

# Beyond simple 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 conceptualised as a simple process: short-term directional adaptation that increases population growth. Here we argue that diverse other evolutionary processes, well studied in population genetics and evolutionary ecology, should also be considered to explore the full spectrum of feedback between ecological and evolutionary processes. Relevant but underappreciated processes include (1) drift and mutation, (2) disruptive selection causing lineage diversification or speciation reversal and (3) evolution driven by relative fitness differences that may decrease population growth. Because eco-evolutionary dynamics have often been studied by population and community ecologists, it will be important to incorporate a variety of concepts in population genetics and evolutionary ecology to better understand and predict eco-evolutionary dynamics in nature.

## KEY WORDS

evolutionary branching, evolutionary ecology, evolutionary rescue and suicide, extinction vortex, genetic drift, mutation, population genetics, rapid evolution, relative and absolute fitness, speciation reversal

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. Bassar et al., 2021; Fussmann et al., 2007; Hairston et al., 2005; Hendry, 2016; Pimentel, 1961; Rudman et al., 2022; Schoener, 2011; Thompson, 1998; Yoshida et al., 2003). Although ecology and evolutionary biology have been neighbouring research areas ever since 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; Hoffmann & Sgrò, 2011; Kinnison & Hairston, 2007).

Studies of eco-evolutionary dynamics have integrated evolution with ecological processes operating at the population (Coulson et al., 2017; Yoshida et al., 2003), 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 simple process: short-term directional adaptation 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, which often involved adaptation 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, and 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 the exploitation of available prey or hosts, or evolution of resistance to chemicals such as environmental toxins, herbicides, pesticides and antibiotics.

Here we propose that it will be useful to conceptualise 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 have been well studied in population and quantitative genetics, whereas complex evolutionary dynamics driven by disruptive selection (that can result in evolutionary branching) and by relative fitness (that can result in decreased population growth) have been intensively investigated in evolutionary ecology (using the Adaptive Dynamics framework assuming slow evolution). We point out that combining rapid evolution with these concepts will deepen our understanding of complex eco-evolutionary dynamics.

## 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 in studies of eco-evolutionary dynamics, but drift and mutation have been relatively neglected. For example, it is well known in population genetics that the effective population size can be much smaller than the census size (Frankham, 1995) and this results in strong genetic drift. Indeed, recent theories (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 models (Wright-Fisher or Moran). 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, greatly reducing drift-effective population size and therefore increasing random drift at all loci, is also seen in natural populations, for example Chen et al. (2019) observed vast variation in lifetime reproduction within a 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 as shown by classical studies on the extinction vortex and mutational meltdown (Gilpin & Soulé, 1986; Lynch & Lande, 1993). These are positive feedbacks between decreased population density and greater fixation of deleterious mutations due to genetic drift (and inbreeding depression). Once population density has decreased sufficiently, eco-evolutionary feedback can drive 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) to understand better evolutionary rescue. 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 separate habitats (De Meester et al., 2019) as the classical shifting balance theory (Wright, 1982) implies.

Mutation rates at loci under selection may also have feedbacks with population density because the absolute rate at which mutations, favourable or unfavourable, arise in a population depends on population size. This relationship is embodied in the ‘fundamental (canonical) equation of Adaptive Dynamics’ (Dieckmann & Law, 1996; Lion, 2018) because Adaptive Dynamics theory posits that evolution is mutation-limited and operates on a slower time scale than ecological dynamics (but see Lion et al., 2023). The 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 (Loreau et al., 2023). 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). By comparing the differences between ODEs and other modelling frameworks with stochastic processes, for example stochastic differential/difference equations or individual-based models (e.g. Constable et al., 2016) as well as empirical results, it may be possible to detect the roles of drift and mutation in eco-evolutionary dynamics.

## 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 extensively using Adaptive Dynamics theory (Geritz et al., 1998), a basic assumption in Adaptive Dynamics theory 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 the 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). A lot more could be investigated in future studies about the integration of micro- and macroevolution including the speed of evolution (Harmon et al., 2021), and this will be an interesting interface of ecology and paleobiology.

## SELECTION THAT REDUCES POPULATION GROWTH RATES

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 the selection that increases absolute fitness, partly because of the prevalence of studies on evolutionary rescue, where adaptive evolution prevents population extinction (Bell, 2017; Gomulkiewicz & Holt, 1995; Kinnison & Hairston, 2007). Indeed, theoretical studies on eco-evolutionary dynamics (e.g. Schreiber et al., 2011; Vasseur et al., 2011; Yamamichi & Ellner, 2016) sometimes 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.

However, because selection acts on relative fitness, it can actually decrease population growth rates, and this can be incorporated by considering frequency-dependent selection (Abrams et al., 1993; Iwasa et al., 1991). Selection on relative fitness may cause extinction resulting in 'evolutionary suicide' rather than 'evolutionary rescue' (Henriques & Osmond, 2020). Again, studies in evolutionary ecology (particularly Adaptive Dynamics theory) have investigated evolution that reduces population growth (e.g. an evolutionary tragedy of the commons: Rankin et al., 2007) and evolutionary suicide (Parvinen, 2005). However, again a basic assumption has been that evolution is slow, and studies in eco-evolutionary dynamics will be enriched by explicitly considering rapid evolution driven by relative fitness. This is important not only for population dynamic studies related to evolutionary rescue but also for studies in community ecology: a recent study suggests that adaptation to intraspecific interactions such as sexual and social interactions may promote stable species coexistence (i.e. negative frequency-dependence in community dynamics) by reducing the population growth rate of species with high abundance ('intraspecific adaptation load' *sensu* Yamamichi et al., 2020).

In addition to relative vs. absolute fitness, there are different fitness measures appropriate for different situations, and it will be important to consider adaptive evolution that maximizes different fitness measures in the context of eco-evolutionary dynamics. For example, the evolution of bet-hedging occurs via maximising the product of time-varying fitness (geometric mean fitness) (e.g. Cohen, 1966), and this may also reduce the short-term population growth rate.

## CONCLUSION

There are many aspects of evolution, other than short-term directional adaptation, that have been considered relatively infrequently in the context of eco-evolutionary dynamics. For example, 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 of considering the difference between hard and soft selection (Bell et al., 2021; Reznick, 2016; Wallace, 1975) 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 the genetic architecture of adaptive trait evolution affects eco-evolutionary dynamics in the future (Rees & Ellner, 2019; Rudman et al., 2018; Yamamichi, 2022) by considering, for example, gene networks underlying phenotypic traits (Melián et al., 2018).

Moreover, ecology in its entire complexity is not well integrated into the eco-evolutionary dynamics literature, as there seems to be bias towards considering population and community dynamics (with less attention to whole-ecosystem dynamics), and more attention to predation and competition as mechanisms of selection (with less attention to mutualism). In addition to expanding the ecological aspects of eco-evolutionary dynamics studies, it will be important to integrate concepts in population genetics, evolutionary biology and ecology carefully to better understand and predict ecological dynamics in nature. Several studies have suggested that conceptual developments can be accelerated by considering analogies between ecology and evolutionary biology (Govaert et al., 2021; 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/behavioural ecology. Through this process, considering eco-evolutionary dynamics will become essential not only for ecologists but also for geneticists and evolutionary biologists.

## AUTHOR CONTRIBUTIONS

Masato Yamamichi conceived the study and wrote the first draft of the manuscript. All authors contributed substantially to writing and revising the manuscript.

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## CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

## DATA AVAILABILITY STATEMENT

This study did not generate new data.

## PEER REVIEW

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