Beyond adaptation: Incorporating other evolutionary processes and concepts into eco-evolutionary dynamics

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Abstract

Studies of eco-evolutionary dynamics have integrated evolution with ecological processes at multiple scales (populations, communities, and ecosystems) and with multiple interspecific interactions (antagonistic, mutualistic, and competitive). However, evolution has often been conceptualized as a single process: short-term adaptive genetic change driven by natural selection. Here we argue that other diverse evolutionary processes should also be considered, to explore the full spectrum of feedbacks between ecological and evolutionary processes. Relevant but underappreciated processes include (1) drift and mutation, (2) disruptive selection causing lineage diversification or speciation reversal, (3) evolution driven by relative fitness differences that may decrease population growth, and (4) topics including multilevel selection, sexual selection and conflict, hard and soft selection, and genetic/genomic architectures/signatures. Because natural selection is not the sole mechanism of rapid evolution, it will be important to integrate a variety of concepts in evolutionary biology and ecology to better understand and predict eco-evolutionary dynamics in nature.

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Beyond adaptation: Incorporating other evolutionary processes and concepts into eco-evolutionary dynamics

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Abstract

Studies of eco-evolutionary dynamics have integrated evolution with ecological processes at multiple scales (populations, communities, and ecosystems) and with multiple interspecific interactions (antagonistic, mutualistic, and competitive). However, evolution has often been conceptualized as a single process: short-term adaptive genetic change driven by natural selection. Here we argue that other diverse evolutionary processes should also be considered, to explore the full spectrum of feedbacks between ecological and evolutionary processes. Relevant but underappreciated processes include (1) drift and mutation, (2) disruptive selection causing lineage diversification or speciation reversal, (3) evolution driven by relative fitness differences that may decrease population growth, and (4) topics including multilevel selection, sexual selection and conflict, hard and soft selection, and genetic/genomic architectures/signatures. Because natural selection is not the sole mechanism of rapid evolution, it will be important to integrate a variety of concepts in evolutionary biology and ecology to better understand and predict eco-evolutionary dynamics in nature.

Main text

Ecologists have revealed that microevolution (i.e., allele frequency changes over a few generations) can be rapid enough to affect contemporary ecological processes (e.g., Pimentel 1961; Thompson 1998; Yoshida *et al.* 2003; Hairston *et al.* 2005; Fussmann *et al.* 2007; Schoener 2011; Hendry 2016; Bassar *et al.* 2021; Rudman *et al.* 2022). Although ecology and evolutionary biology have been neighboring research areas from the age of Darwin, the prevailing assumption had long been that ecological processes occur much faster than evolutionary processes (Darwin 1859; Slobodkin 1961). Thus, the idea of concurrent ecological and evolutionary dynamics and the feedbacks between them is exciting not only for synthesizing the two basic scientific disciplines, but also for its applied aspects, such as the need to predict future eco-evolutionary responses to ongoing environmental change (Gomulkiewicz & Holt 1995; Kinnison & Hairston 2007; Hoffmann & Sgrò 2011).

Studies of eco-evolutionary dynamics have integrated evolution with ecological processes operating at the population (Yoshida *et al.* 2003; Coulson *et al.* 2017), community (Johnson & Stinchcombe 2007), and ecosystem scales (Matthews *et al.* 2011). Researchers have also considered the interplay of eco-evolutionary dynamics in the context of multiple types of interspecific interactions including antagonistic (Post & Palkovacs 2009), mutualistic (Jones *et al.* 2009; Northfield & Ives 2013), and competitive (Hart *et al.* 2019; Pastore *et al.* 2021) interactions.

However, evolution in this framework has typically been reduced conceptually to a single process: short-term adaptive evolution driven by natural selection (Bassar *et al.* 2021), with an emphasis (at least initially) on situations where rapid adaptation to a detrimental change in the biotic or abiotic environment prevents population decline and possible extinction (Bell 2017). This may be a historical legacy from early studies of rapid evolution, that often involved adaptive evolution driven by trophic interactions. For example, a majority of the studies of rapid evolution tabulated by Thompson (1998) involved gain or loss of defense traits — gains in response to selection pressure from predators or pathogens or losses when a threat is diminished (presumably to avoid an unnecessary cost of defense). Most of the other examples involve either the other end of a trophic interaction, rapid consumer or pathogen evolution to improve exploitation of available prey or hosts, or evolution of resistance to chemicals such as environmental toxins, herbicides and pesticides, and antibiotics.

Here we propose that it will be useful to conceptualize eco-evolutionary dynamics more broadly, integrating other kinds of evolutionary processes (including non-adaptive evolution) to understand better the full spectrum of feedbacks between ecology and evolution.

