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A critique for eco-evolutionary dynamics

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Abstract

1. A growing body of empirical work supports and informs the role of genetic variation and contemporary evolution in shaping ecological dynamics at the population, community and ecosystem levels. Although much progress has been made, I contend that reliance on several common empirical and inferential approaches is limiting forward progress in key areas, which leads me to several suggestions.

2. More studies should focus on revealing eco-evolutionary dynamics as they play out in the "real world," as opposed to laboratories and mesocosms.

3. At the community and ecosystem levels, increasing effort should be directed towards the importance of evolution acting through population density, as opposed to only direct per-capita effects.

4. More work should be directed towards the effects of whole-community evolution, as opposed to the evolution of only particular focal species.

5. New and innovative approaches are needed for studying how natural selection resists evolutionary and ecological change, thus generating cryptic eco-evolutionary dynamics.

6. Although simultaneous improvement on all of these fronts is perhaps impossible for any single research programme, even advances in one or more areas could dramatically improve our understanding of the prevalence, power and relevance of eco-evolutionary dynamics.

KEYWORDS
community genetics, foundation species, indirect genetic effects, keystone species, rapid evolution

1 | INTRODUCTION

Eco-evolutionary dynamics is an integrative field of research that focuses on how ecological change influences evolutionary change, how evolutionary change influences ecological change, and how those two pathways (eco-to-evo and evo-to-eco) can sometimes feedback to influence each other (Hendry, 2017). Although these linkages have been discussed from a long-term perspective (millions of years) since the origins of evolutionary biology (Darwin 1859), current emphasis has been placed on how they play out over contemporary time-scales, such as years to centuries. This shift in emphasis started with a growing body of work at the end of the twentieth century showing how the first part of the eco-evolutionary dynamic (ecological change shaping evolutionary change) was reasonably common on contemporary time scales in nature (reviews: Hendry & Kinnison, 1999; Hendry, Farrugia, & Kinnison, 2008; Reznick & Ghalambor, 2001). Acceptance of this eco-to-evo reality set the stage for an expanding cadre of ecologists to begin considering the second (evolutionary change influencing ecological change) and third (feedback) parts of the eco-evolutionary dynamic. In the present perspective, I discuss what this newer work has accomplished and, more importantly, how it can improve into the future.

Much of the early formal work on evo-to-eco and feedback effects emphasized interactions between population dynamics and natural selection (Chitty, 1960; Pimentel, 1968; reviews: Bassar, Marshall, et al., 2010; Kinnison & Hairston Jr, 2007; Saccheri & Hanski, 2006; Travis, Leips, & Rodd, 2013). More recently, a growing number of conceptual reviews and opinion pieces have noted that such effects are likely common and important also at the community and ecosystem levels (Fussmann, Loreau, & Abrams, 2007; Kinnison & Hairston Jr, 2007; Pelletier, Garant, & Hendry, 2009; Strauss, Lau, Schoener, & Tiffin, 2008; Thompson, 1998). Although empirical work illustrating these various effects has been slower to accumulate, it has at least been sufficient to establish several well-supported principles underpinning the evo-to-eco side of eco-evolutionary dynamics (Hendry, 2017).

1. Population growth rate can be as strongly influenced by variation in traits as it can be by variation in other purely "ecological" causes, such as rainfall or temperature (Ezard, Côté, & Pelletier, 2009; Farkas, Mononen, Comeault, Hanski, & Nosil, 2013; Hanski & Saccheri, 2006; Sinervo, Svensson, & Comenant, 2000; Turcotte, Reznick, & Hare, 2011).

2. The effects of evolution on ecology tend to be strongest at the level of population dynamics (as above), weaker at the level of community structure and weakest at the level of ecosystem function (Bailey et al., 2009). However, many instances of strong effects at these later levels are also known.

3. Intraspecific variation can be just as important as interspecific variation in structuring communities and altering ecosystem function (Des Roches et al., 2018; Hughes, Inouye, Johnson, Underwood, & Vellend, 2008).

4. Most eco-evolutionary dynamics at all levels (populations, communities and ecosystems) are probably underlain by *many genes of small-to-modest effect* (Crutsinger et al., 2014; Hendry, 2013), although some dynamics will instead be driven by *a few genes of large effect* (Skovmand et al., 2018).

These evo-to-eco tenets have particularly broad and robust support. Additional assertions regarding eco-evolutionary dynamics also have growing empirical support, such as the fact that contemporary evolution can strongly influence species invasions, range expansions, interspecific competition, host–parasite interactions, predator–prey dynamics and many other phenomena (Hendry, 2017).

The emergence of empirical generalizations such as these has inspired confidence in the importance of eco-evolutionary dynamics, and hence, the field is entering an adolescent phase, where more elegant and involved experiments can address specific predictions and competing hypotheses. This adolescent phase of any rapidly growing research field seems the appropriate time for a re-evaluation of existing methods and approaches. In this sense, the intellectual maturation of eco-evolutionary dynamics as a valuable and useful way of integrating ecology and evolution would benefit from a "mid-term report" and evaluation of sorts. In hopes of providing such constructive criticism, I here outline several common

and increasingly popular approaches to the empirical study of evo-to-eco effects that are perhaps not the best approaches to mature the field into the future. Of course, these approaches—and the criticisms thereof—are not always specific to eco-evolutionary dynamics, but are instead general to many ecological and evolutionary investigations.

