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## *Why Ecology and Evolution Occupy Distinct Epistemic Niches*

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ABSTRACT. Recent examples of rapid evolution under natural selection seem to require that the disciplines of ecology and evolution become better integrated. This inference makes sense only if one's understanding of these disciplines is based on Hutchinson's two-speed model of the ecological theater and the evolutionary play. Instead, these disciplines are more accurately viewed as occupying distinct "epistemic niches." When so understood, we see that rapid evolution under selection, even if it is generally true, does not imply that evolutionary explanations are improved by the inclusion of ecological details. Nor are ecological explanations necessarily improved by the inclusion of information about trait variation, heritability, effective population size, or other standard evolutionary factors. To illustrate, I develop a version of Kitcher's (1984) "gory details" argument to show that, even for some trait that is under strong directional selection, a dynamically sufficient explanation of its ecological relationships should ignore most of the information explaining why that trait is evolving. The wholesale integration of ecology and evolution looks even less appealing when empirical sufficiency, a purely practical requirement, is taken into account. As a way forward, I propose an eco-evo partitioning framework. This strategy enables researchers to estimate the empirical sufficiency of a purely ecological, a purely evolutionary, or a combined eco-evo approach.

## 1. INTRODUCTION

It might come as a surprise to some readers that the disciplines of ecology and evolutionary biology are widely regarded as distinct and that efforts to integrate them have proven difficult. This will be particularly surprising to anyone whose impression of these fields is based on popular studies of natural selection in the wild. Most of us learn about natural selection from examples in which both the trait under selection and the ecological factors influencing it have been worked out in detail. Rosemary and Peter Grant's study of Galapagos finches is a classic example (Grant 1999). After years of meticulous work, the Grants demonstrated that a change in the size and hardness of available seeds, caused by a period of drought, selected for rapid evolution in the structure of finches' beaks (Weiner 1994). John Endler's work on Trinidadian guppies is another popular case (Endler 1980). By manipulating the number and types of predators at different locations in the guppies' habitat, he demonstrated that male guppies' coloration evolves toward an adaptive balance between conspicuousness (to females) and crypsis (from predators). The popularity of such examples might lead many of us—in philosophy, for instance—to regard them as representative of research in these fields. Thus, one might be excused for believing that what Mayr (1976) described as “population thinking” (i.e., where populations are represented not as uniform types but comprised of variable individuals) is standard practice in ecology, or that most evolutionary studies consider the effects of specific ecological factors on wild populations.

In fact, the gulf dividing ecology from evolution has been widely commented upon. For example, in a highly cited review in *Science*, Schoener (2011) describes the integration of evolutionary biology and ecosystem ecology as “the newest synthesis,” but notes that there are few known examples where trait evolution has an ecosystem-level effect. Of course, there are many examples of previously evolved traits influencing ecosystem-level properties. Schoener describes these as “retrospective studies” in which “present day ecological processes can be understood as the outcome of historical events” (2011, 428). They are distinct from genuinely integrative studies, Schoener notes, in which the process of evolutionary change (e.g., the adaptation of some trait to an ecological parameter) is shown to have some ecosystem-level effect. Another review in *Ecology Letters* begins with the observation that “the disciplines of evolutionary biology and ecosystem science are weakly integrated” (Matthews et al. 2011). The authors identify nine examples of traits that are “potentially heritable” and “might directly or indirectly affect ecosystem functions” (692). It is revealing, however, that in this attempt to defend the relevance of evolution for ecosystem ecology the authors are forced to rely on hypothetical examples. Another recent review published in *Functional Ecology*, this time focusing on community ecology rather than ecosystem ecology, puts the point more starkly: “Despite an increasing number of pictures of Charles Darwin in conference presentations of community ecologists, the questions asked in many of these studies do not concern any evolutionary processes”

(Gerhold et al. 2015, 606). Again, the subtext is that more work can and should be done to bring ecology and evolution together.

Why, it might be asked, aren't these disciplines already integrated given their apparent overlap in subject matter? Although an interesting historical answer could be given to this question, this shall not be my approach. Instead of providing a detailed "natural history" of these disciplines I defend a functional hypothesis about the distinct epistemic "niches" that they occupy. Furthermore, I suggest that in at least some cases (perhaps often) the integration of ecology and evolution is undesirable.

The argument in a nutshell is as follows. First, I consider (in section 3) whether ecological details tend to be relevant for evolutionary explanations. The suggestion that they are relevant is usually supported with examples of rapid evolution by natural selection, such as with the Grants' finches or Endler's guppies. The key inference is that if most organisms are evolving rapidly under natural selection, then evolutionary explanations should document the specific ecological factors influencing this process. I begin by questioning the evidence that natural selection is indeed so strong or pervasive. I then propose that even if most traits are indeed evolving rapidly under selection, there are many scenarios in which the driving ecological factors are not explanatorily relevant. Second, I consider (in section 4) whether evolutionary details are always relevant for ecological explanations. Again, a key assumption is that if most traits are undergoing rapid evolution by natural selection, then any adequate ecological explanation will typically have to document those changes. To the contrary, I present a scenario in which the "gory details" (Kitcher 1984) of an evolutionary explanation are ecologically irrelevant, even when a trait is evolving rapidly. Hence, the lesson to be drawn from these two sections is that ecology and evolutionary biology are not always better together. This raises the question of when exactly does it make sense to combine them? I approach this question (in section 5) by drawing on a distinction between a strictly ecological vs. a strictly evolutionary explanation. This framework, which involves partitioning variance between ecological and evolutionary factors, serves as a litmus test for estimating when exactly an integrated (eco-evo) explanation is worth the additional effort that it often requires.

