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Cryptic eco-evolutionary dynamics

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Natural systems harbor complex interactions that are fundamental parts of ecology and evolution. These interactions challenge our inclinations and training to seek the simplest explanations of patterns in nature. Not least is the likelihood that some complex processes might be missed when their patterns look similar to predictions for simpler mechanisms. Along these lines, theory and empirical evidence increasingly suggest that environmental, ecological, phenotypic, and genetic processes can be tightly intertwined, resulting in complex and sometimes surprising eco-evolutionary dynamics. The goal of this review is to temper inclinations to unquestioningly seek the simplest explanations in ecology and evolution, by recognizing that some eco-evolutionary outcomes may appear very similar to purely ecological, purely evolutionary, or even null expectations, and thus be cryptic. We provide theoretical and empirical evidence for observational biases and mechanisms that might operate among the various links in eco-evolutionary feedbacks to produce cryptic patterns. Recognition that cryptic dynamics can be associated with outcomes like stability, resilience, recovery, or coexistence in a dynamically changing world provides added impetus for finding ways to study them.

Keywords: rapid or contemporary evolution; eco-evolutionary feedback; stabilizing selection; evolutionary rescue; community genetics; coevolution

> “Numquam ponenda est pluralitas sine necessitate.”
> [Plurality must never be posited without necessity.]
> (Mis)attributed to William of Ockham (c. 1287–1347)

Introduction

Understanding complex processes in nature is an enduring goal and challenge for ecology and evolutionary biology.[1–4] Part of this challenge is that science has a long history of valuing simple but sufficient explanations with the hope they will offer greater generality and easier prediction with less a priori information. Indeed, this preference is embodied in Ockham’s razor, translated above. This principle of parsimony likely even predates Ockham by more than 1000 years,[5] and has been advanced historically as much on theological grounds as philosophical ones.[6] However, even given their relatively short scientific histories, ecology and evolution have become nearly synonymous with complexity and diversity in nature, and while parsimony might offer us a pragmatic place to begin weighing alternate hypotheses for underlying mechanisms, complexity is rarely far from our minds. Nonetheless, Ockham’s razor may be nearly as useful to us in studying complex systems as simple systems. Certainly, to apply the principle in a modern inferential context requires that we acknowledge and define complex explanations that might be weighed and tested against simpler ones. Importantly for our review here, the principle of parsimony, in recognizing alternative explanations for any given pattern in nature, also serves as a powerful reminder that when complex mechanisms really are at play in ecology and evolution, there is a decent chance that the patterns they generate will look similar to those from simpler expectations and thus be cryptic.

Cryptic dynamics can arise in systems when processes interact in a fashion that effectively conceals the action of one or more of those component processes. As we will show, systems that include

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feedbacks or compensatory mechanisms, or those whose component processes are highly nonlinear (e.g., purifying or stabilizing rather than directional), might be particularly prone to cryptic outcomes. In some cases, cryptic dynamics might appear as an absence of change or as stochastic change in some response metric, leading one to settle for an erroneous but parsimonious null model. In other cases, a cryptic dynamic might hasten or slow a transition already expected under a simpler model and thus be overlooked where predictions are imprecise. Cryptic dynamics thus present clear challenges when it comes to inferring process from observational data. In principle, this challenge might at times be overcome if one were able to add or remove the effects of subprocesses of interest so as to estimate their cryptic effects on the system. But then again, the impetus to build theory, experiments, or data sets to do this will often depend on anticipating the possibility of such complex dynamics in the first place. It is here that insights from theoretical arguments based on first principles, mounting empirical evidence, some good fortune, and some reconsideration of what is parsimonious can all play roles in fostering exploration. The objective of this review is to provide insights from theory and empirical research that might encourage broader and more targeted exploration of potential cryptic dynamics operating at the interface between ecology and evolution.

Eco-evolutionary dynamics are reciprocal interactions of ecological and evolutionary processes over what could be considered contemporary or ecological time scales that span up to a few hundred years, but can often be much shorter. The fundamental question the field seeks to answer is what happens to ecological and evolutionary outcomes when the ecologically pertinent characteristics of organisms evolve while ecological interactions are taking place. The synchronous and reciprocal nature of these interactions is central to this definition and the basis for much of the current interest in such a synthesis because that coupling increases the potential for dynamic feedbacks.[7–11] Hence, while it is certain that there are many ways in which evolution and ecology have shaped one another throughout the long history of life (e.g., evolution of photosynthesis as a basis for most modern food webs), our treatment focuses at microevolutionary scales where short-term feedbacks, as opposed to vast spans of time, can conceal the interplay of ecology and evolution. The operation of reciprocal feedbacks at these scales also partly distinguishes the study of eco-evolutionary dynamics from 20th century approaches to ecological genetics[12] and evolutionary ecology[13,14] that tended to emphasize ecology's role in shaping functionally relevant traits of organisms, and from empirical and theoretical work on community genetics[15–17] and niche construction,[18] which consider the ecological effects of intraspecific genetic variation or the role species play in shaping their own selective environments. However, as others have noted,[7–9,19] there is ample conceptual common ground among these fields that represents a convergence of sorts, with eco-evolutionary dynamics typically focusing on a more closely coupled set of interactions. Hence, our review both draws upon, and has relevance for, many of these related areas of investigation.

In this review, we focus on a broad class of eco-evolutionary dynamics that we suspect are at particular risk of being overlooked because they are *cryptic* (*sensu* Yoshida *et al.*[20]), that is, they may appear outwardly consistent with traditional ecological or evolutionary predictions or with the absence of any ecological or evolutionary change. As we will show, although such cryptic processes might actually reflect strong feedbacks between ecology and evolution, they are unlikely to be discovered without approaches designed specifically for that purpose. As with other types of cryptic dynamics,[21] motivation to develop such approaches and pursue these processes depends on our ability to anticipate them and weigh their likelihood relative to seemingly more parsimonious, but not necessarily realistic, models that do not link ecology and evolution as directly. Hence, we begin by considering some historical context and why we might often expect ecology and evolution to interact dynamically in contemporary time. We then review examples of processes that might lead to cryptic outcomes at different linkages throughout an eco-evolutionary feedback dynamic, and consider some approaches to detect such effects. We conclude with a consideration of why "cryptic" does not imply "less important," and we offer a modest recommendation for how we might remain attentive to the possibility of cryptic eco-evolutionary dynamics without suggesting that all studies must directly tackle these complex processes.

Historical and theoretical context

Most ecologists and evolutionary biologists recognize the operation of an important ecology-to-evolution pathway, where changes in ecological conditions provide the basis for natural selection. The converse pathway, from contemporary evolution to ecology, has received much less attention but is also not an entirely new concept. Sporadic but noteworthy attention to evolution's potential dynamic effects on ecology can be traced back to *The Origin of Species*, in which Darwin[22] placed considerable emphasis on evolution's ongoing role in interactions between varieties as a determinant of their extinction or persistence. This theme reemerges within the context of species coexistence, including Pimentel's[23] "genetic feed-back mechanisms" and Van Valen's[24] coevolutionary arms races (i.e., "Red Queen dynamics;" see also Ref. 25). Some other notable examples include Fisher's[26] suggestion that adapting populations do not grow at ever faster rates because of degrading effects of adaptation on the population's environment and Chitty's[27] hypothesis that selection on alternative behavioral types might explain population cycles in field voles (*Microtus agrestis*). We discuss some of these examples in more detail later, but readers familiar with these works might already note how they often depict outcomes where evolution's effects are suspected to balance other effects and thus risk being overlooked. While these early explorations made the case that ecology and evolution might interact, appreciation for the broader relevance of such interactions was likely impeded by prevailing perceptions about the typical rates of evolution and by the absence of much direct evidence for the ecological significance of intraspecific trait variation.

Although examples of contemporary evolution have been known nearly as far back as Darwin's time (e.g., moth melanism[28]), evolutionary change has historically been depicted to be much slower than most ecological change.[29] It is really only in the last couple of decades that this early perspective has begun to appreciably fade in response to accumulating examples of contemporary evolution in the wild,[30–33] and in turn be replaced by recognition of a near synonymy of evolutionary and ecological time scales.[32,34,35] Indeed, longitudinal studies of trait change in nature show that evolution is a highly dynamic process, readily tracking ecological and selective conditions.[36–40] This synonymy is to be expected given that evolution and ecology are linked at a fundamental level through the individual births, deaths, immigrations, and emigrations that underlie both evolution and population dynamics, and by extension the interactions of those populations with other species and their broader ecosystems. Moreover, this coupling can occur at even finer time scales than generations. Although evolution is often envisioned across generations, the actual changes in genetic frequencies that define evolution accrue almost continuously as products of ecological and reproductive interactions that play out throughout the course of a given generation. Little basis exists to assume fundamentally different time scales for the continuous and demographically associated processes of ecology and trait change.