1. **The unnatural approach.** Most existing evo-to-eco studies examine the ecological effects of evolution in unnatural laboratory or semi-unnatural mesocosm settings. I will argue that it is essential for studies to be conducted in the "real world."

2. **The per-capita approach.** Most studies of how evolution influences communities and ecosystems tend to focus on the direct per-capita effects of individuals, or groups of individuals at fixed densities. I will contend that greater effects likely act through an indirect route: evolution influences the population dynamics of key species, which then influences community structure and ecosystem function.

3. **The focal-species approach.** Most evo-to-eco studies concentrate on measuring the effects of particular focal species, which surely underestimates the overall importance of evolution in shaping communities and ecosystems. I will suggest approaches that can generate some insight into the effects of community-wide evolution.

4. **The dynamical approach.** Evo-to-eco studies currently focus on how evolutionary *change* shapes ecological *change*. However, the primary role of evolution might be to generate and promote ecological *stability*, for which additional research methods are needed.

In the sections that follow, I outline how the above approaches have led to inferential deficiencies, and I suggest improvements and alternatives that could help to alleviate those problems. I then briefly discuss several other methodological and inferential limitations frequently attending eco-evolutionary studies. In these discussions, several general points need to be kept in mind. First, my examples draw from—and my suggestions often apply to—studies of the effects of variation within populations (often discussed as "community genetics": Hughes et al., 2008; Tack, Johnson, & Roslin, 2012; Whitham et al., 2006), as well as the *evolution* of that variation. Both types of studies fall under the umbrella of eco-evolutionary dynamics as they both deal with relatively recent evolution—as opposed to differences between species (Des Roches et al., 2018; Hendry, 2017). Second, I variously refer to the ecological effects of different types, ecotypes, populations, phenotypes or genotypes. Except where explicitly noted, these terms are substitutable in the sense that a given point often applies to a given type of experimental design regardless of whether that design used genotypes, phenotypes, populations or ecotypes. Third, I am mainly concerned with—and therefore usually emphasize—the measurement and quantitative comparison of evo-to-eco *effect sizes*, as opposed to the rejection of particular evo-to-eco *null hypotheses*. Fourth, my focus is on empirical studies, with theoretical developments being the emphasis of a different paper in this present special issue (Govaert et al., 2019).

I close my critique by expressing optimism for the ability of eco-evolutionary researchers to move beyond the current common and relatively "easy," but inferentially limited, approaches towards more difficult, but inferentially richer, approaches. Stated another way, we need more high-risk high-reward studies. I recognize the impossibility of simultaneously implementing all of my suggestions. Indeed, studies that I will hold up as exemplars in one respect (e.g., conducted in nature) are often deficient in other respects (e.g., they consider only one focal species). Hence, a key point is that improvement in any one respect is valuable even without improvement in other respects: that is, a partial solution is better than no solution at all.

2 | THE UN-NATURAL APPROACH

Perhaps the greatest problem facing the advancement of understanding in eco-evolutionary dynamics is that most studies test for the ecological effects of evolution in unnatural laboratory conditions or in semi-unnatural mesocosm or common-garden settings. The reasons for using these controlled venues are clear: they allow increased replication, more precise and focused treatments, better controls, and the avoidance of much unwanted variation (Skelly & Kiesecker, 2001; Stewart et al., 2013; Zuk & Travisano, 2018). The first three of these properties increase statistical power and inferential confidence within an experiment and, hence, are universally desirable conditions—at least to the extent that they do not trade off with other important factors, such as the depth, breadth and quality of data collection. The fourth property (avoidance of unwanted variation) is also often considered desirable because it makes more apparent the precise causal effects of a specific treatment of interest. Conversely, I here contend that this property makes most laboratory and mesocosm experiments inappropriate for relevant eco-evolutionary inference.

Every natural environment is extremely complex, with many co-varying and complicating factors acting alongside any specific causal factor of interest. Thus, although controlled laboratory experiments can reveal how the causal effects of a focal factor (or a few factors) play out at some fixed level of all the other non-focal factors, that controlled and simplified situation would never exist in nature. As a result, laboratory experiments only ever can be "proof-of-principle" that the specific treatment of interest can, under certain conditions, have measurable effects (De Meester et al., 2019; Zuk & Travisano, 2018). Such experiments cannot tell us whether the chosen treatment actually has those, or indeed any, effects in the real world (Carpenter, 1990, 1996). A defence of laboratory experiments might be their utility in generating predictions and suggesting ranges of parameter values to explore in both theoretical and empirical studies. Yet even here we can be misled given that the levels of a treatment that are important in the laboratory could be—and probably are—very different from the levels that would be important in nature. In short, the inferential gap between laboratory studies and the real world is a huge problem for eco-evolutionary dynamics because,

after all, we care about making inferences relevant to the real world, not the laboratory.

