Functional Ecology | BRITISH ECOLOGICAL SOCIETY

## PERSPECTIVE

# Integrating fundamental processes to understand eco-evolutionary community dynamics and patterns

Lynn Govaert[1,2,3,4] (iD) | Florian Altermatt[1,2,3] (iD) | Luc De Meester[4,5,6] (iD) |
Mathew A. Leibold[7] | Mark A. McPeek[8] (iD) | Jelena H. Pantel[9] | Mark C. Urban[10]

[1]Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland; [2]Department of Aquatic Ecology, Eawag: Swiss Federal Institute of Aquatic Science and Technology, Dübendorf, Switzerland; [3]URPP Global Change and Biodiversity, University of Zurich, Zurich, Switzerland; [4]Leibniz Institut für Gewässerökologie und Binnenfischerei (IGB), Berlin, Germany; [5]Laboratory of Aquatic Ecology, Evolution and Conservation, KU Leuven, Leuven, Belgium; [6]Institute of Biology, Freie Universität Berlin, Berlin, Germany; [7]Department of Biology, University of Florida, Gainesville, FL, USA; [8]Department of Biological Sciences, Dartmouth College, Hanover, NH, USA; [9]Department of Computer Science, Mathematics, and Environmental Science, The American University of Paris, Paris, France and [10]Center of Biological Risk and Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, USA

**Correspondence**
Lynn Govaert
Email: lynn.govaert@igb-berlin.de

Handling Editor: Kailen Mooney

## Abstract

1. Recent studies demonstrate that ecological and evolutionary processes can occur over similar temporal and spatial scales and might thus frequently interact. Although concepts such as the evolving metacommunity, diffuse (co)evolution and community genetics integrate multi-species dynamics, most experimental studies usually consider how evolution affects only one focal species. Hence, our understanding of evolution in multi-species communities is still underdeveloped.

2. We highlight key community and evolutionary mechanisms and their interactions to facilitate a broader understanding of evolution in multi-species communities. We propose a framework that explicitly considers interactions between each of the four analogous processes of evolutionary biology (selection, gene flow, genetic drift and mutation) and community ecology (species sorting, dispersal, ecological drift and speciation).

3. Focusing on interactions between processes of evolutionary biology and community ecology enables explorations of the full range of eco-evolutionary dynamics in multi-species communities and guides the design of novel experiments. Furthermore, the proposed framework develops a shared language between evolutionary biologists and community ecologists and indicates new research avenues.

4. Overall, we propose that explicitly incorporating interactions between these evolutionary and community processes to study eco-evolutionary dynamics in multi-species communities will better inform broader questions about the maintenance of diversity and the resilience of diverse communities to disturbances, both natural and manmade.

## 1 | INTRODUCTION

Community ecologists seek a mechanistic understanding of multi-species dynamics to explain and predict patterns of diversity. Despite much progress, ecologists are often surprised by observed community dynamics (Doak et al., 2008), which often cannot be explained by ecological processes alone (Pelletier et al., 2007; Vellend & Geber, 2005; Whitham et al., 2006; Yoshida et al., 2003). Increasingly, evidence suggests that evolution can occur on similar temporal and spatial scales as ecological processes, and thus an evolutionary view might often be needed to understand anomalous ecological dynamics and patterns (Hairston Jr. et al., 2005; Hendry, 2017; Richardson et al., 2014; Schoener, 2011; Urban et al., 2020).

Whereas most eco-evolutionary studies focus on population-level attributes, evolution might often affect ecological levels beyond population ecology, such as communities, shifting the unit of study from populations to communities. Concepts such as community genetics (Antonovics, 1992; Whitham et al., 2006), diffuse (co) evolution (Strauss et al., 2005) and the evolving metacommunity (Urban et al., 2008) have specifically incorporated community aspects either as response variables, as drivers of evolution, or both. Nevertheless, our understanding of species evolutionary trajectories within multi-species communities and of their evolutionary impacts on community dynamics remains in the early stages of development.

Biologists have long recognized the analogous operation of processes that diversify or homogenize both species and genetic diversity in community ecology and evolutionary biology, respectively (Amarasekare, 2000; Holt, 2005; Norberg, 2004; Urban et al., 2008; Urban & Skelly, 2006). Vellend (2010, 2016) highlighted four analogous processes that operate among species at the community level, selection, dispersal, ecological drift and speciation, which are analogous to four processes that operate within species on a population genetics level, natural selection, gene flow, genetic drift and mutation. In natural systems, these processes co-occur and likely interact, ultimately shaping eco-evolutionary dynamics within multi-species communities.

Here, we synthesize how community and evolutionary processes affect genetic and community diversity to facilitate a broader understanding of evolution in multi-species communities by providing key examples and insights from emerging empirical and conceptual advances in the literature. We built from the synthesis by Vellend (2010, 2016) on fundamental processes in community ecology, to address how existing work on eco-evolutionary dynamics in multi-species communities can be evaluated along these analogous evolutionary and community processes. We aim to connect analogous processes in population genetics and community ecology emerging from the traditional evolutionary and ecological view of co-existing phenotypes and populations and from neutral genetic and ecological theories. We highlight (a) how each of the four processes of evolutionary biology can affect each of the four community processes, (b) then identify the reverse, how the equivalent four processes of community ecology can affect each of the four evolutionary processes and consequently evolutionary dynamics of the component species, (c) determine to what extent eco-evolutionary dynamics and feedbacks are governed by interactions between community and evolutionary processes and (d) identify knowledge gaps and future directions with a focus on existing frameworks and suggesting future avenues and experimental designs that include interactions between community and evolutionary processes. This perspective is intended for both community ecologists and evolutionary biologists who want to understand current gaps at the intersection of these two fields and how studying these gaps might shed new light on ecological topics ranging from species assembly dynamics to trophic structure, and on evolutionary topics ranging from neutral genetic structure to adaptive differentiation.

## 2 | FUNDAMENTAL PROCESSES OF COMMUNITY ECOLOGY AND EVOLUTIONARY BIOLOGY

Box 1 introduces the four parallel fundamental processes that steer community and population dynamics and structure (Figure 1; Vellend, 2010, 2016) and determine species or genetic diversity and composition, depending on the unit of study. For evolution, the unit of study often is genetic frequencies, while for community ecology it is often species abundances. These units differ in their focus on proportional versus absolute measures, but both relate to measuring diversity. Traits are important units in both disciplines and can thus provide a common currency between evolutionary biology and community ecology. Importantly, evolutionary and community processes are not only analogues, but can also operate at similar temporal and spatial scales, simultaneously structuring population and community dynamics. In this sense, understanding the interactions of these processes is critical for making more general progress in predicting eco-evolutionary dynamics.

Community and evolutionary processes can directly influence one another, with consequences for community and genetic diversity. For example, dispersal of a predator species can directly alter local selection pressure experienced by its prey species (Vermeij, 1982). Community and evolutionary processes can also indirectly influence one another by modifying population or community size (Carlson
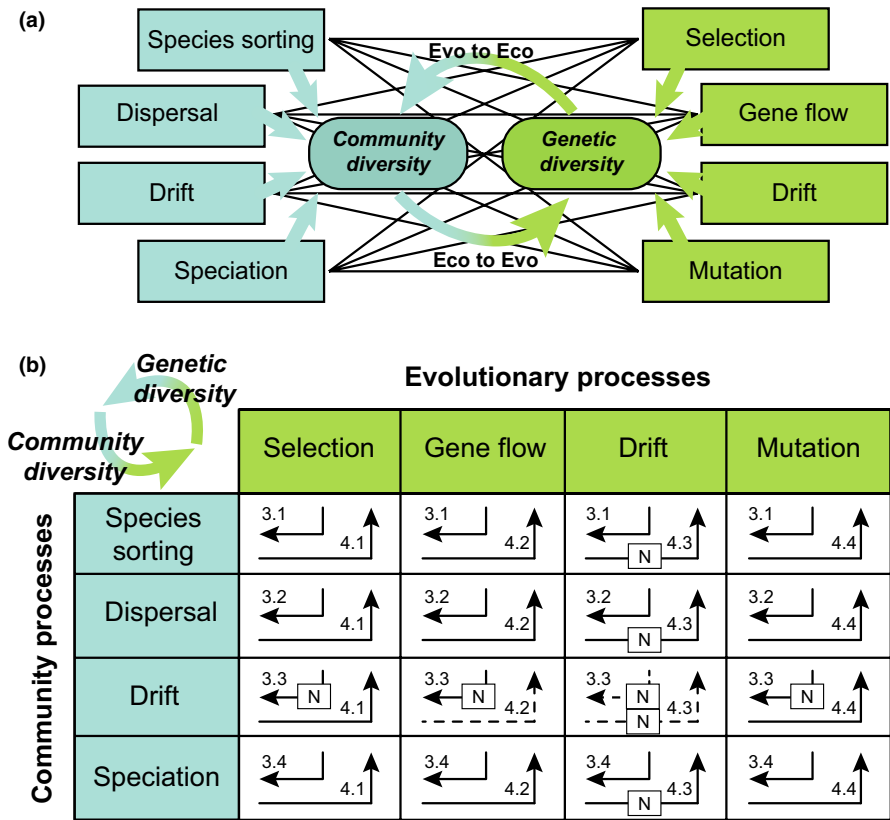
**FIGURE 1** (a) Conceptual figure showcasing the four processes of evolutionary biology and community ecology (definitions see Box 1). Each of these processes influences either genetic or community diversity, respectively. An eco-evolutionary view on community ecology envisions pairwise interactions between evolutionary and community processes resulting in a dynamical interplay between evolution and community dynamics. (b) Overview on the structure of subsections in which we provide examples on pairwise interactions between evolutionary and community processes. Arrows labels represent headings of the respective subsections. Dashed arrows represent those pathways that remain underexplored relative to the others, but we note that most of these boxes have not been explored extensively. Boxes with *N* reflect settings in which processes interact by altering population or community size

et al., 2014; Christiansen, 1975), which could alter the strength of genetic or ecological drift in the population or community. Changes in a single process can also alter both ecological and evolutionary dynamics jointly. For instance, dispersal into a patch inflates the abundance of a species in a community (McPeek & Holt, 1992), but also potentially induces maladaptive gene flow that decreases its fitness (Wright, 1931). When the ecological and evolutionary effects of a process act in opposition, they might dampen observed variation (Yoshida et al., 2007). Alternatively, when they operate in concert, they can amplify their impacts (Urban, 2013). The possible interactions between community and evolutionary processes and the dynamics they create thus have the potential to produce a range of diverse feedbacks.

# 3 | THE INFLUENCE OF EVOLUTIONARY PROCESSES ON COMMUNITY PROCESSES

## 3.1 | Effects of evolutionary processes on species sorting

Species sorting (trait-based selection among species) occurs when abiotic or biotic environments filter species based on species' traits, resulting in a match between local species' traits and local environments (Chase & Leibold, 2003; Leibold et al., 2004). In this way, species sorting is analogous to natural selection on individual traits in a population. Any of the four evolutionary processes can alter trait distributions in ways that affect the local fitness of species in different environments or communities and therefore alter species sorting. Adding new genotypes via mutations or gene flow can alter fitness differences among species and thus influence species sorting. Selection (directional, stabilizing or disruptive) can shift trait distributions among competing species thereby altering trait overlap among these species (e.g. character displacement; Slatkin, 1980). This change in trait overlap can increase or decrease competitive interactions (Ehlers et al., 2016; Hutchinson, 1957), thus changing species composition within the community. Genetic drift can also alter species interactions and species sorting. For example, Müller et al. (2014) showed that genetic drift at an expansion front can create regions where one of two mutualistic partners dominates. The effects of evolution on species sorting might also depend on the role species play in communities. In particular, the evolution of foundation or keystone species can have cascading effects on dependent species and influence species interactions at both higher and lower trophic levels (Miner et al., 2012; Whitham et al., 2006). For example, the evolution of zooplankton species in response to fish predation or cyanobacterial blooms can alter the selective environment of the phytoplankton communities they feed upon (Ekvall et al., 2014). Also, the evolution of dominant trees alters the abundance, diversity and composition of herbivores associated with them and thus creates new filters that sort these associated species (Keith et al., 2017; Whitham et al., 2003). Community genetics focuses on elucidating these effects of evolution on communities (Antonovics, 1992; Whitham et al., 2003).