Likewise, our empirical understanding of the ways in which intraspecific trait variation can have ecological effects has also grown dramatically in recent decades.[41,42] We review numerous examples of such trait effects in later sections of this review, and there is no reason not to expect such effects to be relatively common. At a minimum, every phenotypic trait of an individual requires some acquisition and expenditure of resources to produce; thus, compositional variations in those traits should have somewhat different effects on the individual's environment, however modest. Some might even arise through an organism's death.[43–45] Most traits probably have environmental and ecological effects far in excess of their rudimentary costs—otherwise natural selection would not favor them. Indeed, even the aforementioned compositional differences in tissues can have far-reaching effects, as exemplified by studies of the community and ecosystem consequences of leaf composition traits in trees.[46,47] At a more direct level, interaction strengths in ecology are fundamentally rooted in the trophic, competitive, or antipredator abilities of the interacting organisms. Trait specializations tied to these interactions represent some of the most conspicuous trait variation within species and are common among examples of contemporary evolution in the wild.[34,48]

As more and more examples of contemporary evolution and the ecological effects of phenotypic and genetic trait variation became apparent around the end of the last century and the start of the current one, theory and research on the interplay of ecology and evolution came to focus more explicitly on direct and reciprocal interactions. As noted by Hendry,[49] papers in a 2007 special issue of *Functional Ecology* on "Evolution on Ecological Time Scales" initiated wider use of the term *eco-evolutionary* to describe these directly coupled dynamics.[50–52] Somewhat mirroring the above historical studies, more recent theory and investigations have often been couched in terms of evolutionary contributions to population or metapopulation persistence,[50,53–56] coexistence in communities,[51,57,58] or alternate ecosystem conditions,[8,9,59–62] with some interesting nuances. Specifically, these newer studies and perspectives often highlight a pressing need for theory and insight to accommodate human disturbances to natural systems[50,54,63,64] and advocate for a genes-to-ecosystems synthesis[9,46,47,65] that increasingly looks toward genomic approaches.

To be clear, we do not mean to imply that every instance of trait change will be of primary consequence for every ecological dynamic of interest. Nor are we suggesting that simpler models that lack these coupled dynamics cannot be useful, or even mechanistically justifiable in some contexts, such as where heritable variation is so limited as to be unimportant. Rather, our points are that reciprocal interactions between ecology and evolution have been hypothesized for a very long time and that such eco-evolutionary dynamics might be implicit to many ecological and evolutionary outcomes in nature. To borrow terms from Ockham's translation, we have simply made the case that there is some "necessity" to merit our consideration of "plurality" more broadly. Of course, that recognition might initially appear at odds with the decades of ecological and evolutionary research that have successfully worked within simpler ecological or evolutionary frameworks. However, any seeming paradox depends on the degree to which one expects eco-evolutionary dynamics to produce distinctly different outcomes from those predicted under simpler models of ecology or evolution. We feel this is an expectation worth reconsidering for a nascent synthesis where our enthusiasm for novel insights and outcomes might bias us to overlook eco-evolutionary contributions to more common, but broadly important, patterns in nature.

Forms of cryptic eco-evolutionary dynamics

The variety of processes that might lead to cryptic eco-evolutionary dynamics is diverse and ranges from pragmatic limitations of study design and inference to specific evolutionary and ecological processes that conceal their own traces. To organize our discussion, we first consider some limitations tied to eco-evolutionary inference, what we refer to as *cryptic by oversight*, and then consider examples of processes that might operate at each link of an eco-evolutionary feedback dynamic (Fig. 1) to conceal the broader interplay of evolution and ecology.

Cryptic by oversight

Perhaps the simplest explanation for eco-evolutionary effects appearing cryptic is that we are not likely to identify evolution's interactive effects with ecology if our approaches lack sufficient power, resolution, treatments, or controls. It might seem odd to suggest such a large hole in our picture of the world, but meta-analyses of effect sizes in ecology and evolution suggest the vast majority of R^2 values for specific factors are less than 10%,[66] and that about half of total variation is unexplained even by multifactorial models.[67] This to be expected if the tools we employ to study ecology and evolution tend to be narrowly focused but imprecise. Hence, it is entirely feasible that we might miss effects of evolution on ecology, or vice versa, even where such effects are as large, or nearly as large, as other suspected drivers of interest. As a consequence, studies based on strictly ecological or evolutionary hypotheses can be acceptably supported but at the same time miss important eco-evolutionary contributions, particularly when experiments are not designed to detect such effects.

Many ecological experiments are designed in ways that have limited ability to detect evolutionary effects on ecological response metrics or reciprocal feedbacks. In some cases, ongoing selection and evolution could even confound ecological experiments.[68,69] Certainly, studies where ecological replicates are all derived from single source populations, or that conflate source population with other factors, are unlikely to point to additional evolutionary contributions because they are either obviated by the design or mistaken for other effects. Likewise, studies of laboratory evolution that hold

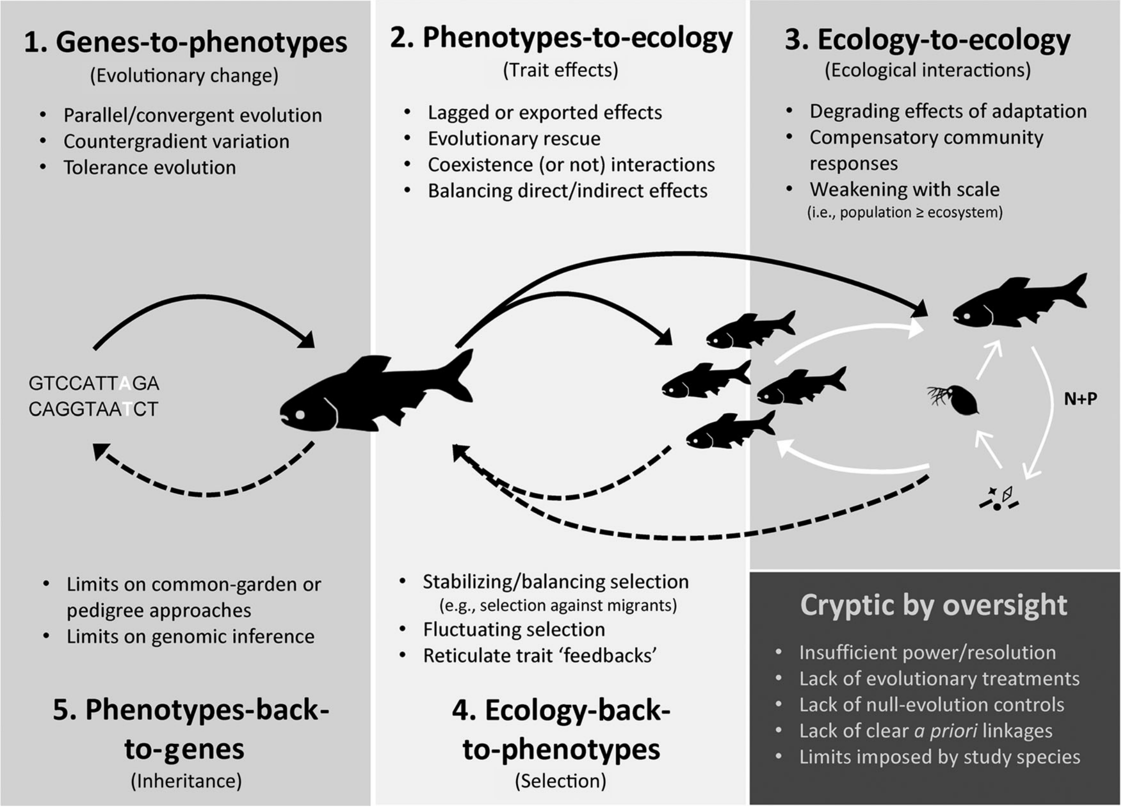

Figure 1. Cryptic links in an eco-evolutionary dynamic. A hypothetical genes-to-ecology pathway (solid black arrows) is shown where genetic differences among individuals (single fish) influence their respective phenotypes (1), that, in aggregate, directly (2) or indirectly (3) (white arrows) influence population (group of fish), community, or ecosystem interactions (food web and excretion). Reciprocally, an ecology-to-genes pathway (dashed arrows) arises where these ecological and environmental conditions have direct and indirect effects on the relative fitness of alternate phenotypes (4), leading to changes in gene frequencies in subsequent generations via trait inheritance (5). Ideally, one would provide evidence for each of these linkages to demonstrate a complete eco-evolutionary dynamic. However, that can be challenging, not only because of various functional mechanisms that can conceal each of these links (examples under 1–5), but also because of observational and experimental biases (*Cryptic by oversight* inset).

ecological conditions constant would miss any ecological feedbacks operating in nature. Another detection challenge arises where the coupled effects of evolution and ecology are to accelerate, decelerate, stabilize, or destabilize an ecological or evolutionary transition qualitatively predicted under a purely ecological or evolutionary model lacking feedbacks. These eco-evolutionary effects could be missed in designs that have sufficient power to detect qualitative changes but inadequate power to distinguish more quantitative nuances of eco-evolutionary predictions. This highlights the importance of not just planning for added evolutionary or ecological effects in a study, but of establishing adequate null expectations or treatments (null evolutionary, null ecological, null feedback) that would be most informative in gauging the potential scope and patterns of those added effects. Encouragingly, when studies are actually designed to detect eco-evolutionary outcomes, those effects are often large, even when compared to more typically considered environmental and ecological drivers.[17,32,39,46,60,70–75] Of course, we might also expect some ascertainment and reporting bias favoring detection and reporting of relatively large effects.

The above considerations, and prior successful studies, suggest some fairly direct ways that ecological studies in particular might be designed to better detect eco-evolutionary effects. For instance, investigators building long-term data sets of ecological patterns could consider including measures of phenotypic, genotypic, and trait variation among the variables assayed in their study systems, and they could simultaneously attempt to set sample sizes and intervals based on the power and resolution needed to detect even transitory responses.[32,39,74,76,77] Various applications of the Price equation to such data can further assist in discerning evolution's effects from plastic and demographic influences.[72,78,79] Investigators conducting experiments can incorporate alternative genotypes or population sources in lab or field experiments[70,71,75,80] or, where actual evolution has the potential to unfold within the design, include treatments with different evolutionary potential or genotypically fixed reference conditions to estimate those effects.[58,81–83]

The odds of detecting significant effects of contemporary evolution on ecology, or ecology on evolution, are likely to be further improved in contexts where there are strong a priori reasons to suspect links between particular traits and particular ecological variables, as well as when or where those effects will be measurable. Some traits appear to have amazingly widespread or consistent ecological effects (e.g., plant condensed tannins and defensive compounds,[46,74] body size,[39,58] trophic specializations[73,84]). By contrast, when traits and ecological responses are selected in a more exploratory fashion, the range of relative ecological effect sizes of evolution within a single system can vary markedly.[60] Hence, upfront investment in identifying variable traits with likely quantifiable ecological effects is well worth the effort, albeit with a trade-off of missing unanticipated contributions from other traits.