Unlike laboratory experiments, mesocosms and common gardens can include many uncontrolled factors that also vary in nature (Stewart et al., 2013), thus increasing the relevance of inferences derived therefrom. Yet even these so-called "semi-natural" venues are also semi-unnatural in numerous aspects, such as predators or competitors being excluded or manipulated, spacings or densities being constant or otherwise manipulated, periods of the life cycle being absent so as to facilitate experimental tractability and so on. In some cases, the potential real-world relevance of mesocosms results can be evaluated by comparing ecological effects in the experiment to ecological patterns in the real world (El-Saabawi et al., 2015; Palkovacs & Post, 2009; Simon et al., 2017). As one example, the effects of landlocked versus anadromous alewife on zooplankton communities in mesocosms tend to mirror the differences in zooplankton communities between lakes containing landlocked versus anadromous alewife (Palkovacs & Post, 2009). Overall, however, mesocosm experiments tend to generate results that are quite different from those observed in nature (Skelly & Kiesecker, 2001; Stewart et al., 2013; Wolkovich et al., 2012). Hence, one important goal for eco-evolutionary dynamics should be to quantify "methodological biases" associated with different experimental venues (sensu Skelly & Kiesecker, 2001).

My strongest point, however, is to encourage researchers interested in eco-evolutionary dynamics to conduct their studies in the "real world," which is admittedly hard—but not impossible. For instance, high levels of replication, precise application of treatments and excellent controls can be implemented in (nearly) real-world eco-evolutionary studies of certain organisms, such as some insects (Farkas et al., 2013; Turcotte et al., 2011) and some plants (Agrawal, Johnson, Hastings, & Maron, 2013; Zuppinger-Dingley et al., 2014). These experiments do often retain considerable unnatural elements, such as artificial spatial distributions of resources or phenotypes. Hence, more natural experiments are also desirable, such as when organisms naturally colonize—or are introduced to—new environments (Gordon et al., 2009; Pérez-Jvostov, Hendry, Fussmann, & Scott, 2017; Mueller et al., 2017), or in the case of other planned or unplanned in situ environmental perturbations (Farkas et al., 2013). Of course, such experiments need to be conducted in ways that minimize ethical concerns and environmental impacts.

A counter argument might be made that simply using *multiple* common-garden or mesocosm environments could enable investigators to move beyond context dependence and towards generalization potentially also applicable to the real world (Stewart et al., 2013). I agree that such expansions are certainly an improvement that can allow extended and improved inference. However, I still contend that all controlled environments remain unrealistic to the point that any emerging generalizations continue to have questionable relevance for natural environments. Of course, any given natural environment at any given time also will not incorporate all of the potentially important factors influencing eco-evolutionary dynamics, leading to considerable context dependence and contingency (for optimists) or

idiosyncrasy (for pessimists). Hence, eco-evolutionary experiments in nature benefit dramatically from "replication" across populations, locations, environments, contexts and years. For instance, such replication has been—in combination with theoretical developments (Schweitzer et al., 2014)—valuable in generating insights into what might be called predictable context dependence, such as plant–soil feedbacks that vary from positive to negative depending on elevation or other factors (Van Nuland, Bailey, & Schweitzer, 2017; Van Nuland et al., 2016).

One option for real-world eco-evolutionary experiments would be extensions of the Before/After Control/Impact (BACI) design originally developed for purely ecological experiments (Underwood, 1992). In particular, I propose an eco-evolutionary Before/After ImpactA/ImpactB (BAAB) design (Figure 1) that is not so different from the current "common gardening" experiments frequently employed in mesocosms (Matthews et al., 2011). For instance, equal densities of two different phenotypes of a fish species (e.g., ecotype A and ecotype B) could be introduced into different natural ponds in which a set of community and ecosystem variables have been measured. Those same variables, along with characteristics of the introduced populations (e.g., growth, survival, biomass), then could be monitored over the subsequent days, weeks and months. Alternatively, the phenotypic distributions of a species already present in those ponds could be manipulated, such as through the removal of large individuals from one set of ponds and the removal of small individuals from another set of ponds. Experiments such as these would first reveal the immediate effects of altered phenotypic distributions of a focal species in otherwise natural environments. Monitoring across subsequent generations then could be used to assess the ecological effects of plastic and evolutionary changes in those phenotypic distributions, ideally by reference to non-evolving control populations in other ponds. (Methods for generating non-evolving populations are discussed in the section on the dynamical approach.).

3 | THE FOCAL-SPECIES APPROACH

Evo-to-eco studies typically take the "focal-species composite-response" approach (Hendry, 2017). That is, they ask how intraspecific variation or contemporary evolution in one species influences a set of emergent community or ecosystem variables. Examples include the effects of different cottonwood genotypes on soil nitrogen mineralization (Schweitzer et al., 2004), different evening primrose genotypes on arthropod diversity (Johnson & Agrawal, 2005), different alewife ecotypes on zooplankton diversity (Palkovacs & Post, 2009), different three-spined stickleback ecotypes on light transmission (Harmon et al., 2009), and different guppy ecotypes on primary productivity (Bassar, Marshall, et al., 2010). Sometimes, these effects of variation within a focal species are compared to the effects of other external variables, such as soil types or geographical distance or different species or species presence/absence (Des Roches et al., 2018; Hendry, 2017). The inference then drawn is
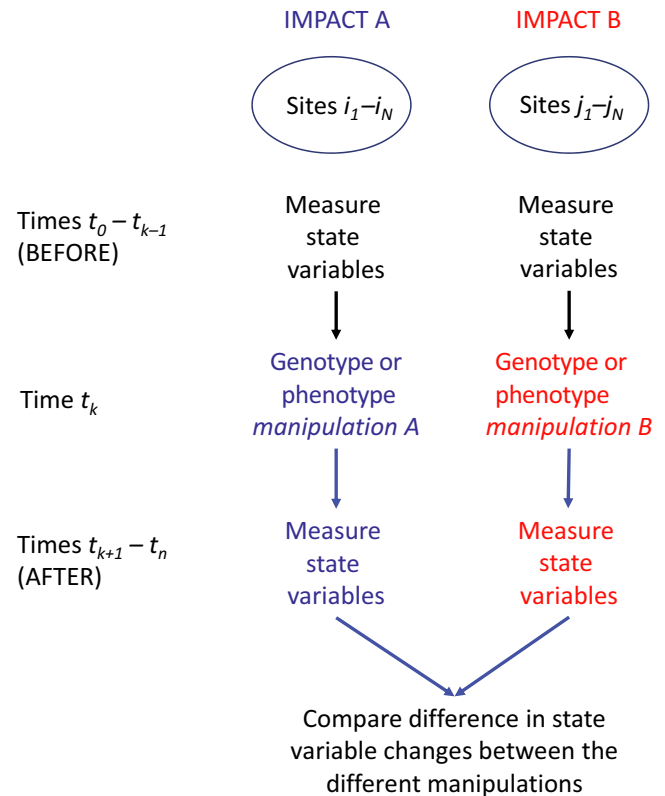