## 2. THE ECOLOGICAL THEATER AND THE EVOLUTIONARY PLAY

Before jumping into the argument, it is important to say a few things about the standard reason one often hears for the separation of ecology and evolution. This idea is often framed in terms of Hutchinson's (1965) metaphor of the ecological theater and the evolutionary play. David Reznick provides a standard summary:

Hutchinson's (1965) "ecological theatre and evolutionary play" . . . argued that ecology shapes evolution. A peculiarity of most of the associated theory is that it models ecological interactions in a fashion that treats

organisms as constants, which implicitly assumes that they do not evolve. The intent is not that evolution does not happen but rather that it happens on a different, much longer timescale than ecology. Evolution is thus seen as something that happened in the past but explains the present. (2013, S1–S2)

This interpretation of Hutchinson's metaphor emphasizes the temporal dimension that was thought to separate ecological from evolutionary processes. As Reznick notes, evolutionary processes were presumed to occur over extended periods (e.g., hundreds of thousands of generations), whereas ecological processes were thought to unfold more rapidly. If this two-speed model were true, then it might be expected that the disciplines of ecology and evolution would follow separate paths. On this view, evolutionary biologists engage in historical reconstructions of how species gradually acquire certain adaptations, while ecologists investigate the ways that those adaptations interact with specific, relatively ephemeral environmental factors.

It is unclear what Hutchinson really meant by his metaphor or how serious he was about the two-speed model. One suspects that he would not have been overly committed to the idea that evolution is always slow. After all, Hutchinson must have been familiar with Darwin's (1859) discussion of rapid evolution under domestication. Darwin's point was that artificial selection provides a close analogue for what happens in the wild and, therefore, that evolution can happen over an "ecological" time scale.

This issue aside, there are two important things to note about the way that Hutchinson's metaphor is deployed in contemporary discussions about ecology and evolution. First, the statement that "evolution" happens over extended periods can be interpreted in a variety of ways depending on which evolutionary process one has in mind. Such macro-evolutionary processes as speciation, extinction, or the emergence of qualitatively novel traits are plausibly quite slow. However, as it will be discussed in the following sections, contemporary authors tend to interpret Hutchinson more narrowly. They take him to be talking about natural selection on continuous phenotypes. This is perhaps the main lesson that tends to be drawn from such examples as Galapagos finches or Trinidadian guppies, that it is possible for continuous traits to undergo rapid evolutionary change. Hence, such studies are taken to suggest that Hutchinson's two-speed model is mistaken, and that the barrier once thought to separate ecology from evolution no longer stands.

A second thing to note about Reznick's comment is his uncharitable interpretation of why ecologists "treat organisms as constants." As I argue in section 5, this is part of what it means to adopt strictly ecological approach to some subject matter. Contrary to Resnick, however, I do not regard this as an "implicit assumption that organisms do not evolve." As I argue below, there are a variety of scenarios in which a trait might be evolving rapidly under selection, but the details of this process are not relevant to a given ecological explanation. Alternatively, those details might be otherwise informative, but end up being too difficult to obtain for practical

reasons. In such cases it is perfectly reasonable to treat populations as if they were static or constant while fully recognizing that organisms do, of course, evolve.

### 3. DO EVOLUTIONARY EXPLANATIONS ALWAYS BENEFIT FROM ECOLOGICAL DETAILS?

Ecologist Andrew Hendry opens his recent book, *Eco-evolutionary Dynamics* (2017), with the following characterization of the relationship between ecology and evolution:

Ecology and evolution are so intertwined as to be inseparable. The reality is obvious on long time scales given that different species are clearly adapted to different environments and have different effects on those environments (Darwin 1859). Yet traditionally, evolutionary and ecological processes have been thought to play out on such different time scales that evolution could be safely ignored when considering contemporary ecological dynamics (Slobodkin 1961). However, the past few decades have seen a shift away from this “evolution as stage—ecology as play” perspective toward the realization that substantial evolutionary change can occur on very short time scales, such as only a few generations (review: Hendry and Kinnison 1999, Reznick and Ghalambor 2001, Carroll et al 2007). If contemporary evolution can be this rapid, and if the traits of organisms influence their environment, it follows that evolution will need to be considered in the context of contemporary ecological dynamics. (2017, xi)

The argument has two steps. First, Hendry takes the growing body of evidence documenting rapid evolution by natural selection to be representative of traits in general. Second, he assumes that if some trait is rapidly adapting to the environment, then an adequate explanation of how it evolves must document the specific ecological factors that bear upon it. This leads to the conclusion that most studies of trait evolution (i.e., where evolutionary change in some trait is the explanandum) should take specific ecological factors into account.

How sure can we be that selection is in fact such a strong or pervasive force in nature? In his classic book on selection in the wild, Endler (1986) provided a list of 125 species from a wide range of taxa—studied between 1921 and 1984—where evolution by natural selection had been empirically confirmed. These are cases in which evolution occurred over fairly short time scales. Hendry cites two relatively recent meta-analyses in which a similarly rapid response to selection is documented in 14 (Hendry and Kinnison 1999) and 47 (Reznick and Ghalambor 2001) species respectively. Although these studies are each impressive demonstrations of the power of natural selection, they hardly provide an adequate basis for estimating the strength or pervasiveness of selection in general. This objection has been developed by Kingsolver and Pfennig (2007), and it is worth considering some of the reasons for their skepticism.

First off, they note that studies failing to detect a rapid response to selection are less likely to be published than ones that do. Hence, meta-analyses estimating the general strength or pervasiveness of selection are likely exaggerated because of a “file drawer” bias. Kingsolver and Pfenning further note that studies on natural selection in the wild tend to have small sample sizes. Again, this casts doubt on their representativeness. Another potential issue is that proxies typically used to measure the strength of selection often examine efficiency at specific stages of an organisms’ life cycle, rather than a more holistic picture of their net effects on survival and reproduction. Thus, researchers might be getting an exaggerated impression of the extent to which ecological performance impacts fitness. For instance, some phenotypic variant that performs relatively well in a foraging context might involve an undetected developmental cost, resulting in a net decrease in organismal fitness. Such cumulative effects are not detectable when ecological performance is evaluated on a trait-by-trait basis.

The problems run deeper than this. Let’s grant Hendry his first premise and assume for the sake of argument that selection is indeed causing most continuous phenotypes to evolve rapidly. Does this imply that explanations of trait evolution must take ecological factors into account?