A further constraint that might contribute to "cryptic by oversight" pertains to attributes of study organisms. A number of field studies have taken advantage of taxa or traits where it is possible to link the traits of individuals to relatively immediate ecological effects measurable at essentially the scale of those individuals or small groups of those individuals. These include studies of invertebrate and microbial dynamics on or in the vicinity of individual plants or groups of plants (i.e., foundation species[46,61,70,74]) or of offspring contributions to population growth in pedigreed animal populations.[77,85] However, it would clearly be much more difficult to link the traits of highly vagile individuals to their respective effects on something as diffuse as a community or ecosystem response at the same time that those individuals traverse throughout open, natural systems. Some evidence for such effects might still be assessed by examining the degree that changes in mean trait values predict ecological changes through time[39,72,79] or by manipulating the composition of genotypes in naturally or artificially isolated systems (e.g., mesocosms[60,73,80] or host plants[86,87]). Alternatively, even in widely free-ranging organisms, genotypes and phenotypes are often heterogeneously distributed over the landscape in space and time, which might be used to detect localized ecological effects if both evolutionary and ecological variation are mapped at the right intrinsic scale and not merely averaged over the whole landscape (e.g., metapopulation dynamics[76] and invasion fronts[88]).

Cryptic by genes to phenotypes

The first cryptic linkage in the eco-evolutionary feedback that we will consider is that from genes to phenotypes or, in other words, the potential that a population undergoes adaptive genetic changes that are largely invisible at the level of phenotypes. One might suspect that the simplest case would be a hypothetical mutation that fails to produce any phenotypic effect. However, such hypothetical mutations would not be of direct relevance to our discussion because they would constitute nonlinkages rather than cryptic linkages per se. For the linkage from genes to phenotypes to be cryptic, different genotypes must be expressed yet result in outwardly similar phenotypes.

One example of eco-evolutionary dynamics rendered cryptic at the genes-to-phenotype link involves cases where selection favors similar phenotypes in either similar or different environments. Beginning with the case of similar phenotypes in similar environments, populations with shared or different histories can adapt to new but similar conditions via parallel or convergent evolution.[89] Were one to compare such populations only under present conditions, one might infer they had not diverged much and thereby miss the extensive genetic changes that occurred in one or both populations to produce this homoplasy. In so doing, one might in turn miss ecological effects tied to such evolution. Interestingly, parallel or convergent patterns might themselves be facilitated by strong eco-evolutionary feedbacks. An example of this comes from studies of landlocked alewives (*Alosa pseudoharrengus*) that adapted to become year-round residents in lakes when human-built dams blocked their ancestral anadromous migrations. The resulting landlocked populations shape zooplankton communities differently than do anadromous populations that are only present in lakes for part of the year, leading to reciprocal selection and repeated parallel evolution of landlocked foraging traits, including narrower gill raker spacing.[90–92] These eco-evolutionary feedbacks would not have been apparent by just comparing landlocked populations. The key for elucidating cryptic eco-evolutionary dynamics associated with parallel or convergent evolution is to recognize that the critical comparison is between contemporary and ancestral genotypes (and phenotypes) and that comparisons among derived populations may not be a good indicator of those rates or patterns.[30]

A similar challenge applies when considering evolution resulting in similar phenotypes in different environments. Most ecologists and evolutionary biologists appreciate that the same genotypes can produce markedly different trait values when exposed to different environments and that this can reflect adaptive phenotypic plasticity.[93,94] However, stabilizing selection can also sometimes oppose the perturbing effects of environment on trait expression. Under these conditions, different genotypes might be favored in different environments because they actually produce outwardly similar phenotypes. This genotype–environment pattern is often referred to as *countergradient variation*,[95,96] and it can be discovered through common-garden or translocation-rearing experiments in which populations that looked similar in the wild end up expressing markedly different trait values when reared under similar conditions. This pattern of divergence has been documented in more than 60 species,[96] suggesting that it might be quite common. Moreover, it can evolve in contemporary time as populations colonize new environments or existing populations face changing conditions.[97,98] A related phenomenon is the evolution of tolerances or resistances to challenging environmental conditions, pathogens, grazers, or toxins.[99–104] Tolerance effects again imply that phenotypes and performance would differ appreciably in the presence of stressors were it not for evolution (Fig. 2). In either case, the potential for different genotypes to produce outwardly similar trait or performance phenotypes when observed in the wild could easily be confused for absence of evolution and, in turn, an absence of associated ecological effects of that evolution.

Countergradient and tolerance effects are interesting in several ways. First, recognizing that these patterns are attributable to adaptation within populations, they again challenge the perception that little or no change (or divergence) in traits equates with little or no evolution or opportunity for eco-evolutionary dynamics. Second, these effects are often associated with attributes like growth, life history traits, and feeding rates[96,105,106] that are particularly important to performance and fitness, and that are suspected of having widespread ecological influences at population, community, and ecosystem scales (examples in Fig. 2). Third, assuming that phenotypic similarity equates to similar ecological function (which is not always the case[107]), they represent a situation where evolutionary effects are not only cryptic but may contribute to greater ecological stability in systems than anticipated under a model that lacks evolution but includes the fundamental dependence of trait expression on environment.

An example of these latter two points comes from a study of experimental adaptation to stoichiometrically challenging dietary environments in the rotifer *Brachionus calyciflorus* (Fig. 2). In that study, DeClerck *et al.*[108] showed that lines not afforded an opportunity to adapt to such conditions showed a strong environmentally induced shift in their reproductive mode when exposed to challenging diets, whereas lines adapted to the challenging diet in contemporary time evolved tolerance and expressed the same reproductive life histories regardless of diet environment. Had one not known the ancestral condition of this tolerant line, it might appear that diet does not matter much, but the authors show that this evolution of tolerance in turn mitigated ecological costs of reduced population biomass and grazing capacity suffered by nonadapted populations.[108]

Finally, it should be pointed out that countergradient and tolerance effects might also lead to ecologically cryptic outcomes when the indirect ecological effects of evolution happen to reinforce the direct ecological effects of an environmental gradient and are in turn misattributed to those direct environmental effects. For example, countergradient adaptation of spotted salamanders (*Ambystoma*

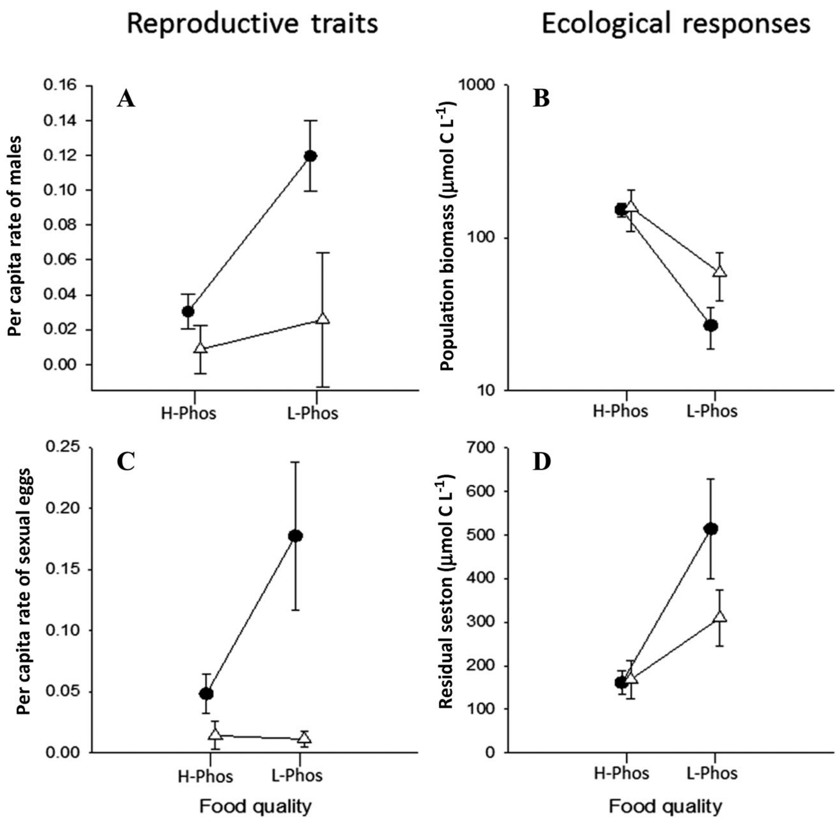

Figure 2. Example of cryptic effects at the genes-to-phenotypes link in an experiment by Declerck *et al.*[108] to assess rotifer adaptation to stoichimetrically imbalanced food conditions. Replicate populations of the facultatively sexual rotifer *Brachionus calyciflorus* were adapted over 209 days in chemostats supplied with algal diets that were either high (H-Phos) or low (L-Phos) in phosphorus content, before being assayed under reciprocal conditions. Rotifers adapted to benign H-Phos conditions (filled circles) showed strong environmental responses to the challenging P-deficient diet in a common garden trial, as reflected in increased facultative expression of sexual reproductive traits (A and B), and a substantial reduction in population biomass (C) and grazing capacity (D). However, the L-Phos–selected lines (open triangles) evolved tolerance, showing similar expression of sexual reproduction under L-Phos conditions as under H-Phos conditions (A and B) at levels sometimes very similar to the H-Phos line under H-Phos conditions (A). This adaptation by the L-Phos line was associated with less reduction in biomass or grazing (C and D). In cases of tolerance or countergradient evolution, like this, the full scope and ecological significance of such compensatory evolution can be outwardly cryptic without experimental or analytical approaches that reveal how nonadapted populations would respond to the same environmental challenge.

maculatum) to a predator-risk gradient improves their ability to consume zooplankton in the presence of predators.[106] As it happens, such adaptation reinforces the zooplankton-grazing effects of the predators themselves and thus might have been misattributed as a direct environmental effect of the predators had the investigator not included both positive- and null-effect treatments to account for salamander evolution.