FIGURE 1 A proposed BAAB (Before/After ImpactA/ImpactB) design for evo-to-eco studies conducted in nature. Two sets of 1-N "sites" in discrete locations (e.g., different ponds) are selected for study and monitored for key ecological state variables over a relevant time frame (t_0–t_{k-1}). The two sets of sites are then (time t_k) subject to different evolutionary manipulations, such as the introduction of different ecotypes of a species or the selective addition or removal of a particular phenotypes from a species already present. All sites are then subject to additional post-manipulation monitoring (t_{k+1}–t_n) of the original state variables, with average differences between the two sets of sites revealing both the short-term impact of different phenotypes and the longer-term impact of the evolution of those phenotypes

typically "How important is evolution, relative to those other factors, in shaping community and ecosystem variables?" Remarkably, evolutionary effects are often thereby revealed to be nearly as important as other already-known-to-be-important factors shaping communities and ecosystems (Des Roches et al., 2018; Ezard et al., 2009).

In reality, however, *all* of the species in a given community are variable and evolving—and *all* of those species could be influencing community structure and ecosystem function (see also De Meester et al., 2019). Thus, an answer to the general question "How important is evolution?" is not attainable through focal-species approaches that instead address the question "How important is the evolution of one focal species?" Of course, the focal species in some of these experiments were chosen specifically for their known importance in ecological processes; that is, the focal species are often keystone species, foundation species, ecosystem engineers and so on. In one sense, this bias might be considered an inferential limitation because

the ecological effects of evolution in such exceptional species presumably do not reflect the ecological effects of evolution in most species. In another sense, however, perhaps the effects of evolution in these exceptional species capture a substantial amount of the overall importance of evolution in the entire community.

Moving substantially beyond the focal-species approach, especially in the real world, might seem so difficult as to be intractable. That is, the effects of interacting genetic variation in multiple species can be studied up to some level (e.g., three species in Zytynska et al., 2014), but expansion quickly becomes infeasible as more and more species are considered. At the extreme, the hypothetical—yet fundamental—question of "What would happen if all evolution, or all natural selection, stopped today?" could never be answered empirically because it would entail simultaneous manipulation of all species in the community. Yet, we might be able to get part of the way to an answer through certain experiments. For instance, an investigator could conduct biodiversity–ecosystem function (BEF) experiments (Hooper et al., 2005) in which genetic variation was manipulated (Hughes et al., 2008) in different numbers of species per treatment. That is, the same set of species could be used in a series of treatments: one treatment where none of the species were genetically variable (e.g., each only a single clone), one treatment where a single species was genetically variable, one treatment where two species were genetically variable, and so on until a final treatment where all species were genetically variable (Figure 2). Depending on practicalities, the single-variable-species treatment could be replicated across the different species, the two-variable-species treatment could be replicated across various pairs of species, and so on. The investigator then could examine the relationship between the number of variable species and the ecological variables of interest, as well as the effect of selection and evolution across future generations. The difference in the ecological variable between the all-species-variable treatment and the no-species-variable treatment would then estimate the total effect of variation and evolution across all species in the experiment. Further, projecting the relationship to its (presumed) asymptote would—at least for the sake of argument—generate an estimate of the total effect of all species that might be in the community. Although experiments of this sort would be difficult, they certainly would be achievable (most likely with plants and most likely in mesocosm settings) given that they are a fusion of existing BEF designs at the interspecific (Hooper et al., 2005) and intraspecific (Hughes et al., 2008) levels.

4 | THE PER-CAPITA APPROACH

Most experimental evo-to-eco studies take the following form: place *equal densities* of two or more "types" (genotypes, ecotypes, populations, etc.) of one species into different arenas, and then quantify their differential effects on the ecological variables of interest. For instance, this design typifies many of the fish examples cited above; that is, the experimental mesocosms were seeded with equal densities of different ecotypes of stickleback

(Harmon et al., 2009), guppies (Bassar, Marshall, et al., 2010) or alewives (Palkovacs & Post, 2009). Moreover, fish that died during the experiments were often replaced with new fish in an effort to maintain reasonably constant densities throughout the experiment. Similarly, many of the plant studies tend to quantify arthropod communities on, or soil properties beneath, individual plants (Johnson & Agrawal, 2005; Schweitzer et al., 2004). In short, most studies equalize densities and thereby assess per-capita effects of different ecotypes or genotypes on community and ecosystem variables. I suggest that this approach to eco-evolutionary dynamics severely underestimates the overall importance of intraspecific variation and evolution for ecological processes and patterns.