**BOX 1   Community and evolutionary processes**

Community and evolutionary dynamics can be described by four parallel processes acting at the community and population levels, semantically described as selection, dispersal, drift and diversification (Vellend, 2010, 2016). These four parallel processes steer community and population genetic dynamics and patterns. Consider a community or population consisting of three species or genotypes (depicted by circles in Figure B1). Mechanisms of **novelty** operate in situ, by adding either a species (i.e. **speciation**) or genotype (i.e. **mutation** defined as alteration in DNA sequence) to the community or population (represented by the dotted circle Figure B1). **Dispersal** reflects the movement of individuals and adds a species or genotype to the community or population from the outside (represented by the striped circle Figure B1). At the population level, this exchange of genetic material from one population to another that changes the genetic composition of the receiving population is called **gene flow**. **Drift** represents random changes in relative abundances of species or genotypes due to stochastic differences in survival, mortality, reproduction and dispersal (e.g. even when all species or genotypes have equal survival rates, the light green species might become extinct by chance: Figure B1). The random drift of species abundances is called **ecological drift**, whereas random drift of genotypic frequencies is called **genetic drift**. The effect of ecological or genetic drift depends on community (Gilbert & Levine, 2017) or population (Lynch et al., 1993) size. **Selection** refers to the process whereby fitness covaries with traits and abiotic and biotic environmental conditions (e.g. larger individuals such as the striped and dotted circles in Figure B1 have a fitness advantage compared to smaller individuals such as the solid colours in Figure B1). Within species, selection can produce evolution by natural selection, whereby the fittest genotypes increase in frequency, if the population harbours heritable variation for the trait under selection. Among species, selection increases the abundances of species with high-fitness traits in a given environment, matching species traits to environments, and generating **species sorting** among different environments. Thus, community and evolutionary processes can alter species and genetic diversity by either reducing or increasing species or genotypic richness and shifting the community or genetic composition. The loss or gain of species or genotypes with particular trait values can alter trait distributions among and within species. Stochasticity affects composition at both levels. Traits provide the common currency that links responses to environmental change and between evolutionary and ecological levels. We note that speciation and mutation differ from the other processes in key ways. First, they are the only processes creating new species or new genetic variants in situ to increase regional species or genetic diversity. The other processes reduce or reshuffle extant species and genetic diversity. Second, speciation usually occurs much slower than mutation (although some cases of rapid ecological speciation also exist, Hendry et al., 2007; Villa et al., 2019). Last, speciation is ultimately an evolutionary process that influences community diversity often over longer time-scales, thus interactions between speciation and evolutionary processes reflect evolutionary interactions albeit potentially at disparate time-scales. However, as speciation adds new species to the community, altering species diversity, it can be seen as a community analogue of mutation. In this study, we focus on these ecological impacts of speciation and include it in community ecology, despite acknowledging it to also be an evolutionary process. Thus, even interactions between speciation and evolutionary processes may have eco-evolutionary consequences.

## 3.2 | Effects of evolutionary processes on dispersal

Dispersal is the displacement of organisms away from their birth location. Dispersal is a behavioral trait that can also evolve (Bonelli et al., 2013; Saastamoinen et al., 2018) via selection (Fronhofer et al., 2015). Dispersal has been shown to evolve in response to inbreeding (Roze & Rousset, 2005), competition (Gandon & Michalakis, 1999), predation (Pillai et al., 2012), parasitism (Altermatt et al., 2007), landscape quality (Olivieri et al., 1995) and landscape structure (Fronhofer & Altermatt, 2017; Schtickzelle et al., 2006). Evolution of dispersal is often important during species range expansions (Travis et al., 2013), both through spatial sorting of alleles or genotypes (Ochocki & Miller, 2017; Williams et al., 2016) and genetic drift. At expansion fronts, strong genetic drift can occur and increase the spread of maladaptive mutations (Excoffier et al., 2009; Klopfstein et al., 2006), slowing down range expansions (Nadeau & Urban, 2019) by preventing adaptation (Polechová, 2018). Last, gene flow can alter dispersal by increasing maladaptation of locally or regionally selected dispersal traits (Lenormand, 2002; Moerman

et al., 2020). For example, at range boundaries, gene flow from central to range populations might reduce dispersal despite selection for greater dispersal (Kirkpatrick & Barton, 1997). Thus, evolution of divergent dispersal strategies can affect local species abundances and corresponding community attributes by altering the balance between local extinction and colonization rates of different species (Mullon & Lehmann, 2018).

## 3.3 | Effects of evolutionary processes on ecological drift

Ecological drift occurs when species' abundances vary randomly through time because species in the same guild are ecologically equivalent (Hubbell, 2001) or because niche-differentiated species with small population sizes become extirpated due to demographic stochasticity (Orrock & Watling, 2010). Although not all species in a community are likely to be ecologically equivalent, drift might occur within a group of related, neutral species within the larger community (Leibold & McPeek, 2006). Species
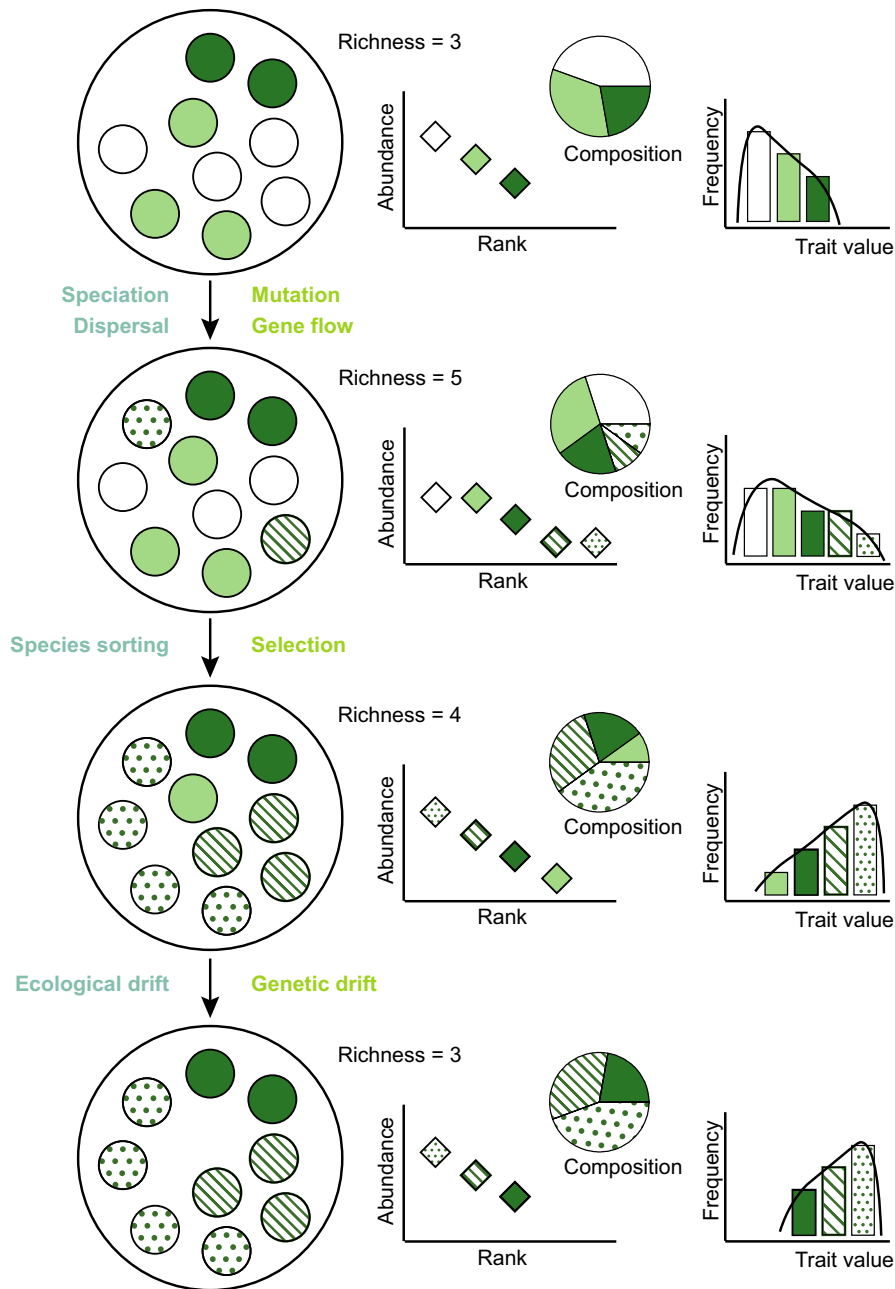
**FIGURE B1** Scheme of community (blue text) and evolutionary (green text) processes depicted from top to bottom as hypothetical sequential steps (given by the arrows) in a hypothetical community or population consisting of different species or genotypes depicted by circles (modified from Vellend, 2016). Each of these processes can alter species or genetic diversity within the community or population. Speciation and dispersal add new species to the community, whereas mutation and gene flow add new genotypes to the population (dotted and striped circle). Natural selection acts on traits, not on species or genes. However, selection can increase the frequency of species or genes that confer traits with higher fitness in a given environment. In this example, species sorting or natural selection favors larger species or genotypes (e.g. the striped and dotted species or genotypes are favored compared to the white and dark green species or genotypes), increasing the abundance of these species or genotypes. On the bottom, ecological or genetic drift could result in stochastic extinction of rare species or genotypes. To evaluate changes in the community and population one can measure analogous properties at the community and population level. For example, the rank-abundance curve can be calculated for either species or genotypes in the community or population, the community or genetic composition is given by relative species or genotype abundances, and when associated traits are measured, trait distribution curves can be constructed (right side of figure). Speciation, mutation, dispersal and drift directly alter species and gene abundances. If species or genotypes have specific trait values (depicted with different colours and filling), then adding or removing species or genotypes with particular trait values also alters the trait distribution of the community or population.

in those groups with lower total population sizes are then more likely to drift towards extirpation compared to more abundant species in the community (Hu et al., 2006; Leibold & McPeek, 2006). Although studies that evaluate interactions between evolutionary processes and ecological drift remain scarce, many studies demonstrate how evolutionary processes affect population sizes of species, consequently indirectly influencing ecological drift. Theoretical studies suggest that evolution by natural selection and random colonization–extinction dynamics can generate the evolution of similar niches among competing species, which then leads to the eventual random extinction of one of the species (Leibold et al., 2019; terHorst et al., 2010). Hard selection (definition given in Supplement A) can reduce species' population sizes and thus render those species more susceptible to drift (Christiansen, 1975). Evolutionary rescue occurs when a population avoids extirpation through adaptation in response to novel selection (Gomulkiewicz & Holt, 1995). In this way, adaptive evolution (either via beneficial mutations or incoming gene flow) of multiple species within the community can increase population sizes (Carlson et al., 2014; Kirkpatrick & Peischl, 2013; Uecker et al., 2014) and consequently the community size (i.e. community rescue; Low-Décarie et al., 2015), potentially reducing ecological drift in a community. However, genetic drift could play an important role in mediating ecological drift during the initial stages of evolutionary rescue when population abundances are low. Genetic drift can also purge beneficial alleles in small populations, which would then reduce population sizes further and enhance the chance for ecological drift within the community.