In the same meta-analysis of 62 studies of selection in the wild, Kingsolver and Pfenning (2007) found that most cases involved directional selection as opposed to stabilizing or disruptive selection. As the authors note, one explanation for this pattern is that “random environmental change causes adaptive peaks to fluctuate over time” (Kingsolver and Pfenning 2007, 569). Let’s suppose that this picture of rapidly shifting adaptive landscapes holds true for most continuous traits. At the extreme, such shifting ecological conditions would demand a treadmill of investigations as evolutionary ecologists chase a constantly shifting adaptive peak. Under these conditions it would often be impractical to consider ecological details when describing the general trend of phenotypic evolution. Trait evolution could be explained more economically by ignoring ecological details and simply assigning a fitness value (perhaps a fluctuating one) to particular traits. Those fitness values can be estimated empirically by counting the number of offspring produced by phenotypically distinct individuals at different ages. This method provides a reliable estimate of dispositional fitness (Brandon and Beatty 1984) without requiring measurement of the specific ecological factors influencing this property (McGraw and Caswell 1996).

To be clear, I am not suggesting that we should hereby assume that adaptive landscapes are in fact fluctuating too rapidly to practically follow. My point is logical, not empirical. Considerations raised by Kingsolver and Pfenning reveal that Hendry’s argument assumes a kind of Goldilocks scenario. On the one hand, environments must be changing to some degree, otherwise it is unlikely that traits would be evolving rapidly in response to ecological selection in the first place. On the other hand, if environments change too rapidly, then at some point it becomes difficult or impossible to track the effects of specific ecological factors on evolu-

tionary outcomes. The point is simply that the inference from rapid adaptation to ecological significance is not necessarily straightforward.

Another consideration is the extent to which traits are subject to drift instead of selection. Although this possibility tends to be overlooked in discussions of eco-evo integration, it ought to be taken seriously. Population geneticists identify a rather narrow range of conditions under which selection drives alleles to fixation. This is thought to occur infrequently in eukaryotes where effective population sizes are typically quite small (Lynch 2007). At the same time, molecular biologists identify alternative (nonselective) processes by which complex structures might evolve (Akins and Lambowitz 1987; Stoltzfus et al. 1999). From this perspective, the case for eco-evo integration looks considerably less promising. If most traits are undergoing drift as opposed to selection, then there is a limited role for ecological factors in explaining their evolution.

Kingsolver and Pfennig drive yet another wedge in the inference from rapid evolution to interdisciplinary integration. Their meta-analysis revealed that “selection acting on traits that influence mating (e.g. elaborate displays in males) appears to be stronger than selection acting on traits that influence survival or fecundity (i.e. sexual selection tends to be stronger than natural selection)” (2007, 570). Again, let’s assume that this is a representative finding and ask what it might mean for eco-evo integration. Granted, some forms of sexual selection are presumably tied to environmental factors. For instance, female guppies are thought to prefer colorful males because color is an honest signal of foraging ability (Grether, Hudon, and Millie 1999). However, other cases of sexual selection are less obviously ecologically driven. Peacock tails and other such exaggerated phenotypes might be explainable in terms of a runaway process (Fisher 1958; Lande 1980) that is decoupled from ecological factors. Again, my point is simply that the inference from rapid selection to ecological significance shouldn’t be drawn too hastily.

One might object that my arguments in this section have been largely hypothetical. *If* the evidence for rapid evolution by natural selection is biased, or *if* most of those traits are either subject to rapidly shifting landscapes or are under sexual selection, then the inference from rapid evolution to ecological significance is blocked. Indeed, there are a few “ifs” here, but that is precisely my point. Before concluding anything about the general significance of ecology for evolution we require a better picture of how selection works in the wild. My aim in this section has been to throw some cold water on what often seems like an unwarranted enthusiasm for the wholesale relevance of ecology for evolution. The fact that some continuous traits are capable of rapid directional selection is undoubtedly interesting. However, it is too soon to demand a radical shift in the ways that evolutionary biologists approach their subject matter. By routinely incorporating measurements of ecological relationships into their studies of trait or genome evolution, evolutionary biologists would add considerable time, complexity, and expense to an already challenging discipline. This might be warranted in some cases, but not without reasonable expectation of an explanatory payoff.



#### 4. DO ECOLOGICAL EXPLANATIONS ALWAYS BENEFIT FROM EVOLUTIONARY DETAILS?

Let's now turn to the other direction of explanatory relevance and ask whether ecological explanations tend to benefit from the inclusion of evolutionary details. Arguments in support of this contention also appeal to the capacity for continuous phenotypes to undergo rapid evolution by natural selection. If traits tend to evolve rapidly, then any ecological factors that are influenced by those traits will fluctuate accordingly. Thus, to fully appreciate the dynamic nature of ecological relationships, the argument goes, one must keep an eye on the direction and magnitude of evolutionary change.

In analyzing this argument let me clarify a few assumptions. Suppose (again, for the sake of argument) that most continuous traits are indeed capable of rapid evolution. Further, assume that the rate of environmental change is typically within the Goldilocks range (not too slow to be irrelevant, but not too quick to be scientifically untractable). Let's also allow (contra Kingsolver and Pfennig) that much of this change results from "ecological" as opposed to purely sexual selection (i.e., that rapidly evolving traits are adapting ultimately to biotic and abiotic features of the environment and not driven by a runaway Fisherian process). Would it then follow that the discipline of ecology ought to systematically embrace an evolutionary perspective?

In fact, this inference relies on at least three additional assumptions. To make them explicit it will help to introduce some terminology. First, consider some trait (T) which is capable of rapid evolution under selection. To say that T is "ecologically effective" means that certain changes in T (e.g., a change in its mean value or variance) cause a corresponding change in some dependent ecological variable E. The nature of E will depend on the ecological scale under consideration (Trombley and Cottenie 2019). At the population level, for example, E might be the abundance or distribution of some other species. At the community level, E is likely to be an aggregate property such as net decomposition rate or biomass production. At the ecosystem level E is often a network property, such as the tendency for energy to pool at a certain trophic level or the rate at which nitrogen flows through an ecosystem (see Linquist et al. 2016 for operational definitions of these three scales of ecological investigation).