The primary challenge of studying countergradient and tolerance effects in an eco-evolutionary context in nature is that, to appreciate evolution's heritable effects on phenotypes and ecology, one needs to not only consider potential ancestral states within populations but also to isolate or quantify the role of the environment. Indeed, it is probably fair to say that the scope and relevance of evolution is not so much measured by how different trait values or ecological conditions come to be but rather by how different the phenotypes and ecology would have been in the absence of such evolution. To use the above rotifer example, the fact that rotifers adapted to their respective dietary environments can express similar reproductive phenotypes (e.g., Fig. 2A) does not imply a lack of evolution or ecological relevance. By contrast, the scope and ecological significance of evolution is captured by comparing the tolerant and nontolerant dietary lines within the challenging dietary environment (right side of all Fig. 2 panels), where the nontolerant lines provide a proxy for what phenotypes and ecology would have been in the absence of tolerance evolution.

Beyond the foresight to look for cryptic countergradient and tolerance effects in the first place, the logistical challenges in studying them are in many ways similar to those faced by any studies of trait evolution in the wild, with the added complications of also demonstrating potential ecological effects tied to such evolution. Common-garden and quantitative genetic breeding studies would ideally be conducted under environmental conditions similar to those actually experienced in nature,[109] but are unfortunately often conducted under artificial laboratory conditions that not only lack environmental realism but risk overriding meaningful ecological outcomes. Reciprocal transplant studies offer an attractive alternative, but can be unfeasible for many species. Both of these approaches are primarily applicable to comparing extant populations and are not easily adapted to dissecting the interactive effects of evolutionary and environmental effects on phenotypes through time within wild populations. However, animal model approaches[110,111] to statistically assess heritable trait changes through time in pedigreed wild populations and "resurrection" of dormant eggs, seeds, or spores from past populations offer at least some opportunities to work around these limitations,[101,112–115] so that one might ultimately reconstruct the interacting contributions of environmental, evolutionary, and ecological effects on traits and ecology through time.[72]

Cryptic by phenotypes to ecology

How genotypes and phenotypes shape ecology is the key missing link between ecology and evolution that launched the field and the one that has received the most recent attention given that the pathway from ecology to evolution (via selection) has been more generally accepted. Nonetheless, the link from phenotypes to ecology is still one of the least understood and presents the most opportunities for cryptic eco-evolutionary effects to be overlooked.

We already mentioned how a priori choice of the "right" traits and ecological responses might improve the power to detect interactions between evolution and ecology. Unfortunately, a trade-off exists in that targeting a few select traits creates a bias that might lead us to miss both cryptic and overt effects elsewhere. For example, one might not initially predict that color polymorphism in an insect would be important to invertebrate community composition or limits on primary production, but such effects are indeed strong for the stick insect *Timema cristinae*.[87] Reasons also exist to be attentive to when and where we look for ecological responses to evolution, as they are not always immediate or local. Evolutionary reversals of population declines (see below) might not be apparent for generations following an initial environmental shift, but thereafter drive rapid population recovery,[50,53,54,116,117] and predator–prey interactions often involve lags such that evolution of one species might not affect responses of the other for several generations.[20,74,118] Such ecological responses to evolution might be cryptic if sampled too early or late in the process. The ability for individuals or their products (e.g., tissues, excretion, offspring) to move or be transported among systems can displace the influences of evolution to other habitats, such as when the genotypes of trees on land influence litter decomposition rates in aquatic habitats[47,119] or bear selection on salmon influences nutrient fluxes into terrestrial systems.[45] The common thread for all of these inferential challenges is that failure to detect an ecological response of evolution might simply reflect our incomplete understanding of the trait-based ecology of the species involved.

However, even presuming that one does correctly identify an ecological response that should be linked to a given instance of phenotypic change, it is still possible that those effects will appear cryptic when the net outcome of trait evolution is to buffer ecological responses that might occur in evolution's absence. In such cases, substantial amounts of evolution might occur with little net ecological change because stability or resilience of the system is the ecological response driven by contemporary evolution. Such cryptic responses in the phenotype-to-ecology link of an eco-evolutionary dynamic could be common but only detectable when we have some understanding of what conditions might be when the potential for evolution is absent or varied. Examples include cases of evolutionary rescue and adaptive tracking in response to environmental perturbations, wherein adaptation permits populations to recover or avoid declines in abundance, respectively (reviewed in Refs. 50, 116, 117, and 120). Replicated laboratory studies and models that manipulate the potential for evolution support such rescue effects under a range of conditions.[53,54,121–126] Unfortunately, similar control and replication are lacking in natural systems, making it notoriously difficult to substantiate evolution's likely pervasive, but easily missed, contributions to population persistence.[116,117] Moreover, when evolution turns out to be insufficient for rescue[127] or deleterious,[128] populations may quickly go extinct, and we would be even less likely to account for evolution's effects (i.e., a winnowing bias[48]).

Many of the best known examples of evolutionary rescue involve cases of species coexistence where populations resist or recover from the initial detrimental effects of a new predator or pathogen,[116–118] which brings us to eco-evolutionary feedbacks at a community scale. As we noted earlier, this theme has its theoretical roots in explorations like Pimentel's[129] "genetic feed-back mechanism" and Van Valen's[24] coevolutionary arms races, among others,[25] with more recent work expanding into geographic mosaics of coevolution,[130] community genetics,[16] evolving metacommunities,[131] community rescue,[132] and, of course, eco-evolutionary dynamics.[51] The simplest place to begin our consideration of cryptic outcomes in communities is with evolution in just one of the interacting species.

Building off anecdotes of populations that recovered from pathogen outbreaks, Pimentel[23] captured the rudiments of such a dynamic in a simple single-locus genetic model. Curiously, rather than couch his model in terms of disease dynamics, Pimentel instead built his model around the population dynamics of an evolving plant and its herbivorous predator. His model included a prescient trade-off between a genotype's ability to negatively affect its consumer and its ability to compete with other individuals of its own species. Much later, parallel laboratory experiments employing plants and herbivores, represented by algae (*Chlorella vulgaris*) and rotifers (*B. calyciflorus*), and disease dynamics, represented by *Escherichia coli* cultures infected by T4 bacteriophages, provided the first examples of eco-evolutionary dynamics to be labelled "cryptic."[20] In both sets of experiments, conditions arose where predator populations underwent clear cycles of abundance but prey densities remained approximately constant. Models and genetic analyses indicate that this outcome is due to nearly counterbalancing, cyclic replacement of "protected" versus "competitive" genotypes of prey in response to varying predator or pathogen densities.[20] Similarly, contemporary adaptation of prey also mediates abundances of prey or predators in experimental systems employing other species pairings: alga–rotifer,[81] protozoan–mosquito,[69] and plant–insect.[74] Moreover, it is quite likely that evolution of species to persist under predatory or pathogenic challenges can further result in cryptic outcomes at ecological scales well beyond the population dynamics of the interacting predators and prey. For example, in the marine cyanobacterium *Synechococcus*, viral infection of populations initially resulted in changes in water column nutrients and bacterial stoichiometry, but these effects faded with evolution of resistance in the cyanobacteria.[133]

Coexistence can, of course, include many other types of species interactions and the evolution of more than one of the involved species. Theory and examples of coevolution associated with diverse forms of species interactions, including competition, are reviewed extensively elsewhere.[51,130,132] But what about evidence that such coevolution might again lead to cryptic ecological outcomes at scales beyond even population persistence and coexistence? In a study of the effects of fish evolution and coevolution in Trinidadian stream communities, Palkovacs *et al.*[80] used stream mesocosms seeded with different combinations of guppy (*Poecilia reticulata*) populations adapted to low- or high-predation regimes, and killifish (*Rivulus hartii*) populations adapted to live alone or coexist with guppies. The experiment showed that guppy evolution influenced algal standing stocks and that killifish coevolution influenced invertebrate biomass. However, a reanalysis of the four major treatments of the mesocosm design to simulate natural or human-mediated invasions of high-predation guppies into habitats previously occupied by only killifish reveal that the combined effects of both guppy and killifish evolution and coevolution is a community state that is very similar in algal and invertebrate stocks to the original preinvasion system (Fig. 3). In another example, adaptation by spotted salamanders to coexist with marbled salamanders (*Ambystoma opacum*) dampens the

