Title: **Individual-based eco-evolutionary framework: towards unifying ecology and evolution**

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Abstract

Evolution is increasingly found to be rapid and entangled with ecological processes in complex eco-evolutionary dynamics, calling for a common conceptual framework. Yet, ecological and evolutionary theory remain largely separated, which constrains the development of integrative research. To overcome this separation, I argue for treating the entangled dynamics as a single eco-evolutionary process rather than as separate ecological and evolutionary processes connected by feedbacks. I propose a unified conceptual framework that integrates ecological and evolutionary processes at population and community levels by considering which of them result from the same individual-based process. The resulting framework is a means to understand the entangled dynamics through the interaction of five basic eco-evolutionary processes: natural selection, drift, dispersal, gene transfer, and mutation. The framework allows systematic comparison of all ecological, evolutionary and eco-evolutionary theories and models. It provides simple means to discuss complex dynamics, and promotes a holistic approach to major topics including diversity, stability, and stochasticity. The framework thus presents a step towards conceptually uniting ecology and evolutionary biology.

Introduction

Ecology and evolutionary biology both study the dynamics of life on Earth, each from a different but overlapping perspective. They are recognized as closely related fields, but the conceptual connection between them remains surprisingly vague, often described by statements like “nothing in evolution or ecology makes sense except in the light of the other” (Pelletier et al., 2009).

Probably the main reason why ecological and evolutionary theory have developed largely in parallel for over a century was presumed separation of ecological timescales (over which population size and community composition change) from evolutionary timescales (over which allele frequencies in a population change) (Holt, 2005; Slobodkin, 1961). This view has been especially prevalent among ecologists (Holt, 2005). However, evidence for rapid evolution that occurs over a few generations has been accumulating in organisms ranging from bacteria to elephants (Campbell-Staton et al., 2021; Hiltunen et al., 2018; Ramos & Schiestl, 2019; Rudman et al., 2022). Evolution can therefore be entangled with ecological processes in complex eco-evolutionary dynamics (Bassar et al., 2021; Evans et al., 2020; Hairston et al., 2005; Hart et al., 2019; Hendry, 2017; Ives et al., 2020; Post & Palkovacs, 2009; Rudman et al., 2022; Urban et al., 2020)**.** For example, Ives *et al.* (2020) demonstrated perpetual eco-evolutionary dynamics in an insect pest and its natural enemies, while Hiltunen *et al.* (2014) found evidence for eco-evolutionary dynamics in about half of consumer-resource dynamics series they investigated. Consequently, increasing numbers of studies are emphasizing the need to consider ecology and evolution together (Barbour et al., 2022; Nosil & Gompert, 2022; Segar et al., 2020; Sigmund & Holt, 2021) to address pressing challenges like managing diseases, invasions and pests (Johnson et al., 2015; Karlson Green et al., 2020; Latombe et al., 2021; Lion & Metz, 2018), mitigating impacts of global environmental change (Faillace et al., 2021; Lasky, 2019; M. C. Urban et al., 2016), and conserving threatened biodiversity (Kahilainen et al., 2014).

Ecology and evolutionary biology have been coming closer together as genetic tools became more widely accessible and as appreciation for the importance of intraspecific variation grew in community ecology (Bolnick et al., 2011; Des Roches et al., 2018; Violle et al., 2012). But despite the achievements of evolutionary ecology and eco-evolutionary dynamics subfields, ecological and evolutionary theory have not yet converged. As a result, research findings in organismal biology are presented using two incomplete theoretical frameworks (Fig. 1). Researchers have found ways to bridge this gap practically using mathematical modelling (e.g. eco-evolutionary feedback, integral projection matrices, evolutionarily stable strategies) (Govaert et al., 2019; Hairston et al., 2005; Hendry, 2017; Lion, 2018; Smallegange & Coulson, 2013), but we lack a common framework which would show how existing theoretical concepts from ecology and evolutionary biology relate to one another. This makes communication between the two fields difficult and especially complicates the framing of eco-evolutionary studies and comparing eco-evolutionary dynamics models.