As we have seen, the argument in favor of eco-evo integration begins with the assumption that in most populations T is capable of rapid evolution by natural selection. This is taken to support the claim that ecologists ought to modify their theoretical understanding of E to incorporate evolutionary changes in T. We can now see that this inference relies on three additional assumptions:

1. Whenever T is under strong selection, it is likely to be ecologically effective for some E.
2. There is some dynamically sufficient theory R relating values of T to values of E.

3. R is an empirically sufficient theory, such that it is possible to measure the relevant values within acceptable levels of tolerance.

The concepts of dynamical and empirical sufficiency were introduced by Lewontin (1974) in his discussion of how to develop a theory of evolutionary genetics. I consider the relevance of these concepts for eco-evo integration momentarily. Before doing so, let's focus on the first assumption.

Even if most traits are under strong selection, this does not imply that they will cause a corresponding change (i.e., be ecologically effective) for some downstream ecological variable. In fact, T's capacity to evolve rapidly can sometimes serve to *stabilize* other ecological variables. To illustrate, consider again the example of Galapagos finches. In this system a change in one environmental parameter—average seed size—caused an evolutionary change in mean beak size. Now consider some other ecological variable that is causally downstream of this trait. For instance, we can imagine that finches play a key role in the rate of seed dispersal. Let's suppose that this second ecological variable systematically depends on the density of the finch population, such that increasing finch population density causes a corresponding increase in the rate of seed dispersal, all things being equal. What would we expect to happen to this ecological relationship once there is a shift toward larger seeds available on the Galapagos Islands?

Since finches possess the requisite genetic variation to adapt to this ecological change, they experience no decrease in population density (within limits, of course). Their population density remains stable despite evolutionary change in average beak size.<sup>1</sup> Hence the ecological relationship between seed size and dispersal rate remains unchanged over this evolutionary process. This consequence might seem counterintuitive at first, since the evolutionary change in beak size is what permitted the finch population to persist in its ecological role as a disperser. However, somewhat ironically, it is this capacity for rapid evolution that effectively stabilizes these ecological variables. If finches had lacked sufficient genetic variation to adapt to the change in seed size, then dispersal rate would have indeed been disrupted by the change in seed size. To put the point differently, the capacity for rapid evolution in beak size provides the necessary “wobble room” to stabilize the ecological relationship between population density and dispersal rate.

The question we must now consider is whether an ecologist studying the relationship between these two variables (seed size and dispersal rate) must incorporate details about the rapid evolution of finch beaks into their explanation. This would involve approaching the system from the perspective of an evolutionary biologist. Not only would this require “population thinking” in which finches are regarded as variable individuals (Mayr 1976), it would also require an estimate of the heritability of those variants. In addition, to calculate the rate of evolutionary

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1. To be clear, I am taking certain liberties with the facts in order to make a conceptual point. In reality, I have no idea whether population density remained constant in the face of changes in average seed size and hardness. The point is that such a scenario is not far-fetched.

change one would have to consider the relative strengths of selection on different phenotypes as well as the effective population size. This quickly becomes quite a detailed and epistemically onerous representation of the system.

Alternatively, it would be much simpler to place a black box around these evolutionary factors and focus just on the effects of population density on dispersal rate. In effect, this treats the finch population as if it were a static type—regarding one finch as good as the next as far as their capacity for dispersal goes. Of course, an ecologist who takes this approach is aware that such a simplified picture is probably false. Finches presumably vary in their capacity for dispersal. Some of that variability might well be heritable and impactful on fitness. However, the benefit of ignoring such differences is that it helps us understand the relationship between two ecologically relevant variables without getting bogged down in the “gory details” (Kitcher 1984) of the underlying evolutionary process.

One might object to this argument by insisting that, on the contrary, it is ecologically relevant whether beak size is capable of rapid evolutionary change. By hypothesis, dispersal rate would have been negatively impacted if finch beaks had not so adapted. Therefore, an ecologist must account for the “evolvability” in finch beaks in order to explain why these variables remain stable.

The first thing to note in response to this objection is that there has been a subtle shift in the explanandum, that is, in the property to be explained. We began by asking whether an ecologist interested in the relationship between two ecological variables (e.g., seed size and dispersal rate) must incorporate evolutionary details into the explanation. It was argued that those gory details would detract from our understanding of the ecological relationship. We then entertained the objection that an ecologist would need to represent the population as evolvable (presumably within some tolerance threshold) in order to provide an adequate explanation of the system. I agree that this information is potentially important, but it is relevant to the further question of *why* the two ecological variables remain stable, not to the initial question of *what* is the relationship between them.

Here is another way to make the point. If our interest is just in the precise relationship between seed size and dispersal rate, then it shouldn't matter what mechanism accounts for their ability to adjust to changes in seed size. We have been assuming that natural selection is the primary mechanism. This is in fact what the Grants uncovered with their meticulous work. However, it could have turned out that other, non-evolutionary mechanisms were either partly or entirely responsible for the change in mean beak size. One possibility is that finch beaks are phenotypically plastic. For example, suppose that prey handling experience early in a finch's life influences the size of beak that it later develops. This would result in the very same outcome at the ecological level, requiring no evolutionary change in the trait. Another possibility is that the phenotypic change in beak size could have been driven by meta-population dynamics. For example, the availability of large seeds might have caused small-beaked birds to depart from the region or perish. This would have opened a niche for larger-beaked individuals migrating

from neighboring populations (Rausher 1992; Stinchcombe et al. 2002). Again, such meta-population dynamics could stabilize the relationship between population density and dispersal rate, just as if the population had been locally adapting by natural selection. Ecologically speaking, it doesn't matter which of these processes buffered population density against the change in seed size. What matters is just that the two ecological factors of interest remain stable over certain environmental perturbations.

Obviously, this argument assumes that it is perfectly fine for ecologists to be interested exclusively in “how questions” without necessarily worrying about the underlying mechanistic “why” questions. I can imagine that some philosophers would push back on this suggestion, maintaining that mechanistic details are always beneficial to a scientific explanation.<sup>2</sup> Since we are assuming that selection tends to be the primary mechanism driving phenotypic change (an assumption I return to momentarily), it would follow that ecological explanations must take evolutionary details into account.

