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The Newest Synthesis: Understanding the Interplay of Evolutionary and Ecological Dynamics

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The effect of ecological change on evolution has long been a focus of scientific research. The reverse—how evolutionary dynamics affect ecological traits—has only recently captured our attention, however, with the realization that evolution can occur over ecological time scales. This newly highlighted causal direction and the implied feedback loop—eco-evolutionary dynamics—is invigorating both ecologists and evolutionists and blurring the distinction between them. Despite some recent relevant studies, the importance of the evolution-to-ecology pathway across systems is still unknown. Only an extensive research effort involving multiple experimental approaches—particularly long-term field experiments—over a variety of ecological communities will provide the answer.

Three-quarters of a century ago, the New Synthesis—an integration of paleontology, systematics, morphology, and genetics—captured the imaginations of evolutionary biologists. Ecology, then less well developed, played a relatively small role in this synthesis, even though the major influence of ecological processes on evolutionary trajectories was recognized. The dynamical effect of evolution on ecology, however, has only recently become widely appreciated. Here I review the emerging field of eco-evolutionary dynamics, whose major precept is that both directions of effect—ecology to evolution and evolution to ecology—are substantial. The general argument is as follows: Many studies have documented that ecological change affects evolution; indeed, natural selection is where ecology and evolution meet. Such studies of “evolution in action,” i.e., over observable time scales, show that evolution can be very rapid. This opens the possibility that evolutionary dynamics can also affect ecology; specifically, evolution can occur so quickly that ecological and evolutionary change may be commensurate in time and may interact in a feedback loop. Despite the potential for a directional influence of evolution on ecology, conceptual bolstering from mathematical theory, and some recent empirical studies, we still don’t know if the evolution-ecology pathway is frequent and strong enough in nature to be broadly important.

Ecology Affects Evolution

Many studies have shown that evolution is shaped by ecology. The most detailed of these concern ongoing observations of natural selection (1) driving phenotypic response to changing environmental conditions. A well-known example is found in work on a Galápagos ground finch, *Geospiza fortis*. In this species, larger beaks dominated the population after dry years when large seeds were more available. Correspondingly, after wet years

the direction of selection reversed, favoring smaller beaks that were more appropriate for handling the small seeds produced in the wet environment. These results demonstrate an immediately observable adaptive response to selection favoring animals with the beak best suited for handling available food (2). A second set of examples involves life histories and morphologies of fish. Intense harvest resulted in Atlantic cod (*Gadus morhua*) evolving earlier maturation and a smaller adult body size (3). A similar pattern was observed among guppies (*Poecilia reticulata*) after experimental predator introduction (4). In these cases, rapid adaptation for smaller body size and an earlier age at reproduction occurred in response

to intense predation. Finally, steelhead and rainbow trout are both members of the species *Oncorhynchus mykiss*; however, steelhead migrate, whereas rainbows do not. In an already classic case not only of adaptation but also of rapid speciation, steelhead trout introduced (in 1910) to a stream isolated above a waterfall evolved a rainbow trout non-migratory life-style. Rainbow-like steelhead later able to move across the falls were reproductively isolated from the ancestral steelhead population (5). In short, here adaptation to local ecological conditions resulted in not only a change in behavior, but also adaptive divergence and subsequent inability to breed with the ancestral population.

Evolution Can Be Fast...

By definition, observations of evolution in action document extremely rapid evolution. The number of reliable studies in which natural selection has been observed has increased markedly since Endler reviewed them in his classic 1986 book, *Natural Selection in the Wild*. The most comprehensive discussions are by Reznick and colleagues (4, 6), who found 47 studies demonstrating or implying rapid evolution for a variety of traits (morphological, physiological, life-history, phenological, and behavioral). Most examples involve colonization events, i.e., invasion, or local changes in semi-isolated populations across a varying environment (7). Although the examples are all from nature (rather than the laboratory), humans, by deliberate or accidental introduction or other environmental modification, have spurred many of them: Human predatory activities are especially effective (8). Indeed, without recent and severe anthropogenic actions, the list