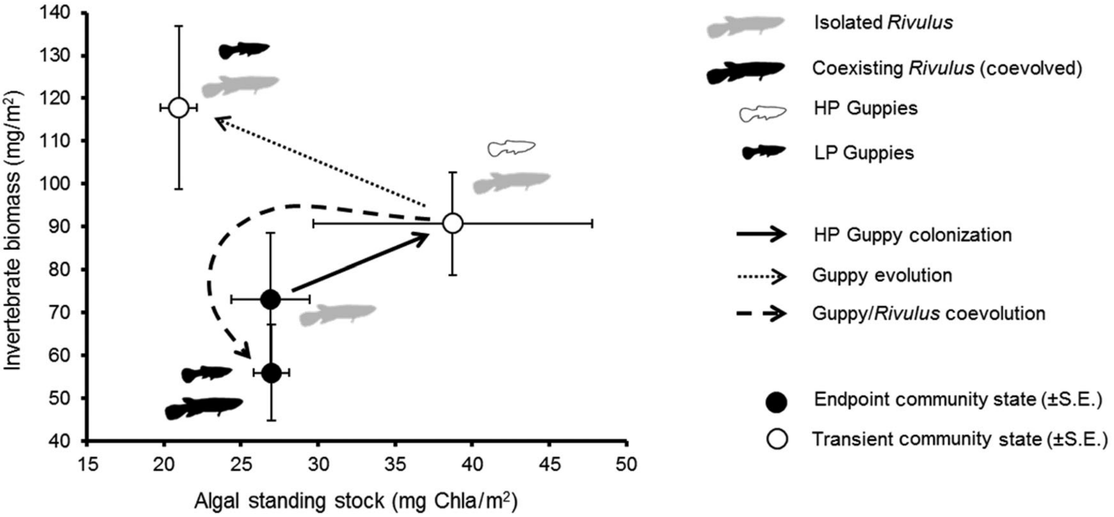

Figure 3. Example of coevolution as a form of cryptic effects at the phenotypes-to-ecology link. The four experimental treatments of Palkovacs *et al.*[80] can be recast in the context of reconstructing eco-evolutionary dynamics during colonization by high-predation (HP) guppies of a low-predation (LP) stream environment inhabited by *Rivulus* previously isolated from guppies. This colonization process would have occurred in classic introduction experiments that elicited contemporary guppy evolution[36,199] as well as in the distant past. Colonization by HP guppies is associated with a change in algal and invertebrate community state (solid arrow), but this is more than reversed by eventual evolution of LP guppy types (dotted arrow). However, this experiment also detected a substantial effect of coevolution, seen here by contrasting community responses to the treatment containing the isolated-type *Rivulus* and LP guppies against a treatment containing the *Rivulus* population that naturally coexists with those LP guppies. The implied community trajectory from evolution and coevolution in this case (dashed arrow) resulted in end point systems (filled points) that are nearly indistinguishable from the initial treatment containing only the isolated *Rivulus.* Had one not quantified the transient community states (open points) that control for evolution in one or both species, it would be easy to miss the cryptic effects of guppy colonization (ecology), guppy evolution, and *Rivulus* (co)evolution on community structure. Total fish biomass was the same in all treatments.

consumer effects of marbled salamanders, a competitor and predator, on zooplankton diversity.[106] And, in a study of two goldenrod (*Solidago*) species, effects of alternate genotypes of one species on plant traits and pollinator communities were often obscured by genotypic effects of its heterospecific neighbors, suggesting that the ability to detect evolution and its ecological effects in one species could again depend on evolution in the other.[134] Hence, evidence suggests that coevolution of species may indeed at times dampen or conceal ecological outcomes at scales beyond population dynamics and predatory–prey coexistence.

As if discerning these cryptic effects tied to coexistence was not challenging enough, one might alternatively consider potentially cryptic outcomes associated with non-coexistence. When adaptation by one species or population prevents coexistence of another, the dynamics leading to that outcome could be very fleeting and difficult to detect. Some indirect evidence of this possibility comes from less extreme outcomes than complete non-coexistence. For example, some genotypes of goldenrod (*Solidago altissima*) more strongly limit the biomass of other colonizing plant species than do other genotypes, potentially impeding invasions.[135] Similarly, contemporary adaptation of *Daphnia magna* to experimentally warmed conditions increased the population's ability to resist replacement by *Daphnia* from other regions.[136] However, more direct empirical support for eco-evolutionary effects leading to non-coexistence comes from a study of experimental evolution in bacteria. Friman *et al.*[137] found that the ability of one *Pseudomonas fluorescens* strain to evolve greater antipredator defense with less of a growth cost than another strain enabled it to competitively exclude that competitor strain in the presence of a predator. Importantly, whether one is concerned with coexistence or non-coexistence, discerning cryptic effects at the phenotype-to-ecology link again not only requires conditions where evolution is present, but also null-evolution treatments (or theory) to infer what community outcomes might be in evolution's absence. In the case of *Pseudomonas*,[137] inclusion of nonpredator treatments, where coexistence was able to occur, was important for demonstrating evolution's role in promoting competitive exclusion.

A final example of a mechanism that might lead to cryptic outcomes at the phenotype-to-ecology link is the ability for evolution to have multiple direct or indirect effects on a given ecological response. Such interactions might be hypothesized to produce additive or multiplicative effects on a particular ecological response,[80] but they might also cancel each other out. Although it might seem improbable that traits would exactly offset each other, the odds their effects might be approximately cancelling are increased by the large number of traits and interactions implicit to most organisms. Direct and indirect pathways can be difficult to disentangle in nature,[138,139] but there is evidence for such cancelling effects. A mesocosm and modeling study by Bassar *et al.*[140] to dissect the aforementioned eco-evolutionary effects of guppy type on algal standing stocks revealed interacting and opposing effects of guppy phenotype mediated via different pathways tied to diet and excretion.

Cryptic by ecology-to-ecology

When predictions are not borne out in ecological studies, investigators typically invoke confounding effects of additional ecological processes. Evolution is increasingly included among these potential confounding factors.[64,68,69] However, our focus in this section is more about ecology's capacity to obscure evolution's effects than the other way around. Even setting aside the aforementioned opposing effects of different evolution-to-ecology pathways, the routes by which a given ecological outcome, evolutionarily mediated or not, might be obscured by another are too diverse to review in detail here. Hence, we focus on a few examples and general patterns that are likely to be of theoretical interest or are best supported from empirical studies.

One of the oldest theories that might be considered an example of evolution's ecological effects concealed by other ecological processes is found in R.A. Fisher's classic work *The Genetical Theory of Natural Selection*,[26] wherein his "fundamental theorem" includes an explanation for why adaptive evolution does not result in a perpetual increase in fitness and population growth. The explanation is that increases in the Malthusian growth parameter due to adaptation are nearly completely offset by deteriorating effects of those adaptations on the population's environment. Fisher defines those deteriorating effects broadly, and thus they can include various aspects of density dependence and population regulation classically studied by ecologists.[141–144] This ecologically insightful evolutionary theory suggests a way in which evolution's effects might be demographically self-cancelling in relatively stable populations. However, evolution's contributions to population growth might become more apparent under conditions where the compensatory effects of ecology are disrupted or not yet in equilibrium with fitness effects.[50,141,143] Examples might include populations undergoing rebound or rescue following a crash[54,85] or colonizing new habitats or resources.[71,121,145–147] In a way, Fisher's theory might even be considered a special case of modern niche-construction theory[18] or vice versa, where both ideas place a priority on the role that phenotypes play in reshaping an organism's ecological environment to determine fitness.

Earlier, we considered how coevolution might conceal the effects of evolution on ecology; here, we consider how species interactions might play important roles in concealing eco-evolutionary effects, even without coevolution. For example, the ecological effects associated with the evolution of competitive versus protected prey (as discussed above) might be dampened or offset by a predator or herbivore's innate functional response to changing prey abundance and susceptibility. Such a functional response is an implicit part of both overt and cryptic eco-evolutionary dynamics in the aforementioned *Chlorella–Brachionus* chemostat system[148] and it is also seen in cryptic bacteria–phage dynamics. Indeed, in the latter case, the compensatory ecological effects associated with predator functional responses and competition among prey genotypes can fully conceal the ecological effects of evolving prey susceptibility (Fig. 4). In another example,[73,149] shifts in zooplankton community composition associated with differences among plankton taxa in their susceptibility to alewife grazing appear to dampen the anticipated cascading effects of alewife evolution on prey densities or biomass (i.e., cryptic trophic cascades[21]). Again, these might outwardly appear as cases where ecology overrides the effects of evolution. However, in each of these examples, the ecological effects of contemporary evolution were not truly

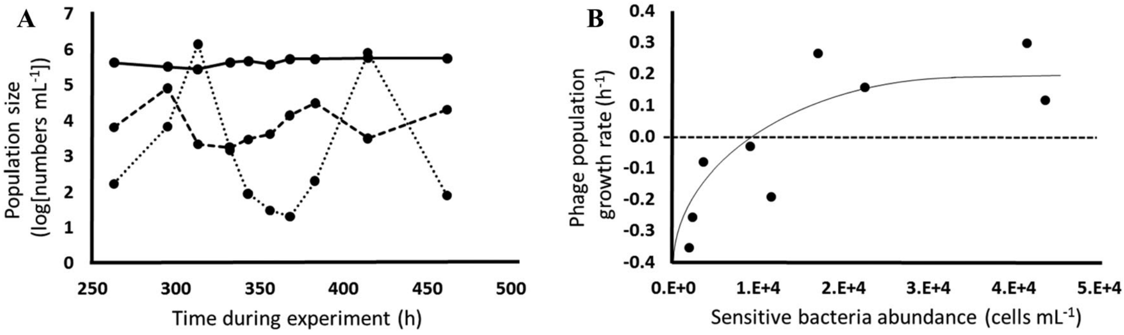

Figure 4. A bacteria–phage example of a predator functional response that conceals cryptic eco-evolutionary consumer–resource dynamics. (A) Temporal patterns of ($\log_{10}$) abundance of phage (dotted line), sensitive bacteria (dashed line), and total bacteria (solid line); note that resistant bacteria make up the difference between total and sensitive cells. Phage abundance oscillates, as does the density of sensitive bacteria, but total bacterial density is essentially constant. Redrawn from Bohannan and Lenski[200] and Yoshida *et al.*,[20] showing only the last half of the 450-h experiment when data are available for all components. (B) Phage population growth rate as a function of the mean density of sensitive bacteria. The data show a saturating numerical response (type II fit to data). At high densities of sensitive cells, the functional response of the phage population drives sensitive "prey" densities lower, whereas at low densities of sensitive cells, the phage population declines (negative population growth rate) and the density of sensitive cells rebounds. Because the sensitive bacteria lineage competes for resources with the resistant lineage, the net effect is little change in total bacterial density as a result of resistance that is effective but not very costly (as explained in Ref. 20).

absent; they were instead balanced by compensatory community processes for which effect sizes would be drastically underestimated if we did not appreciate evolution's contributions. One might even say that the best way to measure the importance of evolution as a cryptic ecological process in such contexts is by the scope of interacting ecological effects required to balance it. For example, while prey abundance did not change over time in the bacteria–phage example, the importance of prey evolution is hinted at by the associated 10,000-fold change in phage abundance (Fig. 4).