## 3.4 | Effects of evolutionary processes on speciation

Evolutionary processes initiate and influence speciation in rather complex ways (Butlin et al., 2012; Coyne & Orr, 2004; Lande, 1980), but here we highlight a subset of scenarios that are particularly relevant for community-level consequences. In 'mutation-order' speciation, different de novo mutations become fixed in different populations (Nosil & Flaxman, 2011). If adaptive, these populations accumulate genetic differences, potentially resulting in subsequent mutations being favoured in one, but not the other population (Butlin et al., 2012; Mani & Clarke, 1990). Divergent selection on ecological traits related to niche differences can also produce reproductive isolation and subsequent ecological speciation (Schluter, 2009; Svensson, 2012). One example involves the recurrent adaptive radiation of *Anolis* lizards across habitats in the Greater Antilles (Losos et al., 2006). Other forms of selection, such as sexual selection, can result in the evolution of assortative mating traits, which then generate reproductive isolation (Butlin et al., 2012). Sexual selection and drift during separation can also generate speciation events not associated with divergence between ecological environments (Czekanski-Moir & Rundell, 2019; Nosil, 2012). For example, in two congeneric damselfly species, male secondary sexual traits (wing melanization) differ between the two species, creating reproductive isolation (Svensson, 2012; Svensson & Friberg, 2007).

Genetic drift can strengthen niche differentiation and reproductive isolation by enhancing the divergence between populations upon which selection can act (Tazzyman & Iwasa, 2010; Uyeda et al., 2009). Last, limited gene flow between diversifying populations can promote speciation, while high gene flow can impede speciation (Nosil, 2008).

# 4 | THE INFLUENCE OF COMMUNITY PROCESSES ON EVOLUTIONARY PROCESSES

## 4.1 | Effects of community processes on selection

Natural selection reflects deterministic trait-based fitness differences between individuals. When these trait-based differences have a genetic basis, evolution by natural selection can occur. Species sorting, species dispersal, ecological drift and speciation can directly affect the type and intensity of species interactions, as well as the abiotic environment and associated selection pressures. While speciation codifies differences among lineages in their past evolutionary responses to natural selection (Futuyma & Moreno, 1988), speciation events can also modify further frequency-dependent selection. This has been frequently modelled by adaptive dynamics in which the occurrence of an evolutionary branching event (viz speciation) alters selection (Geritz & Éva, 2000). The arrival of a new species via dispersal can alter the selection pressures experienced by the local inhabitants. For example, studies on invasive plant species suggest that invaders can alter selection intensity on native plant species (Beans & Roach, 2015; Leger & Goergen, 2017). Although many studies demonstrate altered selection due to increased competition for common resources (e.g. nutrients, pollination), other studies indicate that the arrival of keystone species (Paine, 1969) or habitat-forming ecosystem engineers (Jones et al., 1994) can induce novel selection on populations by altering the abiotic environment (Wright et al., 2012). Species sorting changes species interactions and community composition in ways that can alter the direction and strength of selection experienced by each species within the community (Barraclough, 2015; Lawrence et al., 2012; McPeek, 2017; Stinchcombe & Rausher, 2002; Urban, 2011; Vellend & Geber, 2005). A review by Barraclough (2015) showed that strong species interactions can dampen or promote evolutionary change of member species within the community. A theoretical model by McPeek (2017) demonstrates that temporal changes in the abundances of interacting species not only alters the strength of selection, but can even alter the shape of the selection surface from stabilizing to disruptive selection. As an empirical example, Stinchcombe and Rausher (2002) found that the strength of selection on tolerance to deer damage in the Ivyleaf morning glory (*Ipomoea hederacea*) depended on the presence of insect herbivores on the plant. Last, ecological drift results in random changes in community composition and the potential loss of species. Such changes in community composition and species abundances may also alter the strength and form of selection.

## 4.2 | Effects of community processes on gene flow

Gene flow refers to the exchange of genetic material between conspecific populations, following the successful dispersal of individuals or gametes (Whitlock & Mccauley, 1999). Community processes can alter gene flow. Speciation and the subsequent reproductive isolation resulting from adaptive divergence between populations to distinct environments may prevent gene flow between these populations, allowing separate species to evolve to local conditions without the constraining influence of maladaptive gene flow (Hendry et al., 2007; Schluter, 2000). Gene flow is dependent upon dispersal and sometimes also depends on the dispersal of other species, such as the passive dispersal of zooplankton with migrating birds (Figuerola et al., 2005). However, gene flow could also be reduced when local community members select against maladapted migrants. For example, fine-scaled neutral genetic patterns in spotted salamanders indicated that genes flowed freely between communities with similar predator species regardless of distance, but that dissimilar predator species limited gene flow even at extremely fine scales (Richardson & Urban, 2013). The role of ecological drift on gene flow has not been explored to our knowledge. Yet, because absolute and relative dispersal can depend on population density (Matthysen, 2005), ecological drift and its effect on population densities might commonly affect dispersal rates and thus influence gene flow.

## 4.3 | Effects of community processes on genetic drift

Genetic drift reflects random changes in the genetic composition of a population caused by chance differences in survival, mortality, reproduction and dispersal among individuals (Wright, 1937). The effect of genetic drift is stronger in small and isolated populations, where rare alleles have a greater chance of loss (Kimura, 1983). Thus, straightforwardly, any community process that reduces or increases effective population sizes can alter genetic drift. Dispersal of a predator or mutualist into or away from the community could enhance or diminish effects of genetic drift on a local population depending on how the colonizing species alters local population sizes (Van Buskirk & Yurewicz, 1998). Ecological drift can stochastically increase or decrease species' population size, whether within a group of ecologically equivalent species or on single species within the community (Hubbell, 2001; McPeek & Siepielski, 2019), and thus alter genetic drift. Similarly, species sorting can increase the population sizes of species adapted to local environments or communities, while decreasing the population sizes of species that are not, altering genetic drift. Cyclic population dynamics, such as predator-prey cycles, can have recurrent changes on effective population size (Nakamura et al., 2018), resulting in cyclical changes of genetic drift. Last, effective population sizes can be small during the initial stages of some forms of speciation, and these smaller population sizes can increase genetic drift (Coyne & Orr, 2004; McPeek, 2017).

## 4.4 | Effects of community processes on mutation

Mutation rate is defined as the probability of base changes per nucleotide per meiotic event. The total input of mutations in a population depends on mutation rate and effective population size (Lanfear et al., 2014; Lynch, 2010). Any community process that changes a species' effective population size can also influence the total number of mutations (but not rate). Dispersal can increase or decrease effective population size, if emigration rates are higher or lower than immigration rates (Clobert et al., 2012; McPeek & Holt, 1992). In the early stages of speciation, effective population sizes may be low due to the limited number of individuals that are compatible (Coyne & Orr, 2004). Ecological drift can stochastically reduce or increase effective population size of species within communities, which could then subsequently alter the mutation load within these populations. When species sorting decreases or increases population sizes of particular species, it might also alter the absolute number of mutations in those populations. Selection by biotic factors, such as competition between species, can increase the population size of the stronger competitor, while decreasing the population size of the weaker competitor (Gause, 1934). Community processes not only can affect the number of mutations but can also affect their rate. For example, species interactions commonly induce stress, which is also known to alter mutation rates (Hoffmann & Hercus, 2000). Although this phenomenon has generally been explored in the context of abiotic stress (Foster, 2007), biotic interactions such as predation or bacteriophage interactions are known to induce intense, prolonged stress in organisms and could thus result in elevated mutation rates.

## 5 | MULTI-WAY AND RECIPROCAL INTERACTIONS BETWEEN EVOLUTIONARY AND COMMUNITY PROCESSES

The previous sections demonstrate evidence and potential for evolution to influence community processes and vice versa. However, we expect that in natural communities, these evolutionary and community processes can interact in reciprocal ways, resulting in complex eco-evolutionary feedbacks (Figure 1; Barraclough, 2015; De Meester et al., 2019; Low-Décarie et al., 2015; Rominger et al., 2016). Within a feedback, a community process (e.g. species sorting or dispersal of a new species) altering community diversity or composition can influence any of the evolutionary processes (e.g. selection in response to altered abundance of competitor species or genetic drift in response to arrival of predator species) with consequences for genetic diversity of the focal species which may in turn feedback on any of the community processes (e.g. evolution in response to altered selection may feedback on changing abundance of the competitor species captured by species sorting). Eco-evolutionary feedbacks can also arise when evolutionary processes (e.g. selection) alter traits (e.g. linked to competitive ability) that shape ecological interactions (e.g. competition) within the community which

**TABLE 1** Overview of less explored directions (first column), potential hypotheses (second column), and how they can be experimentally tested (third column). Light green rows reflect questions concerning how evolutionary processes and genetic diversity influence community diversity and processes. White row reflects how ecology (here niche overlap between species) can influence evolutionary processes. Dark green rows reflect broader questions about interactions between evolutionary and community processes. This table does not test all possible ideas or interactions, but highlights a few that are interesting

| Less explored directions | Hypotheses | How to test? |
|---|---|---|
| 1. Does genetic drift affect community structure and dynamics? | We expect a stronger impact of genetic drift on community processes, when species on average have small population sizes with additional potential interactions from ecological drift. Genetic drift in just one species might have a strong effect if that species is a foundation or keystone species | Experimentally vary population sizes and genetic diversities of species to estimate effects of genetic drift on community structure via its interaction with each of the four community processes. This would result in, for example, measuring species abundances (species sorting), or extinction probability of species (ecological drift) |
| 2. Does evolution by natural selection interact with ecological drift? | We expect hard selection to initially reduce community size and therefore increase the effect of ecological drift. This may lead to alternative community assembly trajectories linked to ecological drift, even though community sizes may increase again following adaptive evolution | Experimentally vary the level of hard selection in a multi-species community to determine effects on ecological drift by measuring species abundances and the role of stochasticity in population dynamics |
| 3. Does gene flow interact with ecological drift? | We expect moderate gene flow could increase population sizes by overcoming inbreeding and thus reducing ecological drift. High gene flow could depress absolute fitness by swamping local adaptation, causing population declines, reducing community size, and increasing ecological drift | Experimentally vary the level of gene flow in a multi-species community to determine effects on ecological drift by measuring species abundances and the role of stochasticity in population and community dynamics |
| 4. To what extent does genetic diversity influence the interactions between evolutionary and community processes? | In communities varying in genetic and species diversity, we might expect different interactions between evolutionary and community processes. For example, in communities where species harbour low levels of genetic diversity, species sorting may be more important than evolution in structuring community dynamics | Experimentally vary the genetic diversity of species within the community and evaluate how this alters interactions between evolutionary and community processes. For example, to evaluate how genetic diversity affects the interaction strength of species sorting and selection, one would measure both trait evolution and species-environment trait correlations over time |
| 5. To what extent does interspecific niche overlap affect the interaction between evolutionary and community processes? | In multi-species communities, we expect indirect and higher-order interactions among species to alter the strength and direction of feedbacks between evolutionary and community processes, resulting in different eco-evolutionary dynamics compared to those observed from two-species systems. For example, in communities with large niche overlap among species, we expect stronger interactions between selection and species sorting | Experimentally vary species diversity as well as niche overlap between species, and evaluate community dynamics and trait evolution along different selection gradients |
| 6. How does spatial and temporal scale affect interactions between evolutionary and community processes? | We expect the importance of evolutionary and community processes and their interactions to depend on temporal and spatial scale (i.e. via connectivity of the system). For example, we expect speciation to be more important on larger temporal and spatial scales, and thus also in its interaction with evolutionary processes. We also predict that the effect of genetic diversity on community processes depends on whether species arrive simultaneously or in sequential order. Overall, one expects evolutionary processes to contribute more to community dynamics in more isolated and species-poor systems and over longer time periods | Experimentally vary inclusion of differently adapted species or populations of the same species or manipulate connectivity or the time between colonizations and gene flow and measure either genetic or species diversity as well as community dynamics and trait evolution |

| Less explored directions | Hypotheses | How to test? |
|---|---|---|
| 7. To what extent are legacy effects of evolutionary and community important? | For example, we expect that strong selection could reduce genetic diversity and thereby reduce future evolutionary responses to environmental change, which would in turn increase the relative importance of species sorting over evolution in future responses | First, experimentally vary the strength of a community or evolutionary process of interest (e.g. selection strength). Second, experimentally vary the timing of a second community or evolutionary process and evaluate community dynamics and trait evolution as a consequence of the first manipulation as a function of the timing of the second community or evolutionary process |

then alter community processes (e.g. species sorting or dispersal via competition-colonization trade-off; Levins & Culver, 1971). Such a feedback has been shown by Lankau and Strauss (2007), in which the plant species *Brassica nigra* evolves its allelochemical compounds in response to interspecific competition, consequently altering the abundance of the competitor which then feeds back on *B. nigra*'s expression of these allelochemical compounds. Thus, observations of eco-evolutionary feedbacks governed by interactions between evolutionary and community processes will most likely be through alterations in genetic and community properties as well as traits of species within the community. Moreover, a community process could feed back to further alter the evolutionary process that initially induced the change in the community process (e.g. selection alters species sorting further altering selection) resulting in a closed eco-evolutionary feedback or on a different evolutionary process (e.g. selection alters species sorting that may result in altering the effect of genetic drift in particular species of the community), resulting in a broad eco-evolutionary feedback (as defined in Hendry, 2017).