This is the point in the dialectic where we run into the question of whether some model of mechanistic explanation (e.g., Machamer, Darden, and Craver 2000) is the only suitable ideal for ecology. Although philosophers have written extensively on the suitability of mechanistic explanation for such disciplines as neuroscience (Craver 2007) and evolutionary biology (Skipper and Millstein 2005), there has been surprisingly little discussion of its suitability for ecology (Huneman 2018 is an important exception). Ecologists themselves have debated this issue under the guise of the “holism versus reductionism” debate (Wilson 1988). My sense is that both within the philosophy of science generally (e.g., Lange 2017; Woodward 2013) and in the discipline of ecology (e.g., Leibold and Chase 2018) there is a growing appreciation for the value of nonmechanistic or “holistic” explanations. An overview of this topic is well beyond the scope of this article. However, let us suppose for the sake of argument that some mechanistic model were to emerge as the “winner,” such that any legitimate ecological explanation requires mechanistic detail. This leaves open the question of *how much* and *which sorts* of details are required for a given situation. More specifically, are the sorts of mechanistic details invoked by evolutionary biologists, for example, when explaining the rapid evolution of some trait, typically relevant for the explanations developed by ecologists, for instance, when describing the dynamics of populations or communities?

On this question, I find that Richard Lewontin's (1974) discussion of dynamical and empirical sufficiency offers helpful guidance. According to Lewontin, a dynamically sufficient theory (R) contains an appropriate number of variables to describe, within some accepted threshold of accuracy, the changes in a given

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2. Michael Strevens (2016) explores an interesting possibility, where the underlying causal details always complement “higher level” explanations; however, because of the cognitive benefits associated with an explanatory division of labor, it often makes sense for respective disciplines to remain autonomous. This could serve as yet another argument for the separation of ecology from evolution, which I do not further explore here.

system. The latest objection to the gory details argument can thus be reformulated as the demand that any theory which represents two (or more) coupled variables (e.g., seed size and dispersal rate) is never dynamically sufficient. The purported reason is that this omits at least one additional variable—the tolerance or “wobble room” afforded, in this case, by the capacity for rapid evolutionary change in  $T$ —that is essential for understanding how the other two variables are related.

I accept the basic point that many dynamically sufficient explanations in ecology will require more than a bare bones representation of coupled variables. Since we are assuming, for the sake of argument, that most continuous phenotypes have a capacity for rapid evolutionary change, it would follow that many dynamically sufficient theories in ecology ought to include some additional variable representing the system’s capacity for evolutionary change. However, this need not require anything like what an evolutionary biologist would recognize as an adequate explanation. For instance, there is no need to represent the system as a phenotypically variable population. Nor is it necessary to document the degree of heritability in relevant traits, nor the strength of the selection coefficient, nor the effective population size, etc. Instead, an ecologist could accommodate the relevant “wobble room” with a relatively simple parameter representing the evolvability of  $T$ . The value of this evolvability term can be empirically estimated using a straightforward comparative approach. For example, by measuring variability in  $T$  among related species inhabiting diverse environments (e.g., Hedrick et al. 2019).

At this point, one might object that I have made too large a concession to the proponent of eco-evo integration. By admitting that an evolvability term might be necessary for dynamically adequate explanations in ecology, I am arguably conceding the need for eco-evo integration. In support of this objection, one might point to my suggestion that values of the evolvability term could be estimated using a comparative approach. Such an approach requires phylogenetic reconstruction, which is arguably a tool of evolutionary biology rather than ecology. Hence, by my own lights, it seems that dynamically sufficient explanations in ecology involve a certain amount of “niche overlap” with evolutionary biology.

This objection touches on a point I raised at the outset concerning the various possible meanings of “evolution” in the present context. My sense is that most authors calling for eco-evo integration have something more elaborate in mind besides using phylogenetic trees to estimate evolvability. Instead, they tend to be focused on the more specific details that arise in explaining rapid evolution under selection (phenotypic variability, heritability, selection strength, and effective population size, and the like). Also note that, under the scenario I have proposed, phylogenetic trees do not feature in the explanations of why certain ecological properties remain stable. The explanatory work is done by the evolvability term associated with  $T$ . The use of phylogenetic trees was raised merely as a suggestion for how to empirically assign values to this term. Other means of

estimating evolvability, which do not rely on phylogenetic reconstruction, would do just as well.<sup>3</sup>

Setting aside the gory details argument, let me now raise a separate objection against the argument for the required relevance of evolution for ecology. Up to this point I have allowed that natural selection is the primary mechanism driving most phenotypic changes. However, we have considered two alternative processes (phenotypical plasticity and meta-population dynamics) that might also cause the value of a phenotype to adaptively respond to ecological change. Endler (1986, 108) provides an even more comprehensive list of factors that might produce an adaptive correlation between trait values and environmental variables. These include random correlation, sampling bias, age-related effects, and genetic linkage. Ender argued that evolutionary biologists must rule out these alternatives before inferring that some trait is in fact under selection. With this requirement in mind, it seems rather convenient that proponents of eco-evo integration are pushing for selection as the dominant cause of phenotypic change. This assumption, were it true, makes the job of integration significantly less complicated. Alternative explanations for adaptive covariation could, on this picture, be ruled out with none of the difficult empirical work that Endler encouraged.

The problem, of course, is that this perspective is utterly Panglossian (Gould and Lewontin 1979). As Kingsolver and Pfennig remind us, we are in no position to infer that ecological selection is the primary factor behind most cases of phenotypic change. Indeed, estimating the relative contributions of evolution, phenotypic plasticity, and meta-population dynamics is an extremely difficult empirical problem.

In fact, work done by Endler and the Grants can make this task seem simpler than it often is. The systems they investigated were exceptionally transparent in certain key respects. Migration could be ruled out as a significant cause of phenotypic change in their systems, because the focal populations were isolated (in separate streams or on distant islands). Likewise, heritability of the relevant traits could be established through controlled observation of parent/offspring relationships. For many systems in nature, this level of transparency is simply unattainable. With this in mind, we must ask whether it is reasonable to demand of ecologists that they routinely track such evolutionary variables when conducting their investigations?