The presence of compensatory ecological effects should weaken evolution's perceived influence on further dependent ecological outcomes. In principle, then, the more links in the chain of ecological causation, the more opportunities for such ecological interference and the greater the odds that evolution's effects will be concealed. Along these lines, Bailey *et al.*[150] hypothesized that genetic effects will often be more direct and stronger at the scale of individuals and populations and more indirect and weaker at the scale of communities and ecosystems. A meta-analysis of plant community genetics studies provides some support for this premise,[150] although the authors did not consider population-dynamic responses among the other scales (individuals, community, ecosystem). Time will tell if future meta-analyses uphold this pattern more broadly, but it is worth emphasizing that such a pattern would not necessarily indicate that important evolutionary effects are absent at community or ecosystem scales.

The above line of reasoning pertains to the observed, or net, ecological effects of evolution, as ultimately filtered through interactions with other ecological processes. Consistent with our broader message, just because evolution's effects are concealed in such a fashion does not mean they do not exist; it instead implies they are cryptic. Hence, indirect community and ecosystem responses associated with numeric or biomass effects of evolution shaping population dynamics might be substantial, but we might not be able to discern those evolutionary effects without somehow accounting for other ecological effects that muddle them. Moreover, many community and ecosystem effects of evolution may represent more direct trait effects that could in principle operate even if evolution were to have little effect on abundance or biomass at a population scale. Indeed, the majority of experiments at community and ecosystem scales essentially preclude any indirect evolutionary or genetic effects tied to density by purposefully controlling densities or biomass. Nonetheless, these and other studies provide ample evidence of strong phenotypic and genotypic effects on food-web interactions (e.g., trophic traits, protective compounds or phenology[46,73,74,80,151]) or nutrient stoichiometry and cycling (e.g., body composition, excretion, or decomposition rates).[46,47,152–155] This should perhaps not surprise us, given that decades of theory and empirical studies of trait-mediated indirect effects support that trait effects on community dynamics often rival and mediate many density effects.[42,156]

It is difficult to make general recommendations for how best to detect potential cryptic effects at the ecology-to-ecology link, given the many ways they might arise and the numerous challenges of disentangling interacting direct and indirect ecological effects in nature[138,139] (but see Ref. 140). However, we extend previous guidance[8,9,157] that, despite some risk to generality, there may be initial benefits in focusing on evolutionary effects in taxa with disproportionately large effects on communities and ecosystems, such as keystone, foundation, or ecosystem-engineer species. The effects of evolution in such species should be large and less prone to being muddled by other ecological factors. However, where evolution's ecological effects are not detected in such species, we might uncover evidence for especially important ecological factors that served to conceal, or even truly limit, eco-evolutionary effects.

Cryptic by ecology back to phenotypes

The opportunity for dynamic feedbacks provides one of the most compelling reasons to unite the study of ecology and evolution over contemporary time scales.[7–10,72,154] Hence, it is important to consider not just the genes-to-phenotypes pathway discussed thus far, but also cryptic processes that might conceal elements of the reciprocal pathway from ecology back to genes. Although fewer studies have sought to simultaneously quantify both parts of this feedback, decades of theory and research on natural selection in the wild provide insights into how the ecology-to-phenotypes link might operate in a cryptic fashion.

The easiest conditions for observing the role of ecology back on phenotypes are likely to be cases where selection is strongly and consistently directional, as might occur in cases of species introductions and invasions, harvest by humans, or strong and persistent environmental perturbations like pollution.[48,99,158] However, detailed field and experimental studies,[37,38,83,159] as well as meta-analyses,[34,160,161] provide support that selection and evolution often fluctuate over short time frames, although these fluctuations can be difficult to separate from sampling error.[161,162] Certainly, fluctuating selection seems likely given the pervasiveness of environmental variability[163] and the potential for frequency and density-dependent selection.[38,164–166] Regardless of the exact mechanism, an investigator might miss selection representing an ecology-back-to-phenotypes link if he or she happens to quantify selection and evolution with insufficient resolution to capture transitory fluctuations. Indeed, theory suggests that fluctuating evolution may often contribute to perceptions of stasis in the paleontological record.[34,167] A now classic contemporary example is fluctuating beak- and body-size traits in the medium ground finch (*Geospiza fortis*) on the Galapagos island of Daphne Major,[37,168] where an uncritical comparison of trait change at the start and end of a given time period could easily miss a great deal of intervening selection and evolution. Additional analyses suggest that these selective effects of habitat conditions on finch trait change might actually explain more of the year-to-year variation in finch population growth than the direct effects of habitat conditions themselves.[32] Other high-resolution time series show similar trait variability and putative ecological consequences.[39,40]

While fluctuating selection can easily be missed, trait and environmental variability through time at least hint at its presence; strong stabilizing selection presents a more difficult challenge. Although it might initially seem that absence of trait change is evidence of absence of selection and thus feedbacks from ecology to phenotypes, theory again tells us that genetic and phenotypic stability are often not expected from chance alone. Simultaneous operation of gene flow,[169] genetic drift,[170,171] and mutation[172] ensure that the null-selection expectation for most populations is not an absence of trait change. Rather, the trait distributions of many populations would be expected to change, sometimes quite rapidly (as in the case of gene flow), were it not for effects of stabilizing (purifying) selection.[144] Unfortunately, stabilizing selection is notoriously difficult to directly quantify, not least because it is nonlinear and thus presents challenges associated with the power required to test higher-order model terms.[161,173] However, while stabilizing selection can be difficult to directly quantify, its operation and eco-evolutionary relevance can be inferred by comparing observed trait change and

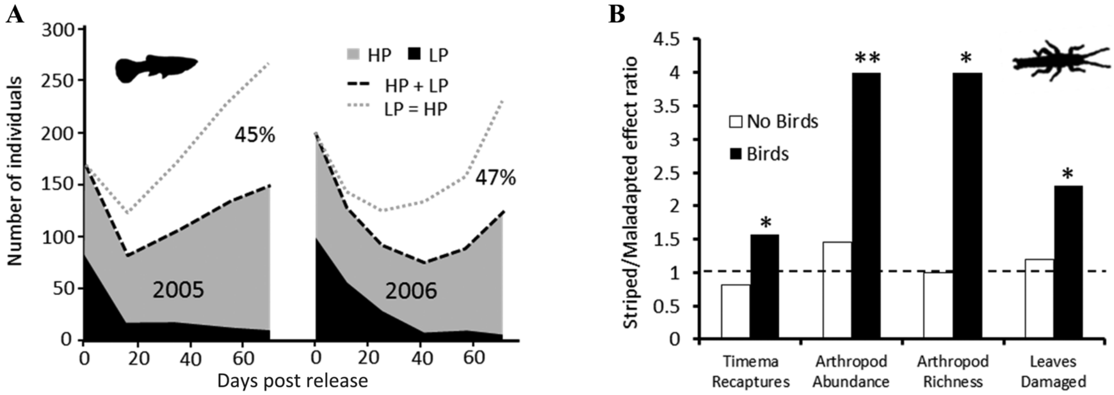

Figure 5. Selection against maladapted migrants as a form of cryptic dynamics at the ecology-back-to-phenotypes link. (A) In a replicated study of guppy (*Poecilia reticulata*) reestablishment following local extirpation in a high-predation risk habitat, Weese *et al.*[85] showed that selection strongly disfavors survival and offspring recruitment by guppies from low-predation sources (LP) that were released (time zero) in equal proportion to high-predation (HP) guppies. This selection maintains local adaptation but reduces peak population recovery (final HP + LP in this figure) by 45–47% compared to the null-selection expectation where LP guppies are assigned the same interval-specific survival and reproduction as HP guppies (final LP = HP). (B) In an experiment on bird selection on *Timema cristinae* stick insects by Farkas *et al.*,[87] striped genotypes that are camouflaged on the host plant *Adenostoma fasciculatum* survive better (recapture ratio > 1.0, dashed line) than maladapted unstriped genotypes that are camouflaged on a different plant host, but not when birds are unable to access the insects (null selection). This bird selection against maladapted migrants maintains color morph–plant associations in mixed-plant metapopulations, but also has spillover effects on the abundance and richness of other arthropods that in turn contribute to leaf damage. In both study systems, selection maintains phenotype–habitat associations that would otherwise change under immigration, and is thus potentially cryptic. (Ratios in B estimated from GLMM effect sizes in Ref. 87. $^{**}P < 0.001$; $^{*}P < 0.05$; no significant morph effects detected in "no bird" enclosures.)

ecological responses with null-selection expectations, as demonstrated by studies of so-called "selection against migrants."