# 6 | FUTURE DIRECTIONS

## 6.1 | Evolutionary and community processes in existing frameworks

Existing eco-evolutionary frameworks often focus on a subset of interactions between fundamental processes. For example, character displacement focuses on natural selection and species sorting (Slatkin, 1980). Community genetics evaluates how intraspecific genetic diversity affects community dynamics (Whitham et al., 2003). This genetic diversity is often the result of natural selection (Johnson & Agrawal, 2005), but it could also result from other evolutionary processes. The geographic mosaic theory of coevolution focuses on how ecological conditions create evolutionary versus coevolutionary patterns by integrating interspecific selection mosaics varying in space and time, and thus including colonization-extinction dynamics governed by dispersal and genetic drift, to produce variable evolutionary trajectories (Thompson, 1999, 2005). Evolving metacommunity aims to test the relative importance of local (species sorting and selection) versus regional (species dispersal and gene flow)

ecological and evolutionary processes on community and meta-community dynamics (Urban et al., 2008). Although the evolving metacommunity framework has generally focused on species sorting, selection and dispersal and gene flow, theoretical models of metacommunity dynamics have also begun to include processes such as mutation and genetic and ecological drift (see e.g. Loeuille & Leibold, 2014; Vanoverbeke et al., 2016). Additional insights have come from extending community frameworks by including evolution (e.g. eco-evolutionary island biogeography) or extending evolutionary frameworks by including community dynamics (e.g. community rescue). For example, eco-evolutionary island biogeography extends classic island biogeography by including local adaptation to understand the fauna and flora of islands (Massol et al., 2017; Rosindell & Phillimore, 2011; Warren et al., 2020). Community rescue extends evolutionary rescue of a single species to a community in which evolutionary rescue of multiple species within the community is crucial for persistence of the community (Low-Décarie et al., 2015). In general, identifying which interactions between community and evolutionary processes are considered in existing frameworks provides a first step towards assessing which interactions are understudied. For example, ecological neutral theory investigates the roles of dispersal, speciation and ecological drift (Hubbell, 2001, 2006), whereas evolutionary neutral theory focusses on evolutionary changes due to genetic drift and random neutral mutations (Kimura, 1983). However, no clear neutral theory for their joint effects has been developed that could answer how genetic and ecological drift interact and how important they are for eco-evolutionary community dynamics.

The incorporation of multiple, joint processes of evolutionary biology and community ecology into existing frameworks provides a way forward to reveal generalities about eco-evolutionary dynamics in multi-species communities and to formulate specific hypotheses (see Table 1 for an overview). Such an evaluation would highlight how similar or different eco-evolutionary community patterns can be depending on which processes are interacting. Detecting similarities could involve comparing whether community (e.g. composition or community trait distribution) or genetic (e.g. composition or population trait distribution) properties at specific time points differ between sets of eco-evolutionary dynamics. Alternatively, one could also assess the characteristics of the temporal patterns of eco-evolutionary dynamics, such as the rate of trait change for the entire
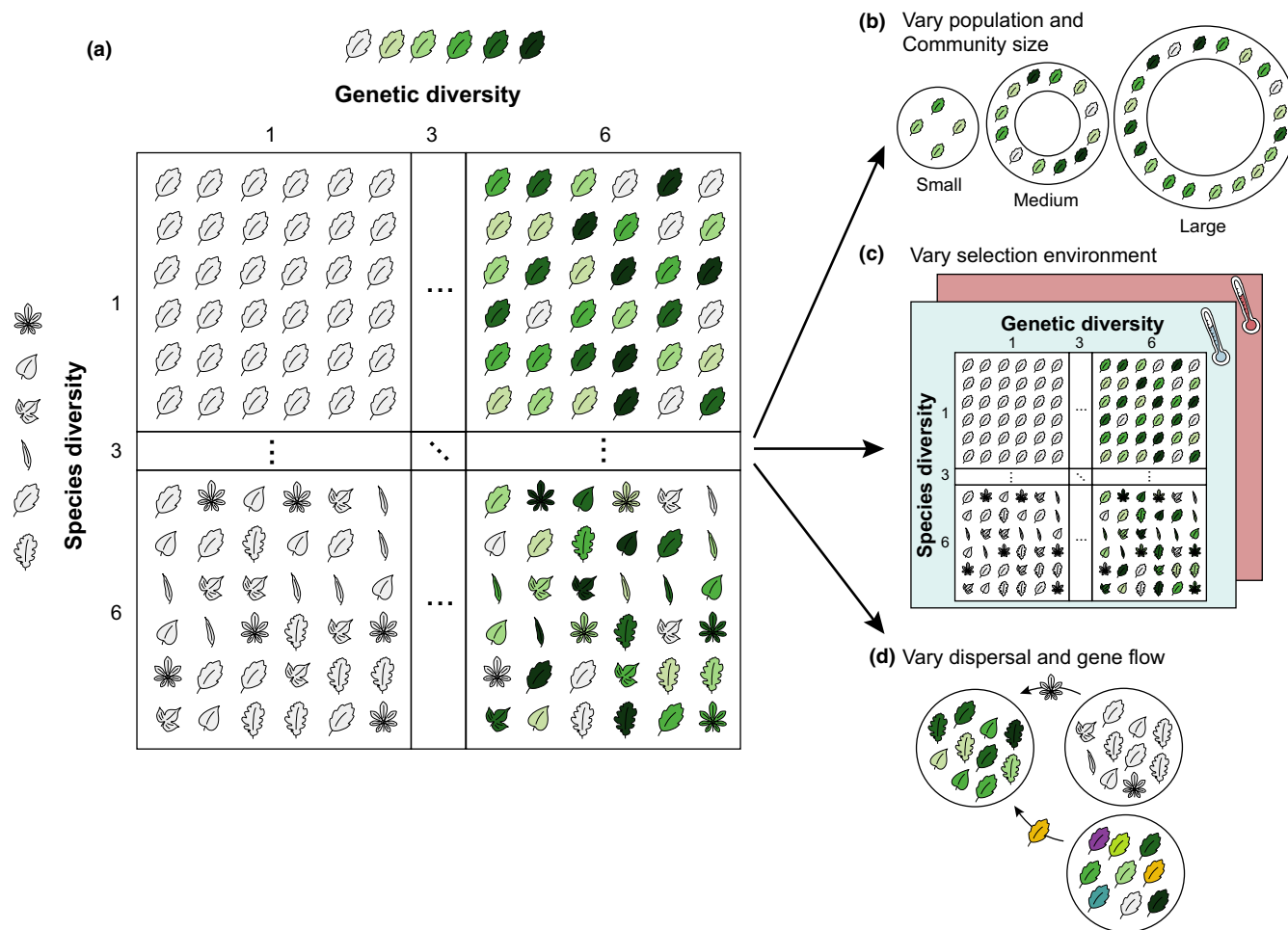
**FIGURE 2** (a) Full-factorial design manipulating genetic and species diversity as used in Crawford and Rudgers (2012). From left to right, one, three or six genotypes per species are used. From top to bottom, one, three or six species are used. Leaf shapes represent different species used in the experiment, and colours represent the different genotypes within each species. (b–d) Experimental design in (a) combined with varying population and community size, varying selection environments [e.g. low (blue) and high (red) temperatures], and varying species dispersal and gene flow, respectively

community, or whether different sets of eco-evolutionary dynamics converge or diverge in the community trait mean. Detailed characterization of temporal dynamics can be found in Ryo et al. (2019). For eco-evolutionary community dynamics, one could quantify changes in the mean, variance or autocorrelation of the temporal dynamics of genes, traits or species and whether changes in these variables reflect, for example, constant, pulse or step changes (see Figure 2 Ryo et al., 2019). Identifying if specific interactions between evolutionary and community processes consistently result in particular characteristics of the eco-evolutionary community dynamic under study would enhance the predictability of eco-evolutionary dynamics in multi-species settings. First steps could involve constructing theoretical models to test whether the inclusion or exclusion of particular interactions between evolutionary and community processes result in similar or divergent eco-evolutionary community dynamics. Constructing such theoretical models could also allow testing the sensitivity of interactions between evolutionary and community processes on eco-evolutionary community dynamics and identify those with the greatest impact.

## 6.2 | Detecting general patterns of interacting evolutionary and community processes

Our perspective highlighted several gaps in the research on interactions among community and evolutionary processes. But are these interactions simply special cases in nature or simply understudied? The literature on these interactions is generally limited, and therefore we probably will not know about the generality or taxon specificity of responses until many more studies are performed. The importance of particular interactions is likely to vary among study systems based on their characteristics. For instance, ecological and genetic drift is likely more important in communities of many species each with small population sizes versus a few species each with large population sizes (Table 1). In some cases, eco-evolutionary interactions could produce legacy effects on consecutive community dynamics (Table 1). For example, a study by Grainger et al. (2021) showed that *Drosophila* populations that varied in selection to interspecific competition differently responded to future environmental change. One future task will be to synthesize (e.g. via meta-analysis)

the relative importance of evolutionary and community interactions across a variety of species, ecosystems and regions, which can help focus future work on the most likely scenarios. Determining the relative importance of evolutionary and community processes could be facilitated by developing methods that quantify the relative contributions of each process and their interactions. Such methods are increasingly used to partition effects of ecological and evolutionary processes to population, community and ecosystem change (Ellner et al., 2011; Govaert et al., 2016; Hairston Jr. et al., 2005). For example, the Price equation (Price, 1970, 1972) partitions population trait change into a component reflecting selection and a component reflecting transmission bias (including mutation). An extension of the Price equation has been used to partition community trait change into effects of species sorting, genotype sorting and within-genotypic trait change (Collins & Gardner, 2009; Govaert et al., 2016), and could be further extended to include species dispersal and gene flow. The development of such partitioning metrics and the accurate assessment of the contributions of each fundamental process to observed eco-evolutionary community dynamics can facilitate understanding when and where these interactions are important. Moreover, it will motivate theory and experiments that consider, if not incorporate, a wider diversity of interacting mechanisms, weighted by their importance in real systems.