Lewontin argued that in addition to dynamical sufficiency, a useful theory must also be empirically sufficient. As he puts it,

While dynamic sufficiency is an absolute and basic requirement for the building of an evolutionary theory, empirical sufficiency adds yet another stricture that may render a formally perfect theory useless.

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3. This line of argument could potentially be taken a step further. Suppose that it is true that all continuous phenotypes have a capacity for rapid evolutionary change, as the proponent of eco-evo integration maintains. Then from a theoretical perspective it might be possible to treat this as a constant background condition instead of assigning it a separate term in a dynamically sufficient explanation. In other words, if the capacity rapid directional selection is pervasive then the ecologist would do well to treat it like any other standing condition and simply ignore it.

If one simply cannot measure the state variables or the parameters with which the theory is constructed, or if their measurement is so laden with error that no discrimination between alternative hypotheses is possible, the theory becomes a vacuous exercise in formal logic. (1974, 11)

The requirement of empirical sufficiency places a practical constraint on the kinds of explanations that researchers should strive for. From the armchair, it is easy to lose sight of this requirement. For instance, in constructing an ecological model it is tempting to plug in variables representing all manner of evolutionary processes. One often does this without considering how those values might be empirically obtained. It is worth noting that Lewontin thought that many population genetic models were already empirically insufficient since real genetic systems were multi-locus. Thus, he would be very skeptical of eco-evo models whose templates were then traditional population genetic models.

To summarize the argument in this section, even when the dynamics of an ecological relationship depend on the capacity for some trait to rapidly evolve, it is not always desirable to include a description of the underlying evolutionary mechanisms driving that change. Sometimes an ecologist is interested simply in how certain variables are related, not necessarily in why they exhibit those dynamics. A dynamically sufficient ecological explanation can be generated with a simple “evolvability” parameter representing the capacity of certain variables to withstand change, while remaining neutral on the exact processes that account for such resiliency. Standard evolutionary factors such as effective population sizes, selection coefficients, degrees of heritability, phenotypic variability, and so on are ultimately “gory details” (*sensu* Kitcher 1984) as far as many ecological explanations are concerned. This argument is only strengthened by the possibility that other, non-evolutionary factors can mimic the effects of selection at the ecological level. Phenotypic plasticity and meta-population dynamics, for instance, can cause phenotypes to rapidly respond to ecological change. In many natural systems, it is extremely difficult if not impossible to determine the relative contributions of such factors. Hence, an empirically sufficient ecological explanation is often better off ignoring the precise mechanisms underlying phenotypic change. At the same time, the idea that ecological explanations are always improved by evolutionary details seems to rest on a pan-selectionist picture that is seriously outmoded (Sarkar 2015). Such a speculative viewpoint can hardly serve as a foundation for the “newest synthesis” (Schoener 2011) in biology.

Up to this point I have been arguing as forcefully as possible for the separation of ecology and evolution. I see this as a corrective to the prevailing trend, which views integration as the desired goal. Let me qualify my position by stating that I do acknowledge that there are bound to be cases where eco-evo integration is informative and perhaps even practical. My issue is with the inference that, given the evidence for rapid evolution by natural selection, we should embrace integration as the default setting. It would be preferable to have an empirical framework for estimating, in advance, whether a given pattern is likely to require either a purely

ecological explanation, a purely evolutionary approach, or some combination of the two. The remainder of this paper outlines one such approach.

## 5. EMPIRICALLY ESTIMATING THE NEED FOR ECO-EVO INTEGRATION

Recent years have seen various extensions of ecological thinking into unconventional domains where the focal entities are not populations or communities of medium-sized organisms. For example, ecological thinking has been applied to gut bacteria (Costello et al. 2012), cancer cells (Amend and Pienta 2015), virus populations (O'Malley 2016), and mobile genetic elements (Brookfield 2005), to name a few. These applications reveal that the “essence” of ecology—so to speak—does not lie in its investigation of any proprietary subject matter. Unlike the disciplines of molecular biology or chemistry, there is no restricted domain of entities which fall under the purview of ecology. In this respect, ecology resembles the study of evolution. Evolutionary thinking is not limited to alleles or biological traits. It has proven useful for characterizing everything from culture (Linguist 2010), to algorithms (Mitchell 1999), to entire ecosystems (Doolittle forthcoming), and elsewhere. Even when ecologists and evolutionary biologists focus on the very same entities, for example when they investigate a population of organisms, their respective approaches often diverge.

The ideas in this section are based on a recent study by Linguist et al. (2013) that focused on an unconventional application of ecological thinking to communities of transposable elements (TEs). TEs are mobile genetic elements capable of autonomously replicating and reinserting into new regions of the genome. The vast majority of DNA in eukaryotic organisms has been generated by TE activity (Elliott and Gregory 2015). Moreover, patterns of TE abundance and diversity across eukaryotic genomes resembles the distribution of species across large geographic regions (Saylor et al. 2013). Such evidence has motivated some researchers to propose an “ecological” approach to the genome, where concepts, models, and methods from ecology are applied at the genomic level (Brookfield 2005; Le Rouzic, Dupas, and Capy 2007; Venner, Feschotte, and Biemont 2009). Linguist et al. (2013) investigated this suggestion, asking how (if at all) an ecological approach to TEs differs from familiar, evolutionary approaches to these elements. This led to a general account of the distinction between ecology and evolution which can be applied to any level of biological organization.

There are three basic steps to this framework. First is a view of the relationship between ecology and evolution as distinct simplification strategies. Second is set of operational definitions outlining the differences between a purely ecological, a purely evolutionary, or a combined eco-evo framework. The third step is a variance partitioning strategy for estimating the extent to which each approach can explain some pattern of interest. I will present this framework at a general level of



detail, saying little about TEs or the specific methods that were used in Linquist et al. (2013). My aim is to show that instead of adopting eco-evo integration as a general methodological goal, it is possible to empirically estimate prospects for successful integration on a case-by-case basis.