In an experimental study by Weese *et al.*[85] of migrant fish contributions to population recovery following catastrophic disturbance, the investigators used genetic assignment tests to show that selection acted strongly against migrants. That selection in turn reduced population abundance at recovery by approximately 45% compared to the null-selection expectation, where migrants were modelled as equivalent to residents in terms of survival and offspring production (Fig. 5A). In another example, Farkas *et al.*[87] used a predator-exclusion treatment as a null-selection expectation to demonstrate stabilizing selection against maladapted migrants in stick insects, as well as spillover effects of that selection on the arthropod community and on herbivory (Fig. 5B). Interestingly, strong stabilizing selection can also operate against migrants in time, such as when maladapted genotypes reemerge from seed or egg banks or diapausing zooplankton eggs hatch from lake sediments.[40,174,175] Fortunately, egg or seed banks can be sampled to infer what genotypic distributions, and possible ecological effects of those distributions, might exist in the absence of ongoing stabilizing selection. The point being, a great deal of selection may often occur to produce little to no evolutionary change in many populations, but even without evolutionary change, such selection could still have measurable ecological consequences.

A final point concerns the definition of what constitutes "feedbacks" between ecology and evolution. For the most part, discussions of reciprocal interactions have focused on ways in which the evolution of particular traits lead to ecological conditions that in turn drive selection back on that focal trait of interest. It is relatively straightforward for us to envision how such feedbacks (in the narrow sense[49]) might be important for producing interesting dynamics.[7,9,64,176] To use the landlocked alewife example, the evolution of gill raker traits (e.g., spacing) that enhance zooplankton grazing efficiency helps shape zooplankton communities in a way that selects for further gill raker specialization.[73,91] However, reciprocal interactions between evolution and ecology may often be more reticulate than this, not just in terms of various direct and indirect effects at the phenotype-to-ecology and ecology-to-ecology links, but also in the selective pathway from ecology back to phenotypes. No reason exists to think that changes in ecology produced by evolution of one trait might not contribute to positive or negative selection on other traits, which could be missed—and thus cryptic—if not anticipated. Indeed, even in the alewife example, early evolution of residency that allowed populations to inhabit lakes year-round likely played the largest initial role in driving zooplankton community structure and in turn instigated the strong selection shaping gill raker traits.[8,73] Importantly, this type of added complexity would not preclude feedback-like behavior of the system (i.e., feedbacks in the broad sense[49]) when the evolution of a particular trait shapes ecology and selection on other traits that, through their own influences on ecology, reinforce selection on the original trait. Indeed, one might even hypothesize that such reticulate feedbacks could contribute to the origins or maintenance of ecologically cohesive character suites associated with alternate ecotypes (e.g., protected versus competitive phenotypes described previously), resource polymorphisms (e.g., benthic versus limnetic[75,177]) or behavioral syndromes (e.g., bold versus shy[178]).

Cryptic by phenotypes back to genes

Only a modest proportion of studies of evolution, and even fewer studies of coupled eco-evolutionary dynamics, explicitly quantify genetic responses to selection. Thus, for most studies of eco-evolutionary dynamics, the phenotypes-back-to-genes link is more assumed than known. Certainly, quantitative genetic and genomic approaches are available to examine this link, but they can be costly or laborious and do not always provide simple insights into the genetics of phenotypic change in the wild. Extensive reviews of the strengths and weakness of these approaches exist elsewhere,[65,109,111,179–181] but the general observation is that the vast majority of traits have some genetic basis, to the point where exceptions can be noteworthy.[182] This reality makes debatable how much time and effort one should invest to merely validate the presence of trait inheritance, and thus "cryptic by oversight" at this linkage might be acceptable in many cases. By contrast, there is clear merit in employing quantitative genetic and genomic studies to pursue more specific questions concerning the functional genetics of eco-evolutionary dynamics,[65] including the potential ways that genetic and environmental (i.e., plastic) components of trait variation determine ecological outcomes.[183] The question for our purposes here is whether there are actual phenotype-back-to-genes mechanisms or biases that would result in important genetic effects being present but missed.

The above arguments concerning stabilizing (purifying) and fluctuating selection at the phenotypic level would naturally apply to variation at the genetic level. Some amount of purging of maladapted genotypes and genetic load resulting from mutation, genetic drift, and gene flow is expected in most populations, which would otherwise suffer significant costs to fitness and population growth potential.[144,184,185] It would be particularly easy to miss recurrent selection against relatively rare but extreme phenotypes and associated genotypes, making the process largely cryptic without very-high-resolution study of genetic diversity. Indeed, in an individual-based simulation, Haller and Hendry[173] modeled an investigator's ability to detect stabilizing selection when it is present. They found that stabilizing selection was only detectable about 5% of the time across all of their simulations, but importantly for our discussion, they also found that detection was worse at the level of genotypic values than phenotypes. Nonetheless, without this commonly undetectable selection, phenotype distributions would come to look quite different.

Another challenge surrounds the underlying genetic architecture of many traits. Although examples exist of single loci with large ecological effects, such as glycolytic enzyme variants that influence dynamics in metapopulations,[76] polygenic inheritance is inevitable for most traits and inescapable for fitness.[65] Polygenic inheritance implies a significant cryptic genetic component for many studies seeking to infer specific loci associated with responses to selection. Major reasons for this cryptic outcome include limitations on power to isolate the marginal effects of numerous loci with modest influences and the potential for different interacting loci to produce comparable phenotypes.[65,181,186] The first of these challenges is well documented by quantitative trait locus (QTL) analyses and genome-wide association studies (GWAS) of known heritable traits contributing to the community genetics effects of foundation plant species.[47,187,188]

As an example, one can consider the largest current GWAS study in trees,[189] which employed a 34K single-nucleotide polymorphism (SNP) genotyping array covering 3518 candidate genes analyzed across 448 accessions of black cottonwood (*Populus trichocarpa*). These traits included a suite of leaf litter and phenology characters that were experimentally shown to produce community and ecosystem responses in aquatic mesocosms.[47] The GWAS results suggested that essentially all of the plant traits investigated were indeed polygenic, with some showing well over a hundred gene associations. Individual SNPs most often explained a few percent of trait variation, and when combined only explained up to about a third of the variation in any given trait.[47,189] The authors concluded that their inability to explain more trait variation was likely due to logistical challenges of detection. Perhaps most telling of the large scope of cryptic genetic effects, the single most explanatory locus in this study accounted for about 10% of phenotypic variation, whereas the estimated heritability for the same trait, a measure of variation explained by polygenic inheritance, was 89%.

The potential for allelic variation at different interacting loci to produce similar phenotypes presents a related but subtly distinct challenge. Specifically, failure to detect anticipated allelic changes at loci previously found to correlate with adaptation is not particularly compelling evidence of absence of genetic change; it could just reflect cryptic genetic responses at other loci. In principle, the more polygenic a trait, the more alternate pathways might exist to produce similar adaptive trait values, and strong selection at some loci in the past might even predispose selection to favor evolution at other loci that retain more genetic variation during subsequent bouts. A striking example of different genetic pathways to the same adaptive phenotypes is shown by a study of gene expression under eco-evolutionary prey cycling in the alga *Chlamydomonas*.[190] As in previously discussed examples of eco-evolutionary dynamics in chemostats, *Chlamydomonas* evolution cycles between predator-protected and competitive phenotypes in response to oscillations of predator density. One might predict that similar phenotypes, cycle to cycle, would likely have a similar genetic basis, but that was not the case. Rather, genes upregulated or downregulated in the first cycle were largely independent of those so regulated in the second cycle (Fig. 6), suggesting convergent routes to comparable phenotypes.[190] This outcome is probably not unusual, even at larger evolutionary scales. Although the authors did not interpret their findings as such, a meta-analysis by Conte *et al.*[191] of gene reuse in candidate gene and mapping studies supports the inference that non-reuse may be as common, or even more common, than reuse in cases of outwardly parallel or convergent evolution.[65]

Finally, various environmental and gene-by-environment effects can complicate both quantitative genetic and genomic insights into the genetic basis of phenotypic change. While we often depict traits as having distinct genetic and environmental components, decades of research on phenotypic plasticity suggests that the environmental liability of traits is itself heritable. Different genotypes can produce different norms of reaction for trait values across a range of environments, and these norms of reaction are subject to selection and can be either adaptive or maladaptive.[94] This outcome holds true for traditional organismal traits and also for genomic expression profiles.[192,193] However, for our current consideration of cryptic outcomes at the link between selection and genetic responses, the biggest issue might be where and how we assess evolutionary responses to selection, as revealed by well-conducted common-garden or reciprocal transplant studies. For example, Pregitzer *et al.*[194] compared different genotypes of narrowleaf cottonwood (*Populus angustifolia*) reared at three different locations along an elevational gradient. As has commonly been the case for such common garden studies since their earliest use,[195] the trait values of the genotypes varied with environment, consistent with norms of reaction. Importantly, however, the different genotypes also showed markedly different norms of reaction, and so two genotypes that differed in phenotype in one environment were often similar in another. Importantly, those patterns cascaded to influence soil chemistry and mineralization,[194] suggesting the same considerations apply to linked ecological effects of evolution. In general, comparing genotypes across a range of environments is preferable to comparing them in one environment,[109] especially if environments are prone to changing, as might be anticipated for some eco-evolutionary feedbacks.