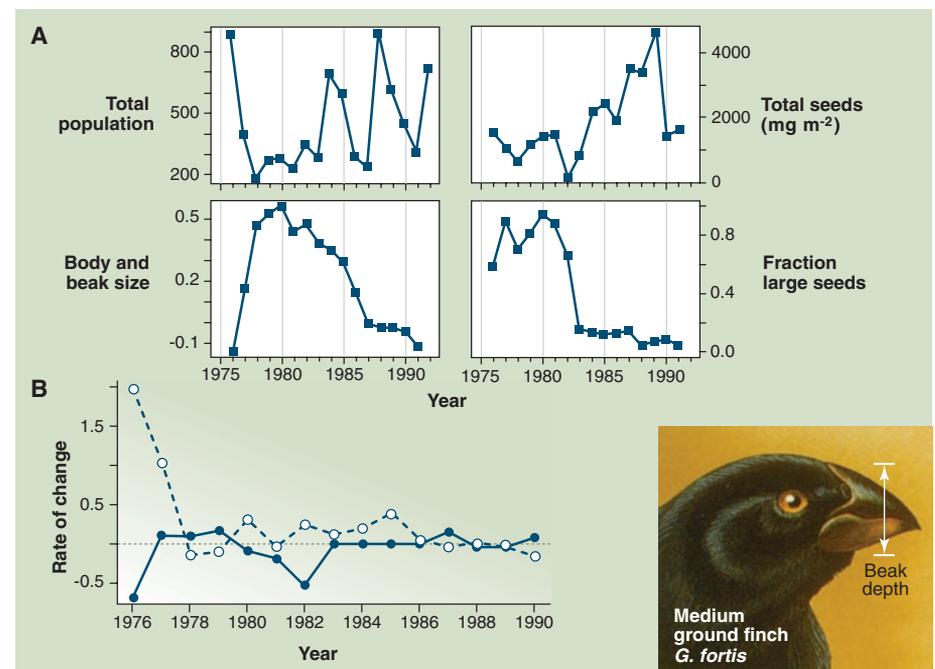


Fig. 1. (A) Dynamics for evolutionary and ecological traits in *G. fortis*. **(B)** The annual ecological (solid line) and evolutionary (dashed line) contributions to the total rate of change (per year) in population growth rate. [From Hairston *et al.* (11)]

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of cases of rapid evolution would be much shorter. In view of such studies, our concept of evolutionary time is also changing rapidly. As Fussmann *et al.* (9) highlight: “By rapid evolution we mean evolution occurring on time scales tractable in laboratory studies of population dynamics—up to about 1000 generations but typically many fewer.” This was much shorter than the half-million years for evolutionary time given by the ecologist Slobodkin in his classic 1961 book, *Growth and Regulation of Animal Populations* (10); his ecological time was “on the order of ten times the generation time of the species involved.” Hairston *et al.* (11) go the farthest in defining “rapid evolution” as “a genetic change rapid enough to have a measurable impact on simultaneous ecological change,” thus coming full circle.

These reinterpretations of how quickly evolution can occur open the door to the possibility that evolutionary dynamics can affect ecological dynamics—in principle. We have just seen that, because evolution can be so fast (4, 6, 8), evolutionary and ecological time can be commensurate. Indeed, natural selection and population dynamics are both affected by births and deaths of individuals (12–14). In fact, in the founding paper on selection gradients (15), mortality in house sparrows (*Passer domesticus*) after a winter storm provided an illustrative example for the computations. To paraphrase Kokko and López-Sepulcre (16): Assessing fitness is ultimately counting offspring that transmit genes to future generations. Therefore, population dynamics (an ecological entity) can depend on the fitness of population members (an evolutionary entity). Similarly, an individual’s fitness can depend on the ecological trait of population density, including densities of conspecifics, heterospecific competitors, prey, or predators. Although tightly related, however, the link between natural selection and population dynamics is not entirely straightforward. Specifically, the measure of fitness used when calculating selection [e.g., (15)] is relative to other members of the population (i.e., how many more offspring does individual A produce relative to individual B, or the rest of the population). In contrast, in population dynamics we are concerned with the absolute output of an individual and how that contributes to population properties.

As summarized, that ecology affects evolution is the cornerstone of the natural selection concept. But can the reverse also happen to a substantial extent? More precisely, what is the contribution to population growth of evolutionary factors, such as genetically based phenotypic change, relative to ecological factors such as changes in the predation or resource regime or abiotic environmental change? The seminal 2005 paper by Hairston *et al.* (11), in which what has come to be called the “Geber method” was introduced, first tackled this question. Using a clever technique based on analysis of variance, Hairston *et al.* partitioned the factors causing year-to-year variation in population growth rate into, roughly speaking, evolutionary and ecological components. In the finch *G. fortis* discussed above (2), evolutionary contributions (via beak shape