Other ways of detecting general patterns may involve determining to what degree evolutionary and community processes occur on similar time-scales, and how this influences eco-evolutionary community dynamics. When an evolutionary and community process occur on similar time-scales they might interact and affect community and evolutionary outcomes in similar ways (Amarasekare, 2000; Urban et al., 2008). For example, the arrival of an adapted species versus the local adaptation of a resident species might generate the same trait distributions (De Meester et al., 2016; Urban et al., 2008). Yet, if the two processes occur on very different time-scales, we might observe more complicated dynamics. For instance, if new species arrive slowly, a resident species might radiate into multiple species in the meantime, and that radiation might prescribe the rules for future species colonizations (Gillespie, 2004; Losos & Ricklefs, 2009). Speciation might often occur over longer time-scales than its analogue, mutation. Therefore, we might expect a divergence in the time-scales at which communities and populations generate novel in situ diversity. If ecological drift is much slower than genetic drift, then genetic drift might dominate, but if they occur at similar time-scales, they might reinforce each other. Perhaps these examples could eventually inform a more general theory of eco-evolutionary community dynamics based on the relative pace of parallel processes. Ultimately, we need to pursue explorations that can generate a more integrative and predictive framework for evolutionary community ecology.

Similarly, one can explore how spatial scale and patchiness affect joint evolutionary and community processes. Evolutionary and community processes are likely to vary in importance and interaction strength across a spatial continuum. For example, at more regional scales, gene flow or dispersal among nearby populations and communities might often interact with other evolutionary and community processes. However, across larger spatial scales, genetic and ecological diversity likely will be affected by the increasing importance of ecotypic divergence, hybridization and speciation. These processes can blur the gradient between evolution and ecology, requiring a more careful consideration about the spatial and temporal scales over which certain evolutionary and community processes dominate. The degree to which populations and communities occur across discrete boundaries versus a continuum might also affect the strength of interactions among processes. For example, ponds and forest fragments may have a clearer boundary to distinguish local versus regional properties compared to more open marine and grassland systems. In more open systems, it remains unknown if eco-evolutionary dynamics experience abrupt transitions in their effects or vary more gradually.

## 6.3 | Moving towards more realistic settings

Most of our current understanding about multi-species eco-evolutionary dynamics either comes from studies focusing on pairwise species interactions (Becks et al., 2012; Hillesland & Stahl, 2010; Yoshida et al., 2003) or from community responses to evolutionary change of a single species in the community (Pantel et al., 2015; Whitham et al., 2006), with the exception of a few bacterial studies (e.g. Fiegna et al., 2015; Lawrence et al., 2012). Using this knowledge to understand multi-species eco-evolutionary dynamics can be problematic because a meta-analysis by Chamberlain et al. (2014) found that the magnitude and sign of species interactions often depends on the presence of other species. Theoretical models also demonstrate that the presence of a third species often alters the strength and direction of selection in two-species communities (de Mazancourt et al., 2008; Strauss et al., 2005; Vellend, 2008). Such indirect ecological effects can occur when genetic trait correlations in one species can alter evolution and abundances of other species in the community (terhorst et al., 2018). Indirect ecological effects may result in nonadditive selection (i.e. indirect ecological effects alter the strength or direction of selection; Strauss et al., 2005). Testing for nonadditive selection can be done by estimating selection gradients for each species pair and assessing whether the sum of these selection gradients equals the resulting selection gradient when all species are present together (terHorst et al., 2015). We thus expect multi-species eco-evolutionary dynamics to differ qualitatively from pairwise species eco-evolutionary dynamics (Friman et al., 2016), and this divergence might be reinforced by alterations to the strength and direction of interactions between community and evolutionary processes in multi-species communities.

Future studies should incorporate experimental designs that explicitly consider a gradient from two to multiple species. We encourage applying experimental designs pioneered
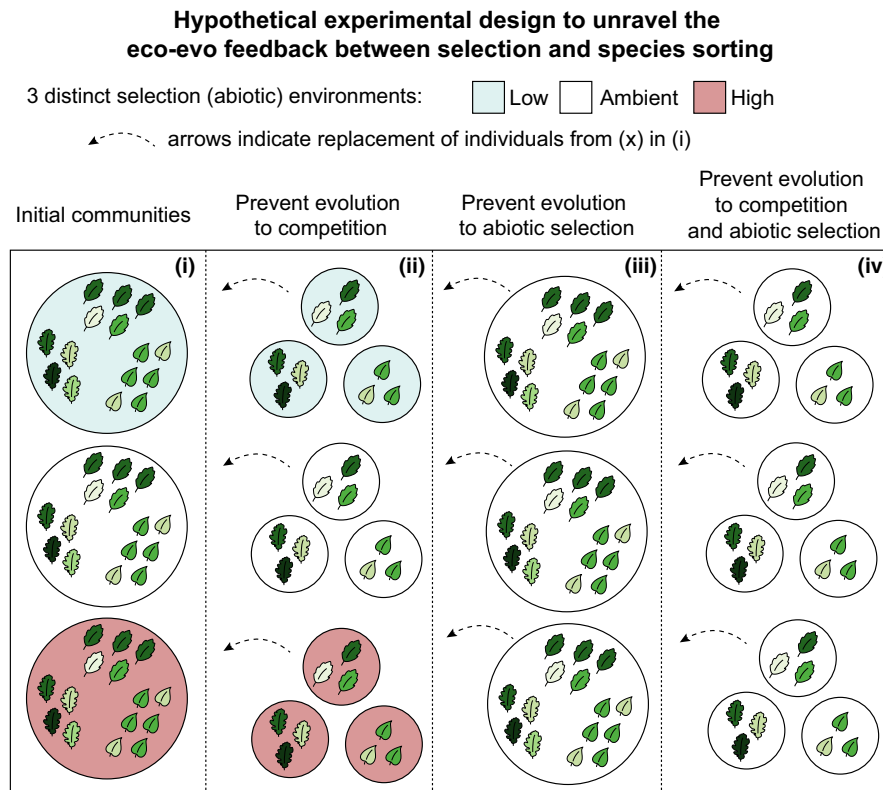
**Hypothetical experimental design to unravel the
eco-evo feedback between selection and species sorting**

3 distinct selection (abiotic) environments:   Low   Ambient   High

arrows indicate replacement of individuals from (x) in (i)



**FIGURE 3** Hypothetical experimental design to test for the interaction between species sorting and selection. (i) Exposing initially similar communities to different abiotic selection environments would account for different strength and direction of selection (e.g. cold, ambient and warm temperature indicated by blue, white and red colored circle) and for interspecific competition determining species sorting. (ii) To prevent evolution in response to interspecific competition, one would replace individuals from (i) with individuals that did not experience interspecific competition. (iii) To prevent evolution in response to the abiotic selection environment, one would replace individuals in (i) with individuals that did not experience the abiotic selection. (iv) To prevent evolution in response to interspecific competition and abiotic selection, one would replace individuals in (i) with individuals from the ambient abiotic environment that did not experience interspecific competition

by Cook-Patton et al. (2011) and Crawford and Rudgers (2012), which vary genetic and species diversity simultaneously. Most studies use an equal number of species and genotypes. However, it would be important to assess whether equal species and genetic diversity is common among natural systems, or whether one or the other is larger. Previous studies have found both positive and negative relations between species and genetic diversity depending on patch size and connectivity as well as species interactions (Lamy et al., 2017). We suspect that genetic and species diversity often diverge substantially in either direction depending on the species and system.

## 6.4 | Integrating interactions between evolutionary and community processes into experimental designs

To quantify eco-evolutionary dynamics, one commonly quantifies the 'evo-to-eco' pathway (i.e. how evolution alters ecological dynamics; Pathway 1) or the 'eco-to-evo' pathway (i.e. how ecology

alters evolutionary dynamics; Pathway 2), resulting in a natural division of experiments related to these two pathways (Figure S1). Approaches such as transplanting entire communities, or performing common gardens on all or most species of the community are promising tools to determine the extent to which evolutionary and community processes interact to determine community and (co) evolutionary responses (De Meester et al., 2019). We detail common experimental practices to assess eco-evolutionary dynamics in Supporting Information and here discuss experimental designs that allow testing interactions between evolutionary and community processes. Space-for-time substitutions could be used in cases where evolutionary and community processes are difficult to manipulate. For example, one of the best examples of the intersection of ecological speciation and dispersal across space and time comes from phylogenetic reconstructions of ecotypic variation in spiders across the Hawaiian islands (Gillespie, 2004).

Beginning with experiments that manipulate genetic and community diversity (Figure 2a), we propose manipulations of the strength and direction of fundamental processes to increase our mechanistic understanding about their interactions. The

extent of such manipulation will also depend on natural history, local ecology and evolutionary history of the studied system. Manipulation of fundamental processes can be achieved for each analogous evolutionary and community process (e.g. by varying selection and species sorting simultaneously) or for multiple interactions between evolutionary and community processes (e.g. varying the interaction of selection and species sorting with genetic and ecological drift). For example, the strength of selection could be manipulated by using more stressful environments (e.g. high pollution or extreme temperatures). The direction of selection could be manipulated by using different selection environments which favour opposite traits (e.g. small vs. large body size). The response to selection can be manipulated by altering genetic diversity (evolution) or trait diversity among species (species sorting). Alternatively, one could manipulate an evolutionary process without manipulating its community analogue (e.g. varying genetic responses to selection but not responses via species sorting) or by manipulating interactions between evolutionary and community processes separately (e.g. varying the interaction between selection and ecological drift but not between species sorting and genetic drift).

We outline three experimental designs that can reveal the operation of specific evolutionary and community processes and that incorporate some of the underexplored interactions between evolutionary and community processes. First, manipulating community and population sizes from small to large sizes (see experimental design of Gilbert & Levine, 2017) in combination with manipulations of genetic and species diversity would alter the strength of ecological and genetic drift and test how these processes jointly influence eco-evolutionary community dynamics (Figure 2b). Moreover, varying community and population sizes in combination with different abiotic selection environments may reveal the eco-evolutionary interactions between selection, species sorting and genetic and ecological drift.

Second, evaluating the full-factorial design of genetic and community diversity in different abiotic environments such as varying temperature or nutrient availability would test alternative scenarios that vary in the strength and direction of selection (Figure 2c). The resulting shifts in trait values could then feedback to alter species sorting. Differences in the resulting eco-evolutionary community dynamics would then be the result of differing eco-evolutionary interactions between species sorting and selection. To decouple this feedback, one could perform three additional experiments that (a) prevent evolution in response to interspecific competition, (b) prevent evolution in response to the abiotic environment and (c) prevent evolution in response to both interspecific competition and the abiotic environment (Figure 3). Preventing evolution to interspecific competition can be done by replacing individuals of each species by individuals experiencing the abiotic selection environment, but not the interspecific competition at regular time points throughout the experiment (see e.g. Hart et al., 2019). Preventing evolution in response to the abiotic selection environment, but not interspecific

competition, can be done by replacing individuals of each species by individuals from a substitute community in the control abiotic environment (Figure 3). Last, substituting individuals in the absence of both interspecific competition and abiotic selection would decouple the feedback between species sorting and selection. In the latter case, one could also substitute individuals from the ancestral population for each species.

Third, manually dispersing individuals or manipulating the connectivity of experimental units in combination with varying genetic and species diversity can test for interactions between dispersal and gene flow with species sorting (Figure 2d). Varying the effects of dispersal and gene flow independently is more challenging. However, one could imagine experiments where individuals are added with the same genetic structure as the recipient population or with a different genetic structure to contrast the effect of dispersal with gene flow. This could be accomplished by sourcing immigrants from populations that differ due to divergent selection. Alternatively, the effects of the dispersal of a new species might be contrasted against gene flow among populations by comparing the effects of species additions versus the immigration of differently adapted individuals.