I propose that community and ecosystem variables are more strongly influenced by an indirect effect of evolution acting through population dynamics than by the direct per-capita effect of evolution. This assertion is partly motivated by the long history of studies showing how adaptive evolution in a focal species can strongly influence that species' population dynamics (Cameron, O'Sullivan, Reynolds, Piertney, & Benton, 2013; Ezard et al., 2009; Farkas & Montejo-Kovacevich, 2014; Hanski & Saccheri, 2006; Pimentel, 1968; Sinervo et al., 2000; Turcotte et al., 2011). To the extent that these species have important influences on their communities and ecosystems, evolutionary changes that influence their population dynamics (e.g., abundance, sex ratios and age structure) should have cascading indirect effects on those communities and ecosystems—even if evolution does not change their per-capita effects. For instance, although the evolution of foraging traits in landlocked alewife does influence zooplankton communities (Palkovacs & Post, 2009), adaptation to a landlocked life style probably has more dramatic effects on the number of alewife in a lake, which probably has an even bigger effect on zooplankton communities.

Several evo-to-eco studies have taken steps to consider indirect density-mediated versus direct per-capita effects on communities and ecosystems. For instance, Bassar, Marshall, et al. (2010) established mesocosms in which two guppy ecotypes (high predation and low predation) were crossed with guppy densities typical of high-predation and low-predation environments. If those different densities are assumed to reflect the influence of evolution on population dynamics, then the experiment can separate total evolutionary effects (comparison between mesocosms with the different ecotypes at their typical densities) from per-capita evolutionary effects (comparison between mesocosms with the different ecotypes at the same densities) from density-mediated evolutionary effects (comparison between mesocosms with the same ecotypes at different densities). However, the assumption that density differences between natural populations mainly reflect evolution is tenuous (they might instead be driven by differences in resources or predators or parasites), suggesting the value of another sort of experiment.

To assess these direct (per-capita) versus indirect (through population dynamics) effects, investigators could place different genotypes or ecotypes of a species into common conditions and then measure ecological effects when densities of that species are or
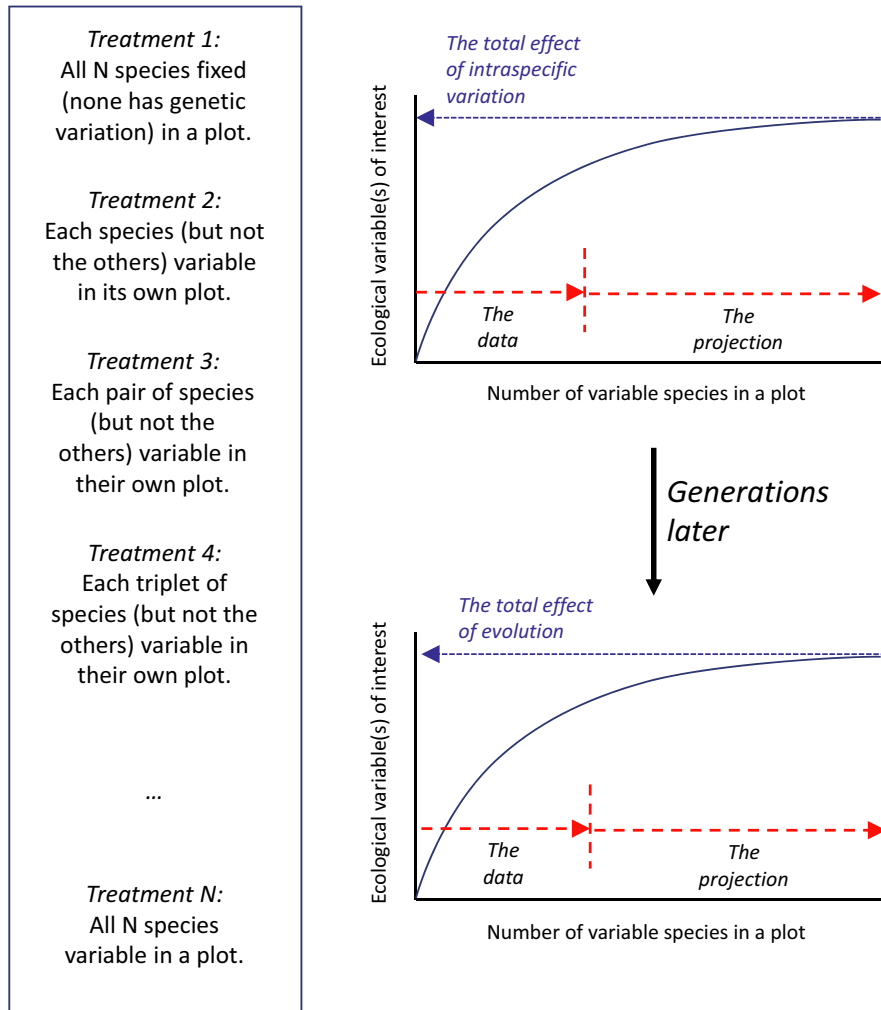
FIGURE 2 One option for moving beyond the focal-species approach in evo-to-eco studies towards an assessment of the total effect of evolution across many species in the community. In the proposed experiment, the same species are present in each experimental treatment but the number of those species with genetic variation differs. To the extent that genetic variation within species increases the ecological variable (e.g., primary productivity, in analogy with biodiversity–ecosystem function [BEF] experiments), an increase in the number of species that are genetically variable should increase productivity. The difference in the ecological variable between the no-species-variable and the all-species-variable treatments then estimates the effects of variation in all of the species in the experiment. Also, as in BEF studies, the effects are expected to be asymptotic: that is, the increase in productivity with the addition of variation in another species is expected to weaken with increasing numbers of variable species. Hence, the projected asymptote arguably generates an estimate of primary productivity if all species in a community were variable. Continued monitoring of the experiment across multiple generations allows similar estimates for the effect of *evolution*, which is only possible (barring contributions from new mutations) in the initially variable species