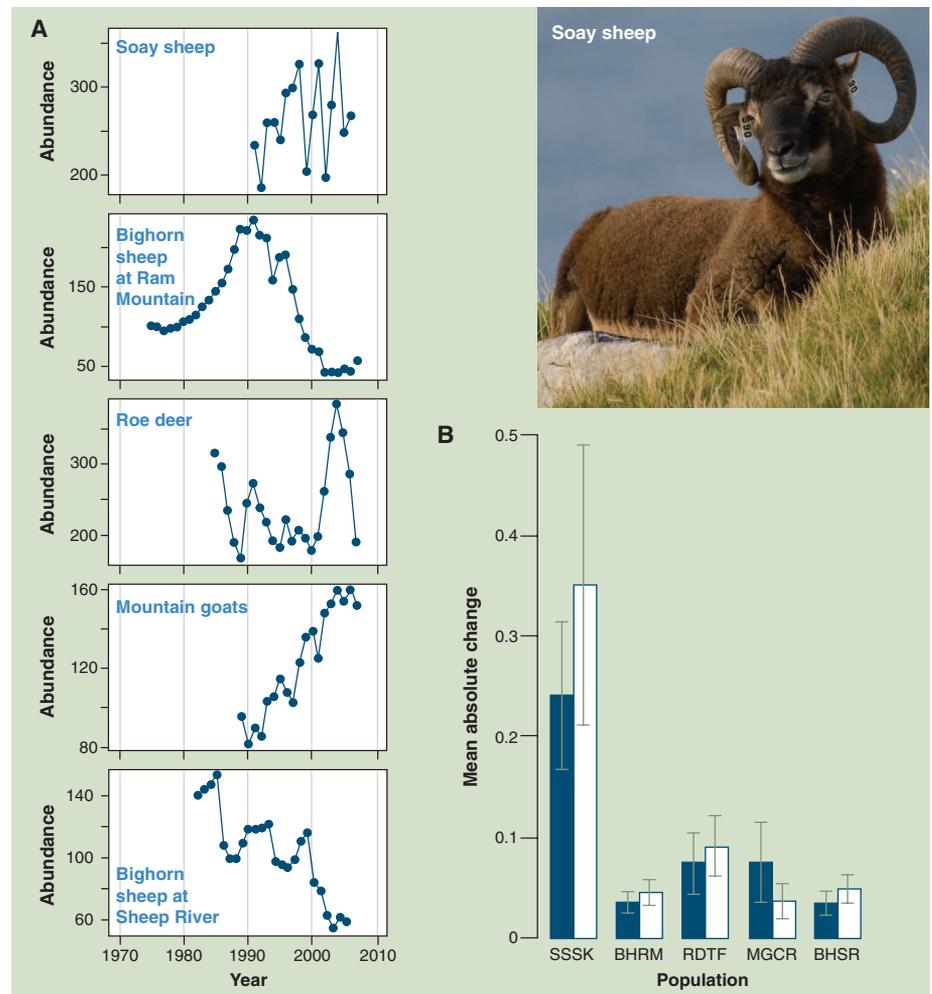


Fig. 2. (A) Population numbers for the five ungulate species in Ezard *et al.*'s (18) study. Time series are shown for the periods of each population analyzed. Species are (from top to bottom) Soay sheep, bighorn sheep at Ram Mountain, roe deer, mountain goats, and bighorn sheep at Sheep River. **(B)** Mean absolute change of environment (blue bars) and phenotype (white bars) with 95% parametric confidence intervals, calculated following Hairston *et al.* (11). The change quantifies the effects on population growth of environmental and phenotypic changes, respectively. Study populations follow the order in the left panel.

and body size) exceeded ecological contributions (via seed density and fraction of large seeds) by a factor of 2.2 (Fig. 1). For Hairston *et al.*'s data on the copepod *Onychodaptomus sanguineus*, the evolutionary contribution (via life history: whether diapausing or immediately hatching eggs are produced) was one-fourth the ecological contribution (via fish predation), which they call “less than in the finch example, but nevertheless substantial.” They also applied a related method to Abrams and Matsuda's (17) model of predator-prey dynamics, showing that evolutionary effects are substantial but not dominant, being 63% of ecological effects. Ezard *et al.* (18) recently used the Hairston *et al.* methodology to partition population change for five ungulate species. They characterize the evolutionary (morphological variables) versus ecological (vegetational and climatic variables) contributions as “statistically indistinguishable” (Fig. 2). Indeed, the best supported model includes both evolutionary and ecological factors, as well as the interaction between them.