## 7 | CONCLUSION

Overall, community ecologists and evolutionary biologists are interested in the same thing: understanding and predicting temporal and spatial variation in biological diversity based on fundamental processes. Although they might focus on understanding biological diversity at different levels (species vs. genetic), emerging work indicates that these issues are often interdependent. Therefore, predicting how either populations and communities respond to environmental changes will often require understanding how ecological and evolutionary processes interact in multi-species communities. Integrating community ecology and evolution will require a deeper understanding and appreciation for the differences and similarities among biological disciplines. Also, disentangling these effects will often require large, collaborative experiments that separate interactive elements in natural systems and a common language between evolutionary biologists and community ecologists. Such a shared language will facilitate collaborations, and promote the integration of currently existing frameworks that differ in their roots, but often share the same or analogous processes. Here we emphasize that such an integration can be achieved by focusing on interactions among four basic and parallel processes that structure both community ecology and evolution.

## COMPETING INTERESTS

The authors declare no competing interests.

## AUTHORS' CONTRIBUTIONS

L.G. and M.U. drafted a first version of the manuscript with input from F.A. and L.D.M. All authors have contributed substantially to multiple rounds of editing and commenting on the manuscript and gave final approval for submission.

## ORCID

*Lynn Govaert* https://orcid.org/0000-0001-8326-3591
*Florian Altermatt* https://orcid.org/0000-0002-4831-6958
*Luc De Meester* https://orcid.org/0000-0001-5433-6843
*Mark A. McPeek* https://orcid.org/0000-0001-7794-9466

## REFERENCES

Altermatt, F., Hottinger, J., & Ebert, D. (2007). Parasites promote host gene ow in a metapopulation. *Evolutionary Ecology*, 21, 561–575.

Amarasekare, P. (2000). The geometry of coexistence. *Biological Journal of the Linnean Society*, 71, 1–31. https://doi.org/10.1111/j.1095-8312.2000.tb01239.x

Antonovics, J. (1992). Toward community genetics. In R. S. Fritz & E. L. Simms (Eds.), *Plant resistance to herbivores and pathogens: Ecology, evolution, and genetics* (pp. 426–449). University of Chicago Press.

Barraclough, T. G. (2015). How do species interactions affect evolutionary dynamics across whole communities? *Annual Review of Ecology, Evolution, and Systematics*, 46, 25–48. https://doi.org/10.1146/annurev-ecolsys-112414-054030

Beans, C. M., & Roach, D. A. (2015). An invasive plant alters pollinator-mediated phenotypic selection on a native congener. *American Journal of Botany*, 102, 50–57. https://doi.org/10.3732/ajb.1400385

Becks, L., Ellner, S. P., Jones, L. E., & Hairston Jr., N. G. (2012). The functional genomics of an eco-evolutionary feedback loop: Linking gene expression, trait evolution, and community dynamics. *Ecology Letters*, 15, 492–501. https://doi.org/10.1111/j.1461-0248.2012.01763.x

Bonelli, S., Vrabec, V., Witek, M., Barbero, F., Patricelli, D., & Nowicki, P. (2013). Selection on dispersal in isolated buttery metapopulations. *Population Ecology*, 55, 469–478.

Butlin, R., Debelle, A., Kerth, C., Snook, R. R., Beukeboom, L. W., Castillo, R. C., Diao, W., Maan, M. E., Paolucci, S., Weissing, F. J. et al. (2012). What do we need to know about speciation? *Trends in Ecology & Evolution*, 27, 27–39.

Carlson, S. M., Cunningham, C. J., & Westley, P. A. (2014). Evolutionary rescue in a changing world. *Trends in Ecology & Evolution*, 29, 521–530. https://doi.org/10.1016/j.tree.2014.06.005

Chamberlain, S. A., Bronstein, J. L., & Rudgers, J. A. (2014). How context dependent are species interactions? *Ecology Letters*, 17, 881–890. https://doi.org/10.1111/ele.12279

Chase, J. M., & Leibold, M. A. (2003). *Ecological niches: Linking classical and contemporary approaches*. University of Chicago Press.

Christiansen, F. B. (1975). Hard and soft selection in a subdivided population. *The American Naturalist*, 109, 11–16. https://doi.org/10.1086/282970

Clobert, J., Baguette, M., Benton, T. G., & Bullock, J. M. (2012). *Dispersal ecology and evolution*. Oxford University Press.

Collins, S., & Gardner, A. (2009). Integrating physiological, ecological and evolutionary change: A price equation approach. *Ecology Letters*, 12, 744–757. https://doi.org/10.1111/j.1461-0248.2009.01340.x

Cook-Patton, S. C., McArt, S. H., Parachnowitsch, A. L., Thaler, J. S., & Agrawal, A. A. (2011). A direct comparison of the consequences of plant genotypic and species diversity on communities and ecosystem function. *Ecology*, 92, 915–923. https://doi.org/10.1890/10-0999.1

Coyne, J. A., & Orr, H. A. (2004). *Speciation*. Sinauer Associates, 545pp.

Crawford, K. M., & Rudgers, J. A. (2012). Plant species diversity and genetic diversity within a dominant species interactively affect plant community biomass. *Journal of Ecology*, 100, 1512–1521. https://doi.org/10.1111/j.1365-2745.2012.02016.x

Czekanski-Moir, J. E., & Rundell, R. J. (2019). The ecology of nonecological speciation and nonadaptive radiations. *Trends in Ecology & Evolution*. https://doi.org/10.1016/j.tree.2019.01.012

de Mazancourt, C., Johnson, E., & Barraclough, T. (2008). Biodiversity inhibits species' evolutionary responses to changing environments. *Ecology Letters*, 11, 380–388. https://doi.org/10.1111/j.1461-0248.2008.01152.x

De Meester, L., Brans, K. I., Govaert, L., Souffreau, C., Mukherjee, S., Vanvelk, H., Korzeniowski, K., Kilsdonk, L., Decaestecker, E., Stoks, R., & Urban, M. C. (2019). Analysing eco- evolutionary dynamics – The challenging complexity of the real world. *Functional Ecology*, 33, 43–59. https://doi.org/10.1111/1365-2435.13261

De Meester, L., Vanoverbeke, J., Kilsdonk, L. J., & Urban, M. C. (2016). Evolving perspectives on monopolization and priority effects. *Trends in Ecology & Evolution*, 31, 136–146. https://doi.org/10.1016/j.tree.2015.12.009

Doak, D. F., Estes, J. A., Halpern, B. S., Jacob, U., Lindberg, D. R., Lovvorn, J., Monson, D. H., Tinker, M. T., Williams, T. M., Wootton, J. T., Carroll, I., Emmerson, M., Micheli, F., & Novak, M. (2008). Understanding and predicting ecological dynamics: Are major surprises inevitable. *Ecology*, 89, 952–961. https://doi.org/10.1890/07-0965.1

Ehlers, B. K., Damgaard, C. F., & Laroche, F. (2016). Intraspecific genetic variation and species coexistence in plant communities. *Biology Letters*, 12, 20150853.

Ekvall, M. K., Urrutia-Cordero, P., & Hansson, L. A. (2014). Linking cascading effects of fish predation and zooplankton grazing to reduced cyanobacterial biomass and toxin levels following biomanipulation. *PLoS ONE*, 9(11), e112956. https://doi.org/10.1371/journal.pone.0112956

Ellner, S. P., Geber, M. A., & Hairston Jr., N. G. (2011). Does rapid evolution matter? Measuring the rate of contemporary evolution and its impacts on ecological dynamics. *Ecology Letters*, 14, 603–614. https://doi.org/10.1111/j.1461-0248.2011.01616.x

Excoffier, L., Foll, M., & Petit, R. J. (2009). Genetic consequences of range expansions. *Annual Review of Ecology, Evolution, and Systematics*, 40, 481–501. https://doi.org/10.1146/annurev.ecolsys.39.110707.173414

Fiegna, F., Moreno-Letelier, A., Bell, T., & Barraclough, T. G. (2015). Evolution of species interactions determines microbial community productivity in new environments. *The ISME Journal*, 9, 1235–1245. https://doi.org/10.1038/ismej.2014.215

Figuerola, J., Green, A. J., & Michot, T. C. (2005). Invertebrate eggs can fly: Evidence of waterfowl-mediated gene ow in aquatic invertebrates. *The American Naturalist*, 165, 274–280.

Foster, P. L. (2007). Stress-induced mutagenesis in bacteria. *Critical Reviews in Biochemistry and Molecular Biology*, 42, 373–397. https://doi.org/10.1080/10409230701648494

Friman, V. P., Dupont, A., Bass, D., Murrell, D. J., & Bell, T. (2016). Relative importance of evolutionary dynamics depends on the composition of microbial predator-prey community. *The ISME Journal*, 10, 1352–1362. https://doi.org/10.1038/ismej.2015.217

Fronhofer, E. A., & Altermatt, F. (2017). Classical metapopulation dynamics and eco-evolutionary feedbacks in dendritic networks. *Ecography*, *40*, 1455–1466. https://doi.org/10.1111/ecog.02761

Fronhofer, E. A., Klecka, J., Melián, C. J., & Altermatt, F. (2015). Condition-dependent movement and dispersal in experimental metacommunities. *Ecology Letters*, *18*, 954–963. https://doi.org/10.1111/ele.12475

Futuyma, D. J., & Moreno, G. (1988). The evolution of ecological specialization. *Annual Review of Ecology and Systematics*, *19*, 207–233. https://doi.org/10.1146/annurev.es.19.110188.001231

Gandon, S., & Michalakis, Y. (1999). Evolutionarily stable dispersal rate in a metapopulation with extinctions and kin competition. *Journal of Theoretical Biology*, *199*, 275–290. https://doi.org/10.1006/jtbi.1999.0960

Gause, G. F. et al. (1934). Experimental analysis of Vito Volterra's mathematical theory of the struggle for existence. *Science*, *79*, 16–17. https://doi.org/10.1126/science.79.2036.16-a

Geritz, S. A., & Éva, K. (2000). Adaptive dynamics in diploid, sexual populations and the evolution of reproductive isolation. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*, 1671–1678.

Gilbert, B., & Levine, J. M. (2017). Ecological drift and the distribution of species diversity. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20170507. https://doi.org/10.1098/rspb.2017.0507

Gillespie, J. H. (2004). *Population genetics: A concise guide*. JHU Press.

Gomulkiewicz, R., & Holt, R. D. (1995). When does evolution by natural selection prevent extinction? *Evolution*, *49*, 201–207. https://doi.org/10.1111/j.1558-5646.1995.tb05971.x

Govaert, L., Pantel, J. H., & De Meester, L. (2016). Eco-evolutionary partitioning metrics: Assessing the importance of ecological and evolutionary contributions to population and community change. *Ecology Letters*, *19*, 839–853. https://doi.org/10.1111/ele.12632

Grainger, T. N., Rudman, S. M., Schmidt, P., & Levine, J. M. (2021). Competitive history shapes rapid evolution in a seasonal climate. *Proceedings of the National Academy of Sciences of the United States of the America*, *118*.

Hairston Jr., N. G., Ellner, S. P., Geber, M. A., Yoshida, T., & Fox, J. A. (2005). Rapid evolution and the convergence of ecological and evolutionary time. *Ecology Letters*, *8*, 1114–1127. https://doi.org/10.1111/j.1461-0248.2005.00812.x

Hart, S. P., Turcotte, M. M., & Levine, J. M. (2019). Effects of rapid evolution on species coexistence. *Proceedings of the National Academy of Sciences of the United States of the America*, *116*, 2112–2117. https://doi.org/10.1073/pnas.1816298116

Hendry, A. P. (2017). *Eco-evolutionary dynamics*. Princeton University Press.