Drift and Mutation: The four fundamental processes in evolutionary dynamics are selection, migration, drift, and mutation. Selection (as noted above) and to a lesser extent migration (e.g., Farkas *et al.* 2013) have received due attention, but drift and mutation have been relatively neglected in studies of eco-evolutionary dynamics. Theory (Snyder & Ellner 2018; Snyder *et al.* 2021) and experimental data (Liu *et al.* 2019) suggest that the magnitude of random genetic drift is often far above that predicted by standard population genetic (Wright-Fisher or Moran) models. Even under tightly controlled laboratory conditions, Liu *et al.* (2019) found that the drift-effective population size for caged *Drosophila* populations was roughly 10 times smaller than the actual population size, because a small fraction of individuals (for unknown reasons, unrelated to genotype) monopolized reproduction. Such extreme reproductive skew is also seen in natural populations, for example Chen *et al.* (2019) observed vast variation in lifetime reproduction within one Florida scrub jay population, the top 10 individuals producing more total nestlings than the bottom 200, which could not be ascribed to any known genetic differences between individuals. Whereas, the primary message of rapid evolution is that the deterministic component of evolutionary change is much larger than we formerly imagined, it may be equally true that the random component of evolutionary change is also much larger than we currently imagine, and too large to ignore when projecting evolutionary responses to changed ecological conditions.

Drift can also mediate eco-evolutionary feedback between population dynamics and deleterious mutations. For example, extinction vortex and mutational meltdown (Gilpin & Soulé 1986; Lynch & Lande 1993) is a positive feedback between decreased population density and greater fixation of deleterious mutations due to genetic drift. Once population density has decreased sufficiently, eco-evolutionary feedback drives extinction. Although the concept of an extinction vortex itself is not new, it will be intriguing to measure the speed of evolution driven by genetic drift and consider a conceptual eco-evolutionary framework incorporating selection and drift (Nabutanyi & Wittmann 2021). This will be especially important when studying eco-evolutionary dynamics in large organisms with small population sizes (e.g., Campbell-Staton *et al.* 2021) and in metapopulation and metacommunity dynamics with many small populations in separated habitats (De Meester *et al.* 2019) as the classical shifting balance theory (Wright 1982) implies.

Mutation may also have feedbacks with population density because the absolute rate at which mutations, favorable or unfavorable, arise in a population depends on population size. This relationship is embodied in the “fundamental (canonical) equation of Adaptive Dynamics” (Dieckmann & Law 1996), because Adaptive Dynamics theory posits that evolution is mutation-limited and operates on a slower time-scale than ecological dynamics. Absence of such a time-scale separation is a defining feature of eco-evolutionary dynamics (Bassar *et al.* 2021), but it still may be interesting to consider feedbacks involving mutation rate, especially in microorganisms such as bacteria. For example, if adaptive evolution is important for population persistence in the face of changing conditions, could reduced population size lead to selection for higher mutation rates?

Theoretical studies of eco-evolutionary dynamics have often employed deterministic models such as ordinary differential equations (ODEs: Govaert *et al.* 2019). As drift and mutation are stochastic processes, we need to employ other modeling frameworks (e.g., stochastic differential/difference equations or individual-based models) to integrate drift and mutation into eco-evolutionary dynamics (e.g., Constable *et al.* 2016).

Disruptive selection causing diversification and fusion of lineages: Compared with directional and balancing selection, disruptive selection is underrepresented in studies of eco-evolutionary dynamics. Although disruptive selection and the resultant lineage diversification (evolutionary branching) have been examined in studies of Adaptive Dynamics theory (Geritz *et al.* 1998), the basic assumption there is that evolution is much slower than ecological processes. What will happen when that evolution is as fast as ecological processes?

Rapid evolution in response to disruptive selection may promote rapid speciation (Hendry *et al.* 2007). Interestingly, some theoretical studies have shown that rapid antagonistic coevolution can drive lineage diversification whereas slow coevolution results in continuous trait changes without divergence (Calcagno *et al.* 2010). The cessation of disruptive selection, on the other hand, may cause speciation reversal, a fusion of two distinct lineages, which have been described in several systems (Vonlanthen *et al.* 2012). It will be interesting to consider ecological consequences of disruptive selection and the resultant eco-evolutionary feedbacks, because rapid (micro)evolution may actually cause long-standing evolutionary change (i.e., macroevolution).

Selection that reduces population growth rate: Despite the recognition that selection is driven by relative fitness within populations rather than absolute fitness (Metz *et al.* 1992), studies of eco-evolutionary dynamics have tended to focus on selection that increases absolute fitness, partly because of the prevalence of studies on evolutionary rescue, where adaptive evolution prevents population extinction (Gomulkiewicz & Holt 1995; Kinnison & Hairston 2007; Bell 2017). Theoretical studies on eco-evolutionary dynamics (e.g., Vasseur *et al.* 2011; Cortez 2018; Yamamichi & Letten 2021) often employ the model of Lande (1976) for quantitative trait evolution, in which a mean trait value ($\bar{z}$) evolves to increase the per-capita population growth rate:

$$\frac{d\bar{z}}{dt} = v\frac{\partial}{\partial\bar{z}}\left(\frac{1}{N}\frac{dN}{dt}\right), \tag{1}$$

where v is additive genetic variance and N is population density.