are not allowed to vary through time (Figure 3). In the first of these treatments, changes in the density of individuals that arise during the experiment are allowed to accumulate; whereas, in the second treatment, any such shifts in density are "corrected" by adding or removing individuals (e.g., clones) as needed in the current genotypic composition. In such an experiment, the density differences that emerge are a consequence of the different genotypes or ecotypes and, hence, reflect past evolution, as well as—if the experiment spans multiple generations—any ongoing evolution. Such an experiment could more confidently estimate total evolutionary effects (comparison between mesocosms with the different ecotypes at the densities they develop), per-capita evolutionary effects (comparison between mesocosms with the different ecotypes in which

densities were "corrected") and density-mediated evolutionary effects (total evolutionary effects minus per-capita evolutionary effects; Figure 3).

5 | THE DYNAMICAL APPROACH

Nearly all studies of eco-evolutionary dynamics ask how ecological *change* causes evolutionary *change*, how evolutionary *change* influences ecological *change*, or both. For instance, several studies have determined how short-term changes in the population size of ungulates are influenced by short-term changes in phenotypic traits (Ezard et al., 2009). Other studies have asked how phenotypic
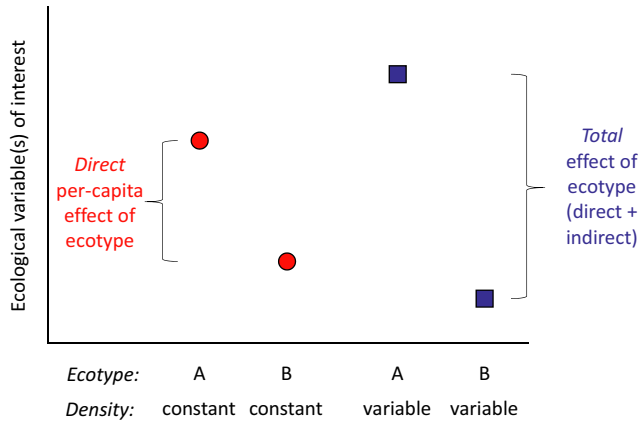
FIGURE 3 Moving beyond the per-capita approach towards a joint assessment of the direct (per-capita) and indirect (density-mediated) effects of intraspecific variation or evolution. In the proposed experiment, each of two or more focal types (genotypes, phenotypes, ecotypes or populations) is placed into different arenas to monitor community and ecosystem responses. In some of the arenas, the two types are maintained at the same density, thus revealing the direct per-capita effects of the different types. In other arenas, densities of the two types are allowed to vary according to their own dynamics, thus revealing the total (direct per-capita plus indirect density-mediated) effects. Indirect density-mediated effects then can be inferred as the difference between the total effect and the direct effect. Of course, the direct effects could depend on density, and so the constant-density treatments should be replicated across multiple relevant densities

differences between ecotypes of fish have generated community or ecosystem *differences*, as in many of the examples presented above (see also review in El-Saabawi, 2017). One reason for this emphasis on dynamics is that it would be challenging to assess the effects of evolution on ecology if no evolutionary change was evident, just as it would be hard to assess the effects of ecology on evolution if no ecological change was evident.

I contend, however, that the main effect of evolution on population dynamics, community structure and ecosystem function might be to resist change. As a result, most eco-evolutionary dynamics might not be readily apparent—that is, they often will be "cryptic" (Kinnison, Hairston, & Hendry, 2015). For instance, one of the most important roles of natural selection is to weed out maladaptive variants that enter the population (or increase in frequency) owing to mutation, recombination, gene flow or genetic drift (Burt, 1995; Hendry, Schoen, Wolak, & Reid, 2018). In short, natural selection in reasonably constant environments tends to keep trait means and variances reasonably stable (Haller & Hendry, 2014), which might thereby enhance ecological stability. Another form of cryptic eco-evolutionary dynamics occurs when traits evolve in ways that stabilize population sizes, for instance, through co-evolution of predators or prey or through adaptation to changing environments. In such cases, the dynamical approach is exemplified by the "evolutionary rescue" literature (Carlson, Cunningham, & Westley, 2014), where investigators seek a signature of declining population size followed by a rebound due to adaptive evolution. However, many populations in

nature are not declining despite changing environments, suggesting that ongoing evolution plays a critical role in counteracting changes in population size (Hendry, 2017; Kinnison et al., 2015; Vander Wal, Garant, Festa-Bianchet, & Pelletier, 2013). Evolution thereby also resists the changes in community structure and ecosystem function that would attend changes in the population dynamics of ecologically important species (i.e., the indirect effect emphasized in the previous section).