The first step involves viewing ecology and evolution as alternative simplification strategies. The aim of simplification generally is to create a tractable representation of a target system that explicitly foregrounds certain properties while strategically ignoring others. This idea is familiar to philosophers and biologists who think about scientific models as simplifications (Weisberg 2013). Somewhat more novel is the suggestion that entire disciplines can be understood as employing simplification strategies (Linquist et al. 2013). This departs from the conventional view of disciplines as defined in terms of their proprietary subject matter, which, I have argued, breaks down in the case of ecology and evolution.

Building on the definitions presented in Linquist et al. (2013) and Linquist (2015):

*A strictly ecological approach regards some class of focal entities (e.g. organisms, cancer cells, transposable elements) as a fixed type, or as a limited number of such types, which possess certain intrinsic causal properties. Changes in the abundance or distribution of those entities are explained exclusively in terms of their relationships to specific features of their environments.*

On this view, ecology (in its “pure” or “strict” form) adopts a typological view of its subject matter. Earlier, we saw that Reznick (2013) uncharitably described this as the implicit assumption that organisms do not evolve. On the contrary, we can better understand this as a calculated simplification. For some explanatory goals, a dynamically sufficient explanation does not require representing variability among individuals or changes in their intrinsic properties over time. This tactic was illustrated in the finch ecology example of the previous section. A dynamically sufficient representation of the relationship between population density and seed dispersal rate regarded finches as a general type, with the addition of an evolvability term specifying the range over which that type remains constant. Similar strategies are routinely employed in ecology; however, critics often disparage such abstract representations as being false or misguided (e.g., Mayr 1976) The idea seems to be that since organisms in reality are Darwinian populations, they must always be represented as such, regardless of explanatory context. The point of the “gory details” argument from section 4 was to challenge this idea.

Of course, there will be occasions when this simplification strategy backfires. Representing individual variability or changes in one’s focal entities is important for understanding some ecological phenomena. These are occasions when a dynamically sufficient explanation requires eco-evo integration. However, we have also seen that attempts to add detail to a scientific representation can violate the condition of empirical sufficiency. It therefore makes sense to assess the prospects of a purely ecological approach before pursuing details that are unnecessary or difficult to obtain.

A defining feature of a purely ecological approach is that it focuses on specific, as opposed to general features of the environment. For example, our earlier example of Galapagos finches identified two specific ecological factors: seed size and dispersal rate. In the example, population density of finches was relatively insensitive to the first factor, but closely coupled to the second. By contrast, a purely evolutionary approach adopts a complementary simplification strategy where specific features of the environment are ignored. Building on the definitions provided by Linquist et al. (2013) and Linquist (2015):

A strictly evolutionary approach views the focal entity as a population of individuals with intrinsic properties that vary and are heritable to some significant degree. The explanatory aim of this approach is to account for changes in the focal population over time. Later stages of the population are explained entirely in terms of its earlier stages (including relationships among individuals at earlier stages). However, relationships to specific features of the environment are ignored.

Much of the work in population genetics provides an illustration of how this approach is profitably applied at the level of alleles. Each allele is defined in terms of certain intrinsic properties such as fitness value and mutation rate. Early stages of the population such as allele frequency and effective population size explain how later stages arise. This is done without any reference to specific ecological factors. This is one of the main points of contrast between evolution and ecology, strictly speaking. When explaining ecological outcomes, it is often necessary to decompose the organism into distinct traits, each with its own ecological performance criteria. However, as Kingsolver and Pfenning (2007) pointed out, this approach can generate an inaccurate picture of organismal fitness. A simpler and often more accurate strategy focuses on a single, aggregate variable: the organisms' relative fitness. This property can be estimated without any attention to specific ecological factors, simply by comparing reproductive outcomes across the life cycle (McGraw and Caswell 1996).

To be clear, I am not suggesting that evolutionary biology reduces to population genetics. Although population genetics provides a useful illustration of a purely evolutionary approach, it is by no means the only example. Accounts of cultural evolution, such as models developed by Richerson and Boyd (2005), are also purely evolutionary in their orientation. These models are non-ecological in the sense that focal entities are considered as variable individuals, whose phenotypes are determined by both genetic and cultural factors. They are also non-ecological in that they regard the population as a closed system, not causally influenced by specific environmental factors. Relations among individuals at early stages of the population explain entirely how the population evolves over time.

It might be argued that this account of a purely evolutionary approach is mistaken because evolutionary biologists often investigate specific ecological factors. As we have seen, this is true of researchers like Endler who considered specific features of guppies' environment. Likewise, the famous study of coevolution between

lactose tolerance alleles and dairy farming practices is a case where evolutionary thinking about culture involved close attention to specific ecological factors (Holden and Mace 2009).

Perhaps the first thing to note in response to this objection is that these studies are not representative of evolutionary biology at large. As I argued earlier, their uniqueness might be due to the exceptional tractability of the specific systems which these researchers investigated. In Endler's system it was empirically feasible to rule out migration and phenotypic plasticity as alternatives to adaptation. The lactose example is also somewhat exceptional in that the genetic underpinning of this trait and its geographic distribution could be precisely determined. It would be a mistake to assume that all evolutionary systems are equally transparent. Nonetheless, there are bound to be occasions when a dynamically or empirically sufficient explanation involves both ecological and evolutionary factors. According to Linquist et al. (2013), these are cases where researchers should adopt a hybrid strategy:

A combined eco-evo approach views the focal entities as members of a population with intrinsic properties that vary to some degree. Relationships between those variants and specific features of the environment are explicitly represented in order to explain, not only how the population changes over time, but potentially also the effects of such changes on features of the environment.

The work of Endler or the Grants exemplify this approach. Such studies also remind us of just how labor intensive this strategy tends to be. Thus, it seems reasonable that evolutionary biologists and ecologists should resort to a combined approach only when there is an expectation of epistemic payoff.