However, because selection acts on relative fitness, it can actually decrease population growth rate (Abrams *et al.* 1993). This can be incorporated in Equation 1 by considering frequency-dependent selection (Abrams 2001). Selection on relative fitness may cause extinction resulting in "evolutionary suicide" rather than "evolutionary rescue" (Henriques & Osmond 2020). Again, studies in Adaptive Dynamics theory have investigated evolutionary suicide (Parvinen 2005), but the basic assumption there has been that evolution is slow. In the context of community ecology, adaptation to intraspecific interactions such as sexual and social interactions may result in an evolutionary tragedy of the commons (Rankin *et al.* 2007a), and promote negative frequency-dependence by reducing the population growth rate of species with high abundance ("intraspecific adaptation load" *sensu* (Yamamichi *et al.* 2020)). In particular, there is currently a heated debate about whether sexual selection increases population growth rate (e.g., by selecting better adapted males) or not (e.g., by wasting energy or attracting predators via male-male competition and female mate choice)

(Kokko & Brooks 2003; Martins *et al.* 2018; Cally *et al.* 2019). Either may be the case depending upon the context of the interaction, and both can result in eco-evolutionary dynamics as population interactions result in evolution (driven by sexual selection) that feeds back to affect population growth rate. It will be important to consider evolution that maximizes geometric mean fitness (e.g., bet-hedging: Cohen 1966) as well, because it may also reduce the short-term population growth rate (unlike Equation 1).

Other evolutionary processes: There are many other aspects of evolution that have been considered relatively infrequently in the context of eco-evolutionary dynamics. For example, one of the central topics in evolutionary biology is evolution of cooperation due to kin or multilevel selection (Nowak 2006). By considering feedbacks between ecological and evolutionary processes, it will be possible to provide a new perspective on the evolution of cooperation: for example, laboratory experiments with yeast have shown transient eco-evolutionary cycles to a coexistence equilibrium of cooperators and cheaters (Sanchez & Gore 2013). Weitz *et al.* (2016) proposed a theoretical framework that combines evolution of cooperation and ecological dynamics, and found similar cycles. Bergstrom and Lachmann (2003) showed that a rapidly evolving species benefits less in coevolution with mutualist partners. On the other hand, Rankin *et al.* (2007b) using eco-evolutionary model simulations showed that interspecific competition may promote evolution of intraspecific cooperation, highlighting the potential importance of multi-level selection.

As with evolution of cooperation, other adaptive evolution, driven by intraspecific interactions such as sexual selection and conflict, has been underrepresented until recently (Giery & Layman 2019; Svensson 2019; Yamamichi *et al.* 2020). Similarly, recent papers have highlighted the value in considering the difference between hard and soft selection (Bell *et al.* 2021) and population genetic aspects in eco-evolutionary dynamics (Osmond & Coop

2020; Yamamichi 2022). Soft selection is affected by environmental conditions as well as population composition and may result in counterintuitive effects on population growth (Bell *et al.* 2021). Seeking population genetic signatures of eco-evolutionary dynamics may be particularly pertinent in this era of “big genomic data.” We may be able to infer past eco-evolutionary dynamics by examining genomic patterns of populations (e.g., selective sweeps due to adaptive evolution in evolutionary rescue: (Osmond & Coop 2020)). It will also be possible to examine how genetic architecture of adaptive trait evolution affects eco-evolutionary dynamics in the future (Rudman *et al.* 2018; Yamamichi 2022).

Because natural selection is not the sole mechanism of rapid evolution, it will be important to integrate concepts in population genetics, evolutionary biology, and ecology carefully to better understand and predict ecological dynamics in nature. Despite the rise of studies of eco-evolutionary dynamics from at most one or two per year prior to 2007 to well over 100 per year since 2017 (Bassar *et al.* 2021), a recent co-citation network analysis by Réale *et al.* (2020) indicates that there has been no trend towards a stronger integration of ecology and evolutionary biology. This may partly be because the number of researchers is increasing and each subdiscipline has expanded. However, conceptual developments can be accelerated by considering analogies between ecology and evolutionary biology (Hairston *et al.* 1996; Vellend 2016). Studying eco-evolutionary dynamics as an interdisciplinary topic presents a great opportunity to promote a synthesis of population/community ecology and population/quantitative genetics as well as evolutionary (behavioral) ecology. In addition, it will be essential for deepening our understanding of microbiology and effects of ongoing environmental changes (Loreau *et al.* 2022). Through this process, considering eco-evolutionary dynamics will become essential not only for ecologists but also for geneticists and evolutionary biologists.

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Conflict of interest

The authors declare no conflict of interest.

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