In retrospect, we can ask why the correspondence of ecological and evolutionary time was not recognized [e.g., (10)]. Kinnison and Hairston (19) suggest two major reasons. First, fitness gains made in the course of selection might not much influence the equilibrium population size, e.g., the carrying capacity, because of strong negative density-dependent regulation. Saccheri and Hanski (20) conclude that explicit demonstrations of this are few, despite theoretical plausibility. Second, the rate of evolution in the paleontological record is “ponderous,” and this is inconsistent with rapid evolution observed in contemporary studies. Thompson (21) suggests this is because episodes of one-way directional selection are interspersed with episodes of stasis or even episodes of selection in the other direction. Hendry and Kinnison (22), building on Gingerich (23), combined data from various studies and showed that the longer the observation period, the weaker the evolution—thus a kind of bias exists [the same trend was found later by Hoekstra *et al.* (24) for studies of

selection measured by survival]. To explore the issue farther, Hairston *et al.* (11) supplemented Hendry and Kinnison's data with per-generation data for two species—the finch and the copepod discussed above—and found that short time intervals could give very low rates of evolution as well as high ones [Fig. 3; see also (6, 25)]. So there is a bias, but it is mainly that the variance of the rates decreases with length of the observation period. Further, that selection can frequently change direction has recently become well established thanks to Siepielski *et al.*'s (26) review of 89 studies incorporating 5519 estimates of selection.

As a result of these and other studies, a frequent correspondence of ecological and evolutionary time is now widely accepted. For example, Carroll *et al.* (27) say “the real distinction between microevolution [short-term] and macroevolution [long-term] may lie only in the degree to which the factors causing evolution are fluctuating or are gradually and persistently directional, and not in the ecological significance of that evolution.” Indeed, the entire issue has been raised almost to the level of a scientific manifesto, where opposition is considered misguided and fruitless. Thus, Kinnison and Hairston (19) could say: “The notion that evolutionary processes are vanishingly slow, and that contemporary evolution is exceptional, does not match current scientific knowledge and is counterproductive.”

...But Few Empirical Examples Exist of Evolution Affecting Ecological Dynamics

Four recent reviews (28–31) have shown that genetic variation within a species can affect its ecological community. It is now even becoming possible to generalize about what ecological units are most affected: Bailey *et al.* (30) showed that effects of within-plant-species genetic variation are strongest at the individual level (phytochemistry, physiology, morphology) and weakest at the community (species richness, total abundance, community composition) and ecosystem (carbon accumulation, productivity, soil-nutrient dynamics) levels.

These reviews generally deal with static properties, or what Losos (32) has called “retrospective studies, how present day ecological processes can be understood as the outcome of historical events.” In contrast, to understand the ongoing effects of evolution on population dynamics, we need studies over multiple generations in real time. How many might there be? An attempt to determine this number precisely was made in 2007 by Fussmann *et al.* (9), who isolated “the handful of [studies] that... come close to providing empirical support for eco-evolutionary community dynamics.” Their criteria were as follows: (i) Does the study document change of abundance of multiple populations over several generations? (ii) Is there a record of genetic frequencies and their changes over time? (iii) Is there a plausible mechanistic link between ecological and evolutionary dynamics? (iv) Is there a control reporting ecological dynamics in the absence of evolution? No single study fulfilled all criteria, and only eight studies came close to qualifying. Of

these, all satisfy criterion 1, but five fail at criterion 2 or 4, and three meet neither (33). Six studies were performed in the laboratory and two in the field (the latter were observational, not experimental, and include the finch study discussed above).

Is the lack of field-experimental studies a deficiency? Two properties of field experiments argue that it is. First, field conditions are natural, incorporating most of the background of the phenomena we are trying to understand. Second, experimental design is rigorous in that it employs

used combinations of guppy and killifish (*Rivulus hartii*) populations with different evolutionary histories to simulate invasion, one-species evolution, and coevolution. They found responses in ecosystem properties such as algal biomass and decomposition. In some cases, the evolutionary treatments had larger effects than the ecological (invasion) treatment. Bassar *et al.* (37), also using guppies, showed that different phenotypes were associated with different values of ecosystem structures (biomasses of various groups) and functions

(productivity, nutrient flux, leaf-decomposition rates), much as Harmon *et al.* showed. Although all experimental and field [or mesocosm (38)] based, none of these studies was dynamic in Fussmann *et al.*'s sense (with the partial exception of Johnson *et al.*, which ran for 2 years). Rather, most fall into Losos's (32) “retrospective” category—how ecology can result from historical events.