Hendry, A. P., Nosil, P., & Rieseberg, L. H. (2007). The speed of ecological speciation. *Functional Ecology*, *21*, 455–464. https://doi.org/10.1111/j.1365-2435.2007.01240.x

Hillesland, K. L., & Stahl, D. A. (2010). Rapid evolution of stability and productivity at the origin of a microbial mutualism. *Proceedings of the National Academy of Sciences of the United States of the America*, *107*, 2124–2129. https://doi.org/10.1073/pnas.0908456107

Hoffmann, A. A., & Hercus, M. J. (2000). Environmental stress as an evolutionary force. *BioScience*, *50*, 217–226.

Holt, R. D. (2005). On the integration of community ecology and evolutionary biology: Historical perspectives and current prospects. In B. E. Beisner & K. Kuddington. *Ecological paradigms lost: Routes of theory change* (pp. 235–271). Academic Press.

Hu, X. S., He, F., & Hubbell, S. P. (2006). Neutral theory in macroecology and population genetics. *Oikos*, *113*, 548–556. https://doi.org/10.1111/j.2006.0030-1299.14837.x

Hubbell, S. P. (2001). *The unified neutral theory of biodiversity and biogeography (MPB-32)*. Princeton University Press.

Hubbell, S. P. (2006). Neutral theory and the evolution of ecological equivalence. *Ecology*, *87*, 1387–1398.

Hutchinson, G. (1957). Population studies: Animal ecology and demography: Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, *22*, 425–427.

Johnson, M. T., & Agrawal, A. A. (2005). Plant genotype and environment interact to shape a diverse arthropod community on evening primrose (*Oenothera biennis*). *Ecology*, *86*, 874–885. https://doi.org/10.1890/04-1068

Jones, C. G., Lawton, J. H., & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos*, *69*, 373–386.

Keith, A. R., Bailey, J. K., Lau, M. K., & Whitham, T. G. (2017). Genetics-based interactions of foundation species affect community diversity, stability and network structure. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20162703. https://doi.org/10.1098/rspb.2016.2703

Kimura, M. (1983). *The neutral theory of molecular evolution*. Cambridge University Press.

Kirkpatrick, M., & Barton, N. H. (1997). Evolution of a species' range. *The American Naturalist*, *150*, 1–23. https://doi.org/10.1086/286054

Kirkpatrick, M., & Peischl, S. (2013). Evolutionary rescue by beneficial mutations in environments that change in space and time. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*, 20120082. https://doi.org/10.1098/rstb.2012.0082

Klopfstein, S., Currat, M., & Excoffier, L. (2006). The fate of mutations surfing on the wave of a range expansion. *Molecular Biology and Evolution*, *23*, 482–490. https://doi.org/10.1093/molbev/msj057

Lamy, T., Laroche, F., David, P., Massol, F., & Jarne, P. (2017). The contribution of species-genetic diversity correlations to the understanding of community assembly rules. *Oikos*, *126*, 759–771. https://doi.org/10.1111/oik.03997

Lande, R. (1980). Genetic variation and phenotypic evolution during allopatric speciation. *The American Naturalist*, *116*, 463–479. https://doi.org/10.1086/283642

Lanfear, R., Kokko, H., & Eyre-Walker, A. (2014). Population size and the rate of evolution. *Trends in Ecology & Evolution*, *29*, 33–41. https://doi.org/10.1016/j.tree.2013.09.009

Lankau, R. A., & Strauss, S. Y. (2007). Mutual feedbacks maintain both genetic and species diversity in a plant community. *Science*, *317*, 1561–1563. https://doi.org/10.1126/science.1147455

Lawrence, D., Fiegna, F., Behrends, V., Bundy, J. G., Phillimore, A. B., Bell, T., & Barraclough, T. G. (2012). Species interactions alter evolutionary responses to a novel environment. *PLoS Biology*, *10*. https://doi.org/10.1371/journal.pbio.1001330

Leger, E. A., & Goergen, E. M. (2017). Invasive *Bromus tectorum* alters natural selection in arid systems. *Journal of Ecology*, *105*, 1509–1520.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M., & Gonzalez, A. (2004). The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters*, *7*, 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Leibold, M. A., & McPeek, M. A. (2006). Coexistence of the niche and neutral perspectives in community ecology. *Ecology*, *87*, 1399–1410.

Leibold, M. A., Urban, M. C., De Meester, L., Klausmeier, C. A., & Vanoverbeke, J. (2019). Regional neutrality evolves through local adaptive niche evolution. *Proceedings of the National Academy of Sciences of the United States of the America*, *116*, 2612–2617. https://doi.org/10.1073/pnas.1808615116

Lenormand, T. (2002). Gene flow and the limits to natural selection. *Trends in Ecology & Evolution*, *17*, 183–189.

Levins, R., & Culver, D. (1971). Regional coexistence of species and competition between rare species. *Proceedings of the National Academy of Sciences of the United States of the America*, *68*, 1246–1248. https://doi.org/10.1073/pnas.68.6.1246

Loeuille, N., & Leibold, M. A. (2014). Effects of local negative feedbacks on the evolution of species within metacommunities. *Ecology Letters*, *17*, 563–573. https://doi.org/10.1111/ele.12258

Losos, J. B., Glor, R. E., Kolbe, J. J., & Nicholson, K. (2006). Adaptation, speciation, and convergence: A hierarchical analysis of adaptive radiation in Caribbean anolis lizards. *Annals of the Missouri Botanical Garden*, *93*, 24–33.

Losos, J. B., & Ricklefs, R. E. (2009). Adaptation and diversification on islands. *Nature*, *457*, 830–836.

Low-Décarie, E., Kolber, M., Homme, P., Lofano, A., Dumbrell, A., Gonzalez, A., & Bell, G. (2015). Community rescue in experimental metacommunities. *Proceedings of the National Academy of Sciences of the United States of the America*, *112*, 14307–14312. https://doi.org/10.1073/pnas.1513125112

Lynch, M. (2010). Evolution of the mutation rate. *Trends in Genetics*, *26*, 345–352. https://doi.org/10.1016/j.tig.2010.05.003

Lynch, M., Bürger, R., Butcher, D., & Gabriel, W. (1993). The mutational meltdown in asexual populations. *Journal of Heredity*, *84*, 339–344. https://doi.org/10.1093/oxfordjournals.jhered.a111354

Mani, G., & Clarke, B. C. (1990). Mutational order: A major stochastic process in evolution. *Proceedings of the Royal Society of London. B. Biological Sciences 240*, 29–37.

Massol, F., Dubart, M., Calcagno, V., Cazelles, K., Jacquet, C., Kéfi, S., & Gravel, D. (2017). Island biogeography of food webs. *Advances in Ecological Research*, *56*, 183–262.

Matthysen, E. (2005). Density-dependent dispersal in birds and mammals. *Ecography*, *28*, 403–416. https://doi.org/10.1111/j.0906-7590.2005.04073.x

McPeek, M. A. (2017). *Evolutionary community ecology* (Vol. 58). Princeton University Press.

McPeek, M. A., & Holt, R. D. (1992). The evolution of dispersal in spatially and temporally varying environments. *The American Naturalist*, *140*, 1010–1027. https://doi.org/10.1086/285453

McPeek, M. A., & Siepielski, A. M. (2019). Disentangling ecologically equivalent from neutral species: The mechanisms of population regulation matter. *Journal of Animal Ecology*, *88*, 1755–1765. https://doi.org/10.1111/1365-2656.13072

Miner, B. E., De Meester, L., Pfrender, M. E., Lampert, W., & Hairston Jr., N. G. (2012). Linking genes to communities and ecosystems: *Daphnia* as an ecogenomic model. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 1873–1882.

Moerman, F., Fronhofer, E. A., Wagner, A., & Altermatt, F. (2020). Gene swamping alters evolution during range expansions in the protist *Tetrahymena thermophila*. *Biology Letters*, *16*, 20200244.

Müller, M. J., Neugeboren, B. I., Nelson, D. R., & Murray, A. W. (2014). Genetic drift opposes mutualism during spatial population expansion. *Proceedings of the National Academy of Sciences of the United States of the America*, *111*, 1037–1042. https://doi.org/10.1073/pnas.1313285111

Mullon, C., & Lehmann, L. (2018). Eco-evolutionary dynamics in metacommunities: Ecological inheritance, helping within species, and harming between species. *The American Naturalist*, *192*, 664–686. https://doi.org/10.1086/700094

Nadeau, C. P., & Urban, M. C. (2019). Eco-evolution on the edge during climate change. *Ecography*, *42*, 1280–1297. https://doi.org/10.1111/ecog.04404

Nakamura, H., Teshima, K., & Tachida, H. (2018). Effects of cyclic changes in population size on neutral genetic diversity. *Ecology and Evolution*, *8*, 9362–9371. https://doi.org/10.1002/ece3.4436

Norberg, J. (2004). Biodiversity and ecosystem functioning: A complex adaptive systems approach. *Limnology and Oceanography*, *49*, 1269–1277. https://doi.org/10.4319/lo.2004.49.4_part_2.1269

Nosil, P. (2008). Speciation with gene ow could be common. *Molecular Ecology*, *17*, 2103–2106.

Nosil, P. (2012). *Ecological speciation*. Oxford University Press.

Nosil, P., & Flaxman, S. M. (2011). Conditions for mutation-order speciation. *Proceedings of the Royal Society B: Biological Sciences*, *278*, 399–407. https://doi.org/10.1098/rspb.2010.1215

Ochocki, B. M., & Miller, T. E. (2017). Rapid evolution of dispersal ability makes biological invasions faster and more variable. *Nature Communications*, *8*, 1–8. https://doi.org/10.1038/ncomms14315

Olivieri, I., Michalakis, Y., & Gouyon, P. H. (1995). Metapopulation genetics and the evolution of dispersal. *The American Naturalist*, *146*, 202–228. https://doi.org/10.1086/285795

Orrock, J. L., & Watling, J. I. (2010). Local community size mediates ecological drift and competition in metacommunities. *Proceedings of the Royal Society B: Biological Sciences*, *277*, 2185–2191. https://doi.org/10.1098/rspb.2009.2344

Paine, R. T. (1969). A note on trophic complexity and community stability. *The American Naturalist*, *103*, 91–93. https://doi.org/10.1086/282586

Pantel, J. H., Duvivier, C., & Meester, L. D. (2015). Rapid local adaptation mediates zoo-plankton community assembly in experimental mesocosms. *Ecology Letters*, *18*, 992–1000. https://doi.org/10.1111/ele.12480

Pelletier, F., Clutton-Brock, T., Pemberton, J., Tuljapurkar, S., & Coulson, T. (2007). The evolutionary demography of ecological change: Linking trait variation and population growth. *Science*, *315*, 1571–1574. https://doi.org/10.1126/science.1139024

Pillai, P., Gonzalez, A., & Loreau, M. (2012). Evolution of dispersal in a predator-prey metacommunity. *The American Naturalist*, *179*, 204–216. https://doi.org/10.1086/663674

Polechová, J. (2018). Is the sky the limit? On the expansion threshold of a species' range. *PLoS Biology*, *16*, e2005372. https://doi.org/10.1371/journal.pbio.2005372

Price, G. R. (1970). Selection and covariance. *Nature*, *227*, 520–521. https://doi.org/10.1038/227520a0

Price, G. R. (1972). Extension of covariance selection mathematics. *Annals of Human Genetics*, *35*, 485–490. https://doi.org/10.1111/j.1469-1809.1957.tb01874.x

Richardson, J. L., & Urban, M. C. (2013). Strong selection barriers explain microgeographic adaptation in wild salamander populations. *Evolution*, *67*, 1729–1740. https://doi.org/10.1111/evo.12052

