Ellner, G. F. Fussmann, and N. G. Hairston. 2002. Predator-prey cycles in an aquatic microcosm: testing hypotheses of mechanism. *Journal of Animal Ecology* 71:802–815.
- Travis, J., J. Leips, and F. H. Rodd. 2013. Evolution in population parameters: density-dependent selection or density-dependent fitness? *American Naturalist* 181(suppl.):S9–S20, doi:10.1086/669970.
- Turcotte, M. M., D. N. Reznick, and J. D. Hare. 2011*a*. Experimental assessment of the impact of rapid evolution on population dynamics. *Evolutionary Ecology Research* 13:113–131.
- . 2011*b*. The impact of rapid evolution on population dynamics in the wild: experimental test of eco-evolutionary dynamics. *Ecology Letters* 14:1084–1092.
- . 2013. Experimental test of an eco-evolutionary dynamic feedback loop between evolution and population density in the green peach aphid. *American Naturalist* 181(suppl.):S46–S57, doi:10.1086/668078.
- Turley, N. E., W. C. Odell, H. Schaefer, G. Everwand, M. J. Crawley, and M. T. J. Johnson. 2013. Contemporary evolution of plant growth rate following experimental removal of herbivores. *American Naturalist* 181(suppl.):S21–S34, doi:10.1086/668075.
- Yoshida, T., N. G. Hairston, and S. P. Ellner. 2004. Evolutionary trade-off between defence against grazing and competitive ability in a simple unicellular alga, *Chlorella vulgaris*. *Proceedings of the Royal Society B: Biological Sciences* 271:1947–1953.
- Yoshida, T., L. E. Jones, S. P. Ellner, G. F. Fussmann, and N. G. Hairston. 2003. Rapid evolution drives ecological dynamics in a predator-prey system. *Nature* 424:303–306.

Editor: Judith L. Bronstein