Nine studies appearing after Fussmann *et al.*'s review went to press are multigenerational. Three were field-observational and on mammals: Pelletier *et al.* (39) on Soay sheep, Ozgul *et al.* (40) on yellow-bellied marmots (*Marmota flaviventris*), and Ezard *et al.*'s ungulate study (18) discussed above. The six others were experimental but were conducted in the laboratory: Kerr *et al.* (41), Bull *et al.* (42), and Brockhurst *et al.* (43) on bacteria and phage; Lennon and Martiny (44) on cyanobacteria and viruses; terHorst *et al.* (45) on protozoans and mosquitoes; and Becks *et al.* (46) on algae and rotifers. To elaborate on one, Kerr *et al.* devised a metapopulation using plates on which the bacterial host *Escherichia coli* inhabited media-filled wells. The pathogenic phage always wiped out the bacteria within each well

and then went extinct, resulting in an empty well that could be recolonized by bacteria. The setup selected over time for “prudent” phage if migration between wells was restricted, whereas “rapacious” phage was selected under unrestricted migration. The evolution of the prudent variety is reminiscent of *Myxoma* virus and rabbits, one of Fussmann *et al.*'s qualifying examples: Less virulent virus strains were selected for. These laboratory studies provide valuable insights into the mechanics of the eco-evolutionary feedback process, and the observational studies analyze long-term field data in fundamentally new ways. Still, no field-experimental study has yet been published. An example of the form such a study can take is given in Fig. 4, which sketches an ongoing study using two species of island lizards.

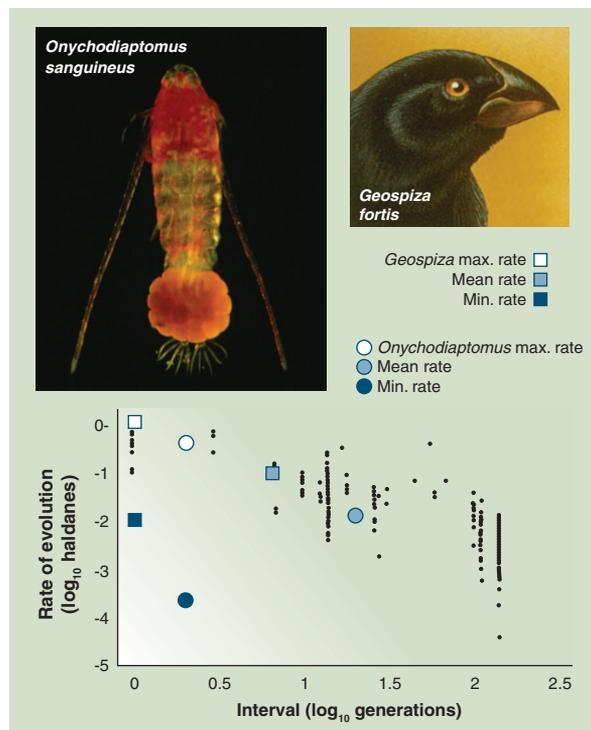


Fig. 3. Relation between rate of phenotypic evolution and number of generations over which measurements were made. Original figure (small dots) is from Hendry and Kinnison (22) with new calculations added for the finch *G. fortis* and the copepod *O. sanguineus*, showing the slowest, most rapid, and the average rates of evolution (per generation) over the 30- and 10-year, respectively, periods of study. [From Hairston *et al.* (11)]

random selection of arenas for the various treatments. Four field-experimental studies of how evolution affects ecological properties have appeared since the review of Fussmann *et al.*—would any meet their criteria? Harmon *et al.* (34) showed that combinations of two species of sticklebacks *Gasterosteus aculeatus* (from different habitats and with unique morphologies that had evolved repeatedly from a common ancestor) differentially affected community-ecological properties (primary production, dissolved organic matter, prey species diversity). Johnson *et al.* (35) experimentally generated selection on biomass, life history, and herbivore resistance of the primrose, *Oenothera biennis*. The resulting evolutionary changes affected abundance and diversity of the associated arthropods. Palkovacs *et al.* (36)