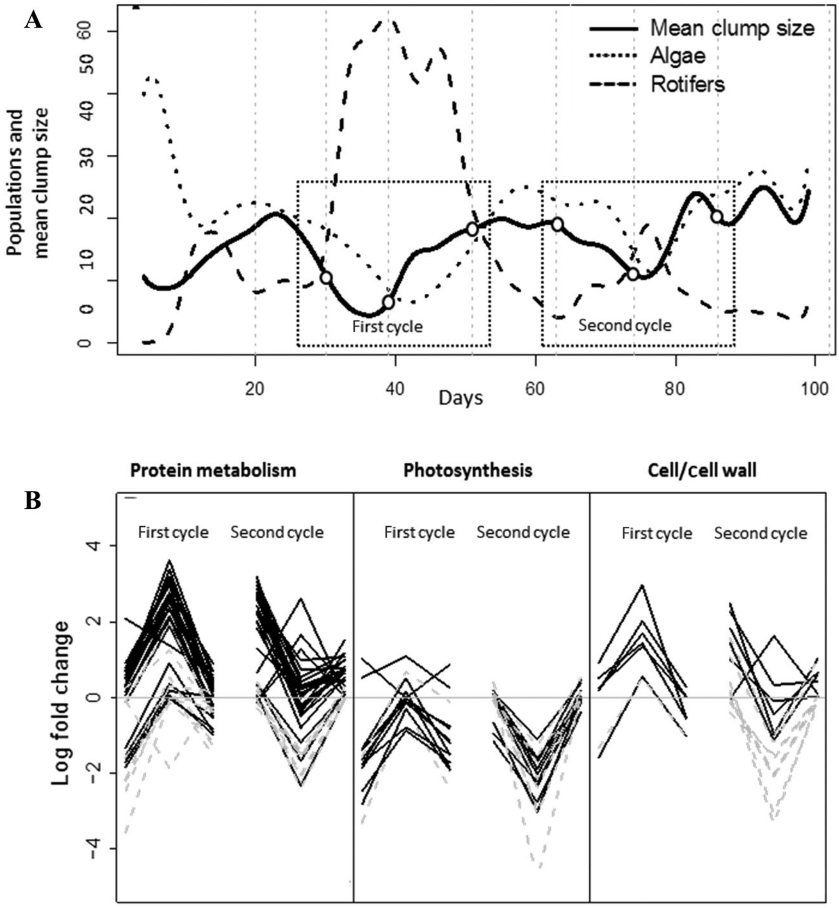

Figure 6. Example of cryptic at the phenotypes-back-to-genes linkage due to different genetic responses underlying similar phenotypic responses to selection. Gene expression profiles associated with evolution of a defensive cell-clumping phenotype in the alga *Chlamydomonas reinhardtii* differ dramatically between successive cyclical bouts of selection in an eco-evolutionary predatory–prey dynamic with rotifers (*Brachionus calyciflorus*). Modified from Figures 1a and 5e of Ref. 190. (A) Temporal density changes (smoothed fits) in rotifers (females/mL) and algae (10^4 cells/mL) with mean number of cells per palmelloid algal clump. Open circles on algal-clump line show times when gene expression was measured using microarrays. (B) Levels of gene expression (log fold change relative to day 0) for genes with significant twofold change in both (solid black lines) or only one (dashed gray lines) of the two clump-size cycles. See Ref. 190 for identity of genes included in the three functional groupings (protein metabolism, photosynthesis, and cell/cell wall).

Cryptic eco-evolutionary dynamics and pragmatism

It is straightforward enough to make an argument on logical grounds that eco-evolutionary dynamics of some sort are to be expected in many contexts, and even to provide diverse examples of processes that might conceal some of these complex interactions in nature. Indeed, if eco-evolutionary dynamics are often cryptic, then it is not unreasonable to suspect that they might frequently have been overlooked in favor of simpler, if incomplete, explanations. However, it is another matter to make a case for their general importance, to the point that a pragmatist might reasonably question whether giving up on seemingly simpler explanations to hunt down cryptic eco-evolutionary dynamics is really worth the effort when it comes to (1) predicting system responses or (2) meaningful effect sizes. In this light, we feel it is important to emphasize that “cryptic” does not somehow imply “less important,” and that the value in pursuing such dynamics is not only context specific, but also best answered with empirical research supported by pertinent theory.

Predicting versus explaining system responses

If we rely only on our ability to predict a given ecological or adaptive response as our sole criterion for assessing the success of simple models, and if we allow for some imprecision, then missing some cryptic eco-evolutionary effects might not be so bad, and could even justify some use of parsimony for convenience where doing so basically gets us the right answer for the wrong or incomplete reasons. Nonetheless, most ecologists and evolutionary biologists seek explanatory theory over mere prediction because explanation offers more scope for generalization,[196] and not all outcomes in ecology and evolution are simply deterministic.[197] The prediction-centric justification also does not apply well where eco-evolutionary outcomes are cryptic by virtue of compensatory effects that lead to little or no apparent net change in a system response. As we have discussed, failure to consider an eco-evolutionary model in such cases could actually lead us to significantly underestimate the importance of a key ecological (or evolutionary) process of interest. At the same time these null, muted or transient system responses are actually areas of enduring interest to ecologists and evolutionary biologists when cast in terms of processes like stability, resilience, regulation, persistence, and stasis.

It is no coincidence that much eco-evolutionary theory invokes the above types of cryptic outcomes (e.g., populations;[50,53,54] communities and ecosystems[9,51,64,103,118,130,132]). Indeed, these types of outcomes often bear directly on societal interests tied to conservation, natural resource management, and control of unwanted pests or pathogens, where sustainability or control are high priorities. If one major lesson has emerged from eco-evolutionary explorations along these lines, it is that these types of system dynamics can be challenging to predict, and likely even more difficult to manage, without an understanding of the underlying dynamics. To invoke a fairly stark example, while we could certainly use the costly history of resistance emergence in pathogen and pest populations to predict billions of dollars of future economic loss and a great deal of human suffering, our best hope to actually mitigate such outcomes depends on our ability to predict and manage evolutionary rescue dynamics in such systems.[33,198]

Effect sizes

If the effect sizes of cryptic eco-evolutionary processes are typically modest, then associated outcomes may not be all that different from those anticipated under simpler models that ignore those added dynamics. Indeed, we have no reason to believe that all eco-evolutionary effects are large, and we have already noted how more modest cases might be cryptic by oversight. Although a number of the studies that drew initial attention to the field provided evidence of relatively large effects of evolution or trait variation on ecological responses (examples in Refs. 17, 32, 39, 71, 72, 74,80, and 87), it is early yet to suggest that such effect sizes will be typical of eco-evolutionary outcomes in general. Clearly not all responses are large when assessed more broadly, at least on short time scales.[60] Inevitably, some studies pursuing cryptic eco-evolutionary effects will not be rewarded with much return on investment, but even those findings, if properly documented, will ultimately contribute to a broader synthesis of the conditions favoring strong or weak eco-evolutionary dynamics. We also caution that what constitutes a biologically important eco-evolutionary effect size is highly context dependent and not defined by our limits of statistical power to detect them. For example, small evolutionary alterations to population vital rates (e.g., a few percent) may make the long-term difference between extinction and persistence and yet still be difficult to detect statistically. While we do not discourage exploratory studies that survey many traits and ecological responses, the use of theory and modeling to guide empirical study could improve the odds that investigators invest limited time and resources into study systems and approaches that will reveal cryptic dynamics.

A pragmatic return to parsimony

While it would certainly hasten our understanding of eco-evolutionary dynamics and their relative importance if more ecologists and evolutionary biologists were to dedicate their labs to that mission, that is of course not realistic and would come at a considerable cost to our understanding of many other important processes and patterns in nature. Moreover, few ecological or evolutionary research programs have the time or resources to explore all possible factors contributing to a given observation of interest, and thus even asking investigators to regularly include evolutionary treatments or response variables in their ecological studies, much less fully dynamic feedbacks, is a lot to expect. So, in closing, we advocate for something much more modest and more attainable by ecologists, evolutionary biologists, and eco-evolutionary biologists alike: a return to thoughtful use of parsimony in practice.

Most investigations begin with some assessment of the factors that might contribute to a pattern in nature, often with the pragmatic objective that these factors must be measured or controlled. Likewise, essentially all studies reflect back on these factors and assumptions when analyzing and interpreting their findings. We merely ask that, as part of this process, investigators challenge themselves to explicitly define some cryptic, or even not-so-cryptic, eco-evolutionary mechanisms that might hypothetically operate in their study systems. What are the likely traits influencing a population's growth, the interaction of species, or even fluxes of nutrients and energy? What changes in ecological conditions might maintain or alter selection on those traits? Could those processes be coupled, and if so, how would they need to be coupled to produce outcomes similar to seemingly simpler alternatives? This last question is likely to be as useful to investigators already studying eco-evolutionary dynamics as it would be to those pursuing primarily evolutionary or ecological insights. To be sure, this thought exercise will not always change how a study is ultimately conducted. Some cryptic dynamics will be deemed too improbable or impractical to pursue much further. However, we suspect that in some cases investigators will reward themselves with interesting possibilities. Defining and weighing such possibilities is what it means to apply parsimony in a conscientious fashion that does not ambiguously dismiss cryptic interactions of evolution and ecology without ever stating why, or worse still, on the basis of unwarranted caricatures of their disparate time scales and the simplicity of nature.

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Conflicts of interest

The authors declare no conflicts of interest.

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