The study of eco-evolutionary dynamics thus would derive much benefit from the development and application of methods for inferring cryptic eco-evolutionary dynamics. Some excellent strides have already been made. (a) Characteristic statistical signatures of evolution can be detected in simple time series of predator–prey abundances (Hiltunen, Hairston, Hooker, Jones, & Ellner, 2014). (b) Tracking genotype frequencies can sometimes reveal how evolutionary change underpins population stability (Yoshida et al., 2007). (c) The measurement of additive genetic variance in fitness can indicate the likely effectiveness of natural selection in maintaining fitness despite environmental change and various forms of genetic degradation (Burt, 1995; Hendry et al.,). (d) Perturbation experiments that ask how ecological systems remain in, or return to, their original state (Bender, Case & Gilpin 1984) could be combined with manipulations of evolutionary potential (e.g., genetic variation) to infer how evolution favours resilience and robustness. (e) Studies can be conducted where the ecological effects of a species (or multiple species) are compared between situations where that species evolves versus situations where it does not. These experiments can be forward-looking, wherein some treatments allow evolution and others do not (right-hand side of Figure 4); or they can be backward-looking, wherein current and past gene pools are compared in current environments (left-hand side of Figure 4).

One forward-looking approach compares experimental treatments where populations have genetic variation present to facilitate short-term evolution to experimental treatments where populations are genetically invariant to prevent short-term evolution (e.g., multiple clones vs. single clones: Yoshida et al., 2007; Turcotte et al., 2011). A limitation of this approach is that effects of genetic variation per se are difficult to separate from effects of the *evolution* of that variation. To circumvent this limitation, both experimental treatments can incorporate the same starting genetic variation, with one treatment then allowing that variation to evolve and the other not (Pimentel, 1968; Williams, Kendall, & Levine, 2016). Genotype frequencies in both treatments will change within a generation due to natural selection, but evolution across generations is prevented in the latter (non-evolving) treatment by removing the post-selection individuals at the end of each generation and replacing them at the start of the next generation with new individuals according to the original (pre-selection) genotype frequencies.

One backward-looking approach uses "resurrection experiments" that rely on organisms with dormant stages, such as seeds in plants or resting eggs in some zooplankton (Franks, Hamann, & Weis, 2017; Orisini et al., 2013). In such experiments, current and
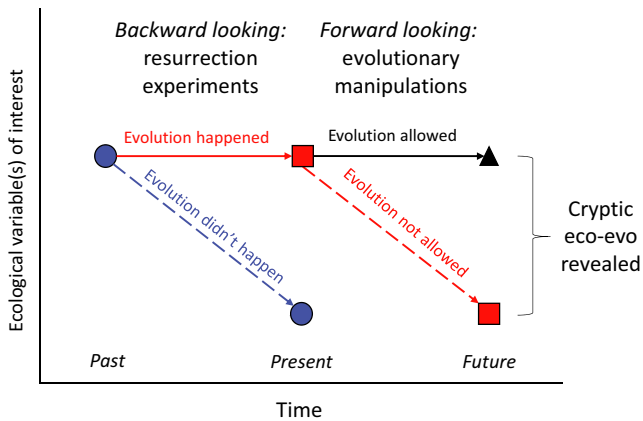
FIGURE 4 Inferring cryptic eco-evolutionary dynamics by comparing the ecological effects of evolving and non-evolving populations. The left-hand side of the figure depicts the backward-looking approach of resurrection experiments that compare the ecological effects—in current ("present") environments—of populations that have evolved up to the present (current gene pools) versus ancestral ("past") population preserved in a dormant non-evolutionary state. The right-hand side of the figure depicts the forward-looking approach of experiments that compare the ecological effects of populations allowed to evolve under new ("future") conditions versus populations prevented from evolving under those new conditions.

past genotypes (or gene pools) can be compared for their ecological effects under common conditions. These common conditions are typically generated for controlled settings, such as a laboratory or greenhouse, but, as encouraged above, assays for ecological effects also could be conducted in natural settings. A potential limitation of such work is that gene pools resurrected from dormant stages might be a biased subsample of the past gene pool. It is sometimes possible to avoid this concern by combining forward-looking and backward-looking approaches by preserving current gene pools in a state of dormancy until the future, when they can be resurrected for comparison to natural gene pools that evolved into that future (Franks et al., 2017).

6 | OTHER CONCERNS, ISSUES AND OPPORTUNITIES

Implementation of the above experimental design suggestions is important but also likely to be difficult or (at the least) time-consuming, expensive and risky. By contrast, a number of other inferential problems attending some current eco-evolutionary studies—and also many purely ecological or evolutionary studies—are relatively easy to solve.

1. *Replication at the appropriate level?* Many studies examine how ecological effects differ between populations of two different *types*, such as (in fish) benthic versus limnetic, lake versus stream, or high predation versus low predation. In each case, inferences are typically desired about the effects of adaptation

to those different environment *types*, and yet many studies examine only a single population of each type. Unfortunately, any study that does not examine multiple independent populations of each type lacks the replication necessary for inferences about those population *types*. Editors, reviewers and authors should pay much closer attention to this extremely common inferential problem.