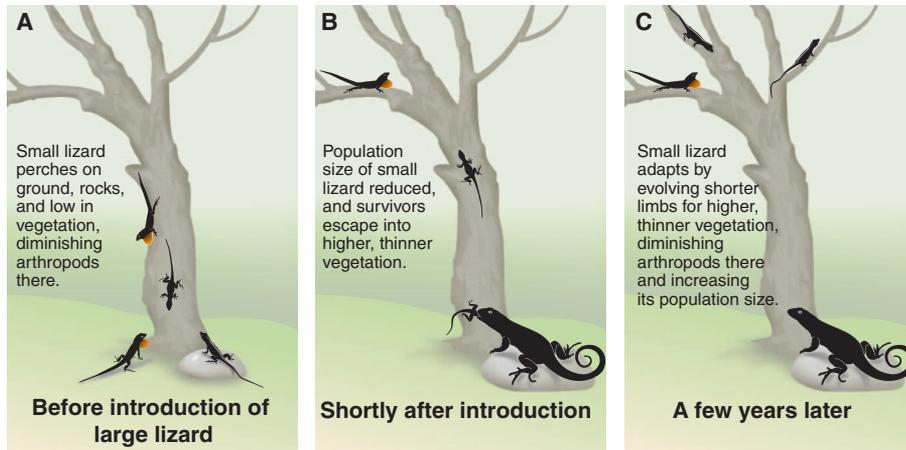


Fig. 4. Experimental approach used in ongoing study of eco-evolutionary dynamics in Caribbean lizards. **(A)** Before introduction of the large predatory lizard *Leiocephalus carinatus* (curly-tailed lizard), the smaller *Anolis sagrei* is found both on the ground and trunks of trees. **(B)** Introduction of predators may result in reduced population size and change in habitat use by *A. sagrei*. **(C)** Rapid evolution of *A. sagrei* could be precipitated by change in selection pressures, and this may have amplifying effects on the system in the form of altered arthropod densities and distributions, as well as increased population size of *A. sagrei* [as argued in Strauss *et al.* (54)].

Feedback Loops Between Evolution and Ecology: Will They Be Important or Trivial?

Dobzhansky notoriously said in 1964: “Nothing in biology makes sense except in the light of evolution.” This was supplanted half a century later by Grant and Grant’s (2): “Nothing in evolutionary biology makes sense except in the light of ecology.” Pelletier *et al.* (12) quickly followed with “Nothing in evolution or ecology makes sense except in the light of the other,” and this sentiment is pretty much where we are today. If ecology affects evolution (long supported) and evolution affects ecology (becoming increasingly supported), then what? The transformed ecology might affect evolution, and so on, back and forth in a feedback loop. Kokko and López-Sepulcre (16) call this “ecogenetic feedback”: “If density influences everyone’s reproductive prospects to the same extent, one has merely restated the ecological concept of density dependence. But if density variation has a differential effect on individual fitness depending on...phenotype, we have a feedback loop. In this loop, individual behavior or life history, influenced by genes, has an effect on population dynamics...and the resulting change in population dynamics in turn...[may] differentially favour...[certain] genotypes...in the population...”

The idea of feedback between evolution and ecology is not itself new. One of Fussmann *et al.*’s examples, Pimentel (47), developed his genetic feedback concept and tested it in the lab half a century ago. Taper and Case’s 1985 character displacement theory (48) modeled coevolution of competing species’ phenotypes and food niches while allowing food resources to change dynamically. Chitty also used a feedback idea to explain cycling selection between dispersers and homebodies in rodents (49); however, little supporting evidence was found and explicit modeling gave the opposite result—natural selection diminished cyclical behavior (50, 51).

Given this long history, what then is new about the emerging field of eco-evolutionary dynamics? Palkovacs *et al.* (36) say: “it remains a frontier to experimentally examine the ecosystem effects of dynamically evolving (and coevolving) populations in the wild...one potentially critical element that can only be captured using dynamic experiments is the eco-evolutionary feedback...” Herein lies the novelty current researchers are exploring. Because our investigations to reveal the role of such feedback are just beginning, it is hard to guess at the outcome. There are large open questions, the most important of which, according to Thompson (21), “is whether the persistence of interactions and the stability of communities truly rely upon ongoing rapid evolution...or whether such rapid evolution is ecologically trivial.” It is a question well worthy of the large research effort it will take to learn the answer.

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- Strictly speaking, observing natural selection is not the same as observing evolution. Evolution is defined as a change in gene frequency, and that selection resulted in genetic change is not always demonstrated. Among Reznick *et al.*’s (4) 47 studies, 30 provide “reasonable evidence for a genetic basis” such as estimates of trait heritability, reciprocal transplants, and common-garden experiments.
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