The final step of the eco-evo partitioning framework is to estimate the prospects of each explanatory strategy by measuring the extent to which ecological and evolutionary factors covary with some dependent variable that is of explanatory interest. Specifically, this framework provides a method for evaluating the empirical sufficiency of these alternative approaches. This framework was employed by Linquist et al. (2013) to evaluate the extent to which patterns of abundance and diversity in TE communities called for each type of explanation. However, this example is complicated by the fact that TEs are unconventional entities, not often viewed from an ecological perspective and presumably unfamiliar to many readers. Let me therefore illustrate the application of this framework with a simpler, hypothetical example.

Imagine a meta-population of butterflies with a broad geographic distribution and suppose that there is considerable variation among those populations in wing pattern. An advocate for eco-evo integration might recommend launching into a detailed analysis of how both evolutionary and ecological factors interact to generate this pattern. However, a more prudent strategy would be to gauge in advance the prospects for each of the "pure" strategies. To evaluate the prospects for a purely ecological explanation one must determine the amount of variability

in wing pattern that correlates with specific features of the butterflies' environment. For example, we might look at such likely environmental factors as predator gradients or variability in specific food types to see whether they covary with phenotypic differences in wing pattern. A significant degree of covariation between ecological factors and trait values indicates that ecological factors potentially explain those phenotypic differences. This analysis would not tell us how those ecological factors are causally related to the trait. For instance, we would not be able to distinguish habitat preference from natural selection or phenotypic plasticity. However, an estimate of the covariation between the focal trait and ecological factors would indicate to a researcher the expected benefit of pursuing those questions. If there is no correlation between trait values and environmental factors then the decision is simple, an ecological approach is unlikely to pay off. If there is weak correlation, a researcher is in the position of having to weigh costs and benefits of an ecological study. Such factors as the tractability of the system will come into play at this point. In this respect, the eco-evo partitioning framework is a tool for making decisions about how scientists should invest their resources.

A similar approach could be used to evaluate the prospects for a purely evolutionary investigation. In this case, the relevant question is the extent to which variability in wing pattern among butterfly populations covaries with patterns of historical divergence. In other words, to what extent does the branching pattern of butterfly populations covary with differences in their wing pattern? At one extreme, historical relationships among populations might show little or no covariation with the focal pattern. This would be the case, for example, if population differences were due largely to phenotypic plasticity or meta-population dynamics. Under these conditions a researcher should be dissuaded from an evolutionary or combined eco-evo approach, especially if the system is relatively intractable or if the associated research costs are large. At the other extreme, it might turn out that there is a high degree of covariation between wing pattern and the order in which butterfly populations branched off from one another. This would be a reliable indication that evolutionary factors are indeed relevant in explaining the pattern of variability. For instance, the pattern might be largely due to a series of founder effects or high rates of drift.

Adopting this strategy can also inform a researcher of the prospects for a combined eco-evo investigation. It might turn out that the pattern in question is explained by both types of factors. For instance, we might discover a statistical interaction between ecological and evolutionary factors in their covariation with wing pattern. Perhaps predator intensity (an ecological factor) interacts with historical divergence patterns (an evolutionary factor) in their relationship to wing pattern variability. This would be a good indication that the trait is under selection and therefore that either of the "pure" strategies, taken on its own, is unlikely to be dynamically sufficient.

Applying this framework to TE communities in the genome led to a clear result (Linquist et al. 2013). Among relatively closely related TE communities, diversity

and abundance covaried significantly with ecological factors, but not with evolutionary factors. Conversely, among more distantly related TE communities, abundance and diversity covaried with evolutionary factors, but not with ecological factors. Interestingly, there was no interaction among these variables. In this system at least, eco-evo integration would not have been a profitable explanatory strategy.

This outcome is somewhat predictable in that it aligns with the expectation of Hutchinson's two-speed model. Recall that, on this view, "ecology" explains relatively short-term patterns while "evolution" explains deep historical time. However, for Hutchinson, this prediction was based on an ontological assumption about the rate of evolutionary change. By contrast, the eco-evo partitioning framework, described above, treats this as an empirical question. It could have turned out that ecological factors were relevant for distantly related communities, or that evolutionary factors were relevant over shorter time scales. Or, both types of factors might have been relevant across both periods.

Also note that this eco-evo partitioning framework can be applied on a case-by-case basis. Arguably, the problem with Hutchinson's two-speed model was its broad scope. Hutchinson assumed that evolutionary processes are never relevant over the short term. Hence, only a handful of counterexamples were sufficient to overturn it. The pendulum has swung to the other extreme with the recent wave of enthusiasm for eco-evo integration. It is now popular to assume that evolution and ecology are *always* better together. Viewing these disciplines as simplification strategies serves as a corrective to this "all-or-nothing" way of thinking. Trade-offs are central to the process of model-building. A modeler will often hesitate before adding detail to a model, asking whether the inclusion enhances its explanatory power or compromises its empirical tractability. The same sorts of considerations ought to apply more generally when considering disciplinary approaches to scientific questions. The eco-evo partitioning framework outlined here can help researchers to make these decisions in an empirically informed way, strategically evaluating the explanatory prospects of different approaches.

## 6. CONCLUSION

The disciplines of ecology and evolution have each hit upon distinct, but complementary simplification strategies. Ecology views focal entities as if they were fixed types with certain intrinsic properties that interact with specific features of the environment. It then explains changes in their abundance and distribution in terms of those specific ecological relationships. Evolution regards focal entities as members of a variable population but assumes for simplicity that they are not causally connected to specific features of the environment. Changes in the population are then explained in terms of relations among focal entities. It is also possible to combine these approaches, viewing the focal population as consisting of variable entities while also considering how their respective interactions with

specific environmental features affect population changes. This combined eco-evo approach is much more onerous than either of the pure strategies. It therefore makes sense for researchers to estimate the empirical sufficiency of different alternatives before launching into a particular mode of investigation. The idea that researchers must adopt by default an integrated eco-evo approach is based on a couple of misconceptions. One of these is Hutchinson's two-speed model, which treats the distinction between ecology and evolution as an ontological difference concerning the rates of different processes, rather than an epistemic difference about the most profitable mode of simplification. The other misconception is that the (supposedly) pervasive tendency for traits to undergo rapid evolution under selection implies that ecological and evolutionary details are always mutually informative.

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