2. *Plastic or genetic effects?* I have here frequently discussed studies of fish ecotypes (Bassar, Marshall, et al., 2010; Gordon et al., 2009; Harmon et al., 2009; Palkovacs & Post, 2009) as revealing some community and ecosystem consequences of *evolution*. However, nearly all such studies use wild-caught individuals and, hence, more specifically demonstrate the consequences of *phenotypic* differences, which will reflect a mixture of genetic (evolutionary) and plastic effects. In many cases, the trait differences thought to be having the differential ecological effects are known to have a strong genetic basis, yet the genetic basis for any particular ecological effect remains unknown. A first-glance solution might be for experimenters to use fish raised in a common-garden environment; however, genotype-by-environment interactions mean that effects observed for common-garden fish might not reflect the genetic effects manifest in nature. An improvement is to use multiple types of common garden (Johnson & Agrawal, 2005; Matthews, Aebischer, Sullam, Lundsaard-Hansen, & Seehuasen, 2016), ideally mimicking at least some of the environmental differences seen in nature. Of course, it would be equally interesting for studies to focus on the ecological effects of non-genetic inheritance, including epigenetics, cultural transmission, microbiomes and the like (Bonduriansky & Day, 2018).

3. *Statistical significance or effect size?* Many studies report and emphasize whether or not particular effects are statistically significant. However, in eco-evolutionary dynamics—as in many other enterprises—what matters is not whether there *is* an effect but rather what is the *type and magnitude* of that effect. All studies therefore need to report and emphasize effect sizes, regardless of their (also reported) statistical significance. It is also extremely useful for the observed evo-to-eco effect size to be compared to other potential drivers of the same ecological response variable. For instance, how community and ecosystem variables are influenced by intraspecific variation can be compared to how those same variables are influenced by interspecific variation (Des Roches et al., 2018), species presence/absence (Des Roches et al., 2018; Palkovacs & Post, 2009), geographical distance (Tack et al., 2012), focal-species density (Bassar, Marshall, et al., 2010), or several other possibilities (Hendry, 2017). Without such comparisons, one does not know what to make of a given evo-to-eco result.

4. *Prediction?* Studies on the community and ecosystem effects of evolution might be criticized for their apparent (everything but the) "kitchen sink" approach to response variables, wherein investigators measure everything they can think of (or that they can measure), and then search for which of those variables show significant effects. The criticism is that such investigations are not

hypothesis-driven but rather a fishing expedition for significant results, which runs the risk of happening on some outcomes merely by chance. Instead, as the argument goes, investigators should be testing a priori predictions such as from theoretical models or laboratory experiments. Although I certainly see the value of developing and testing predictions, community and ecosystem variables are so numerous and complex that it is often hard to know in advance which will be most interesting or important. Moreover, a given effect is always context-dependent, such that it might be present only in some replicates of some experiments. Hence, kitchen sink approaches—combined with multivariate analyses (e.g., MANOVA) of overall effect sizes—remain extremely useful in generating new ideas, which can thereby generate future predictions for testing in new studies.

Although my emphasis in the present paper has been on new and improved experimental approaches to eco-evolutionary dynamics, it is important to note the need to solidify and expand improvements in other areas of eco-evolutionary inference. For instance, data compilations and reviews strongly benefit from adopting and implementing formal meta-analytic approaches (Koricheva, Gurevitch, & Mengersen, 2013). Additionally, empirical efforts should be coupled, when possible, to theoretical developments that facilitate interpretation and generalization (Fussmann et al., 2007; Govaert et al., 2019).

7 | CODA

I have been so enamoured with, and enthused by, eco-evolutionary dynamics that I took seven years to write a book about empirical support for the burgeoning field (Hendry, 2017). Much of my approbation stemmed from pioneering experiments of the very sorts I have just criticized. My current concern is that these simple approaches have proliferated beyond the proof-of-principle spirit in which they were originally valuable. That is, the approaches are often now viewed as the end-point goal of experimental and inferential innovation, as opposed to a valuable spur for further improvements. Stated another way, empirical work in eco-evolutionary dynamics might now be stuck on a local adaptive peak of inference, where incremental improvements in design and implementation will lead to only incremental improvements in inference about the real world. Perhaps instead, the field needs a shake-up that forces us off that peak of limited profitability and into other areas of inferential space that have greater potential to make the massive inferential improvements that are needed if the field is to grow, evolve and expand in the scope and spread of its influence.

Clear insights into how our world will change into the future, how that change will influence the environment and ourselves, and what we can do about it is sure to depend on a robust understanding of the role of contemporary evolution in shaping ecological dynamics. If you are not fully convinced, attempt the counterfactual thought experiment "What would happen if all natural selection stopped working today?" Existing work in eco-evolutionary dynamics provides us

with the *inspirational* insight that the consequences would be massive, likely even catastrophic. What that same existing work does not typically provide us with are the *useful* insights that would allow evolutionarily informed management strategies for mitigation and improvement. In short, current eco-evolutionary work is woefully inadequate to answer questions such as: "Which ecological variables in which environments are most critically dependent on what type of evolution in which species?" Answering questions such as this requires experimental work in the real world, a consideration of how ecological effects are shaped by evolutionary changes in population density, insight into how multiple ecologically important species in communities are evolving together, and how evolution resists ecological change.

DATA ACCESSIBILITY

This manuscript does not use data.

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