Richardson, J. L., Urban, M. C., Bolnick, D. I., & Skelly, D. K. (2014). Microgeographic adaptation and the spatial scale of evolution. *Trends in Ecology & Evolution*, *29*, 165–176. https://doi.org/10.1016/j.tree.2014.01.002

Rominger, A. J., Goodman, K. R., Lim, J. Y., Armstrong, E. E., Becking, L. E., Bennett, G. M., Brewer, M. S., Cotoras, D. D., Ewing, C. P., Harte, J., Martinez, N. D., O'Grady, P. M., Percy, D. M., Price, D. K., Roderick, G. K., Shaw, K. L., Valdovinos, F. S., Gruner, D. S., Gillespie, R. G., & Ricklefs, R. (2016). Community assembly on isolated islands: Macroecology meets evolution. *Global Ecology and Biogeography*, *25*, 769–780. https://doi.org/10.1111/geb.12341

Rosindell, J., & Phillimore, A. B. (2011). A unified model of island biogeography sheds light on the zone of radiation. *Ecology Letters*, *14*, 552–560. https://doi.org/10.1111/j.1461-0248.2011.01617.x

Roze, D., & Rousset, F. (2005). Inbreeding depression and the evolution of dispersal rates: A multilocus model. *The American Naturalist*, *166*, 708–721. https://doi.org/10.1086/497543

Ryo, M., Aguilar-Trigueros, C. A., Pinek, L., Muller, L. A., & Rillig, M. C. (2019). Basic principles of temporal dynamics. *Trends in Ecology & Evolution*, *34*, 723–733. https://doi.org/10.1016/j.tree.2019.03.007

Saastamoinen, M., Bocedi, G., Cote, J., Legrand, D., Guillaume, F., Wheat, C. W., Fronhofer, E. A., Garcia, C., Henry, R., Husby, A., Baguette, M., Bonte, D., Coulon, A., Kokko, H., Matthysen, E., Niitepõld, K., Nonaka, E., Stevens, V. M., Travis, J. M. J., … del Mar Delgado, M. (2018). Genetics of dispersal. *Biological Reviews*, *93*, 574–599. https://doi.org/10.1111/brv.12356

Schluter, D. (2000). *The ecology of adaptive radiation*. Oxford University Press.

Schluter, D. (2009). Evidence for ecological speciation and its alternative. *Science*, *323*, 737–741. https://doi.org/10.1126/science.1160006

Schoener, T. W. (2011). The newest synthesis: Understanding the interplay of evolutionary and ecological dynamics. *Science*, 331, 426–429. https://doi.org/10.1126/science.1193954

Schtickzelle, N., Mennechez, G., & Baguette, M. (2006). Dispersal depression with habitat fragmentation in the bog fritillary buttery. *Ecology*, 87, 1057–1065.

Slatkin, M. (1980). Ecological character displacement. *Ecology*, 61, 163–177. https://doi.org/10.2307/1937166

Stinchcombe, J. R., & Rausher, M. D. (2002). The evolution of tolerance to deer herbivory: Modifications caused by the abundance of insect herbivores. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 269, 1241–1246.

Strauss, S. Y., Sahli, H., & Conner, J. K. (2005). Toward a more trait-centered approach to diffuse (co) evolution. *New Phytologist*, 165, 81–90. https://doi.org/10.1111/j.1469-8137.2004.01228.x

Svensson, E. I. (2012). Non-ecological speciation, niche conservatism and thermal adaptation: How are they connected? *Organisms Diversity & Evolution*, 12, 229–240. https://doi.org/10.1007/s13127-012-0082-6

Svensson, E. I., & Friberg, M. (2007). Selective predation on wing morphology in sympatric damselies. *The American Naturalist*, 170, 101–112.

Tazzyman, S. J., & Iwasa, Y. (2010). Sexual selection can increase the effect of random genetic drift – A quantitative genetic model of polymorphism in *Oophaga pumilio*, the strawberry poison-dart frog. *Evolution: International Journal of Organic Evolution*, 64, 1719–1728. https://doi.org/10.1111/j.1558-5646.2009.00923.x

terHorst, C. P., Lau, J. A., Cooper, I. A., Keller, K. R., Rosa, R. J. L., Royer, A. M., Schultheis, E. H., Suwa, T., & Conner, J. K. (2015). Quantifying nonadditive selection caused by in-direct ecological effects. *Ecology*, 96, 2360–2369. https://doi.org/10.1890/14-0619.1

terHorst, C. P., Miller, T. E., Powell, E. et al. (2010). When can competition for resources lead to ecological equivalence? *Evolutionary Ecology Research*, 12, 843–854.

terHorst, C. P., Zee, P. C., Heath, K. D., Miller, T. E., Pastore, A. I., Patel, S., Schreiber, S. J., Wade, M. J., & Walsh, M. R. (2018). Evolution in a community context: Trait responses to multiple species interactions. *The American Naturalist*, 191, 368–380. https://doi.org/10.1086/695835

Thompson, J. N. (1999). The evolution of species interactions. *Science*, 284, 2116–2118. https://doi.org/10.1126/science.284.5423.2116

Thompson, J. N. (2005). *The geographic mosaic of coevolution*. University of Chicago Press.

Travis, J. M. J., Delgado, M., Bocedi, G., Baguette, M., Bartoń, K., Bonte, D., Boulangeat, I., Hodgson, J. A., Kubisch, A., Penteriani, V., Saastamoinen, M., Stevens, V. M., & Bullock, J. M. (2013). Dispersal and species' responses to climate change. *Oikos*, 122, 1532–1540. https://doi.org/10.1111/j.1600-0706.2013.00399.x

Uecker, H., Otto, S. P., & Hermisson, J. (2014). Evolutionary rescue in structured populations. *The American Naturalist*, 183, E17–E35. https://doi.org/10.1086/673914

Urban, M. C. (2011). The evolution of species interactions across natural landscapes. *Ecology Letters*, 14, 723–732. https://doi.org/10.1111/j.1461-0248.2011.01632.x

Urban, M. C. (2013). Evolution mediates the effects of apex predation on aquatic food webs. *Proceedings of the Royal Society B: Biological Sciences*, 280, 20130859. https://doi.org/10.1098/rspb.2013.0859

Urban, M. C., Leibold, M. A., Amarasekare, P., DeMeester, L., Gomulkiewicz, R., Hochberg, M. E., Klausmeier, C. A., Loeuille, N., De Mazancourt, C., Norberg, J. (2008). The evolutionary ecology of metacommunities. *Trends in Ecology & Evolution*, 23, 311–317. https://doi.org/10.1016/j.tree.2008.02.007

Urban, M. C., & Skelly, D. K. (2006). Evolving metacommunities: Toward an evolutionary perspective on metacommunities. *Ecology*, 87, 1616–1626.

Urban, M. C., Strauss, S. Y., Pelletier, F., Palkovacs, E. P., Leibold, M. A., Hendry, A. P., De Meester, L., Carlson, S. M., Angert, A. L., & Giery, S. T. (2020). Evolutionary origins for ecological patterns in space. *Proceedings of the National Academy of Sciences of the United States of the America*, 117, 17482–17490.

Uyeda, J. C., Arnold, S. J., Hohenlohe, P. A., & Mead, L. S. (2009). Drift promotes speciation by sexual selection. *Evolution: International Journal of Organic Evolution*, 63, 583–594. https://doi.org/10.1111/j.1558-5646.2008.00589.x

Van Buskirk, J., & Yurewicz, K. L. (1998). Effects of predators on prey growth rate: Relative contributions of thinning and reduced activity. *Oikos*, 20–28. https://doi.org/10.2307/3546913

Vanoverbeke, J., Urban, M. C., & De Meester, L. (2016). Community assembly is a race between immigration and adaptation: Eco-evolutionary interactions across spatial scales. *Ecography*, 39, 858–870. https://doi.org/10.1111/ecog.01394

Vellend, M. (2008). Effects of diversity on diversity: Consequences of competition and facilitation. *Oikos*, 117, 1075–1085. https://doi.org/10.1111/j.0030-1299.2008.16698.x

Vellend, M. (2010). Conceptual synthesis in community ecology. *The Quarterly Review of Biology*, 85, 183–206. https://doi.org/10.1086/652373

Vellend, M. (2016). *The theory of ecological communities (MPB-57)*. Princeton University Press.

Vellend, M., & Geber, M. A. (2005). Connections between species diversity and genetic diversity. *Ecology Letters*, 8, 767–781. https://doi.org/10.1111/j.1461-0248.2005.00775.x

Vermeij, G. J. (1982). Phenotypic evolution in a poorly dispersing snail after arrival of a predator. *Nature*, 299, 349–350. https://doi.org/10.1038/299349a0

Villa, S. M., Altuna, J. C., Ruff, J. S., Beach, A. B., Mulvey, L. I., Poole, E. J., Campbell, H. E., Johnson, K. P., Shapiro, M. D., Bush, S. E., & Clayton, D. H. (2019). Rapid experimental evolution of reproductive isolation from a single natural population. *Proceedings of the National Academy of Sciences of the United States of the America*, 116, 13440–13445. https://doi.org/10.1073/pnas.1901247116

Warren, B., Ricklefs, R., Thébaud, C., Gravel, D., & Mouquet, N. (2020). How consideration of islands has inspired mainstream ecology: Links between the theory of island biogeography and some other key theories. in book: Encyclopedia of the World's Biomes, pp57-60, Elsevier.

Whitham, T. G., Bailey, J. K., Schweitzer, J. A., Shuster, S. M., Bangert, R. K., LeRoy, C. J., Lonsdorf, E. V., Allan, G. J., DiFazio, S. P., Potts, B. M., Fischer, D. G., Gehring, C. A., Lindroth, R. L., Marks, J. C., Hart, S. C., Wimp, G. M., & Wooley, S. C. (2006). A framework for community and ecosystem genetics: From genes to ecosystems. *Nature Reviews Genetics*, 7, 510–523. https://doi.org/10.1038/nrg1877

Whitham, T. G., Young, W. P., Martinsen, G. D., Gehring, C. A., Schweitzer, J. A., Shuster, S. M., Wimp, G. M., Fischer, D. G., Bailey, J. K., Lindroth, R. L., Woolbright, S., & Kuske, C. R. (2003). Community and ecosystem genetics: A consequence of the extended phenotype. *Ecology*, 84, 559–573.

Whitlock, M. C., & Mccauley, D. E. (1999). Indirect measures of gene ow and migration: $F_{st} \neq 1/(4 nm + 1)$. *Heredity*, 82, 117–125.

Williams, J. L., Kendall, B. E., & Levine, J. M. (2016). Rapid evolution accelerates plant population spread in fragmented experimental landscapes. *Science*, 353, 482–485. https://doi.org/10.1126/science.aaf6268

Wright, J. T., Gribben, P. E., Byers, J. E., & Monro, K. (2012). Invasive ecosystem engineer selects for different phenotypes of an associated native species. *Ecology*, 93, 1262–1268. https://doi.org/10.1890/11-1740.1

Wright, S. (1931). Evolution in Mendelian populations. *Genetics*, 16, 97. https://doi.org/10.1093/genetics/16.2.97

Wright, S. (1937). The distribution of gene frequencies in populations. *Proceedings of the National Academy of Sciences of the United States of the America*, 23, 307.

Yoshida, T., Ellner, S. P., Jones, L. E., Bohannan, B. J., Lenski, R. E., & Hairston Jr., N. G. (2007). Cryptic population dynamics: Rapid evolution masks trophic interactions. *PLoS Biology*, 5. https://doi.org/10.1371/journal.pbio.0050235

Yoshida, T., Jones, L. E., Ellner, S. P., Fussmann, G. F., & Hairston, N. G. (2003). Rapid evolution drives ecological dynamics in a predator-prey system. *Nature*, *424*, 303–306. https://doi.org/10.1038/nature01767

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.