Eco-evolutionary feedback is a particularly widely used approach for modelling entangled ecological and evolutionary dynamics through partitioning dynamics into ecological processes, evolutionary processes, and their interactions (Govaert et al., 2019; Hairston et al., 2005; Post & Palkovacs, 2009). This is a powerful modelling approach, and it gradually became the main conceptual framework through which we currently understand eco-evolutionary dynamics as a feedback between two separate processes – ecology and evolution. However, this separation leads to emphasizing differences over commonalities and precludes the integration of ecological and evolutionary concepts. I argue here that a transition towards conceptualizing eco-evolutionary dynamics as a single eco-evolutionary process can present an important step in integrating ecology and evolutionary biology.

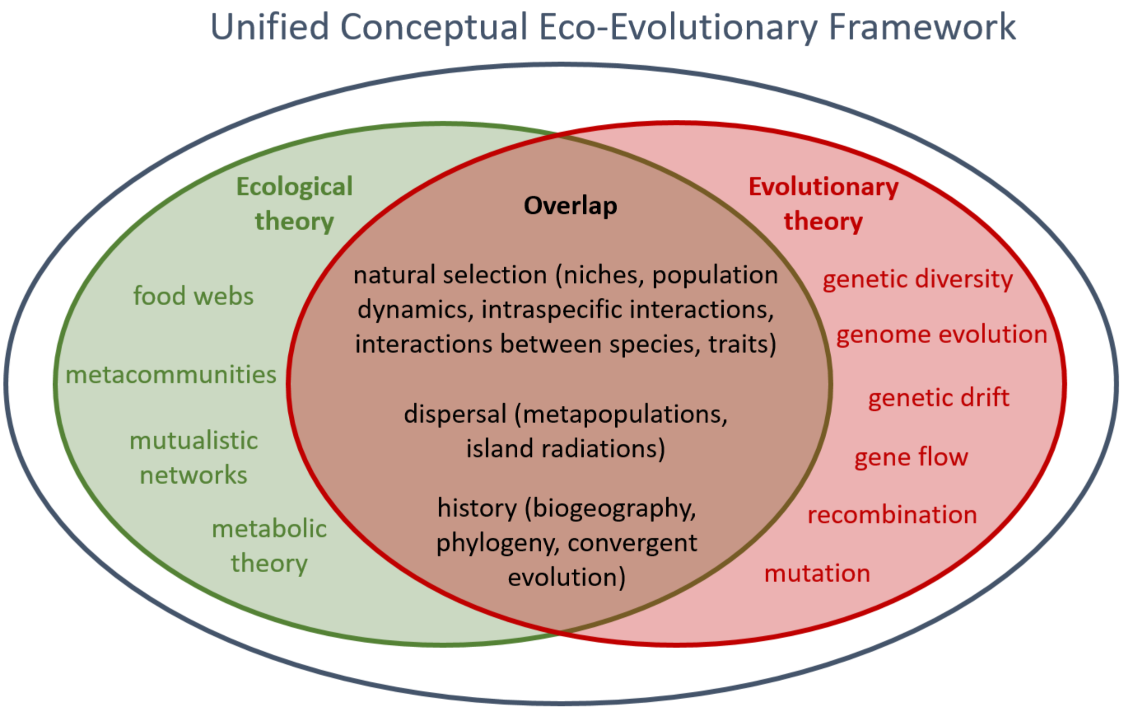

Fig. 1. Ecological and evolutionary theory largely overlap, although each field has developed unique aspects. *The emphasis in ecology is on interactions of organisms with their environment and between themselves, while the emphasis of evolutionary biology is on modification of genetic components of organisms through generations. The Unified Conceptual Eco-Evolutionary Framework unites both disciplines within a common overall framework. Alternatively, the new framework can be used for eco-evolutionary dynamics only, i.e. in situations where ecological and evolutionary processes interact at the same timescale.*

There has been a clear recent interest in developing a conceptual framework for eco-evolutionary dynamics (De Meester et al., 2019; Govaert et al., 2021; Lowe et al., 2017). Govaert *et al.* (2021) worked with four community level processes proposed by Vellend (2010) (discussed further in the Synthesis section) and four widely used population genetic processes, and examined how all 16 pairwise interactions between the two sets of processes influence eco-evolutionary dynamics. De Meester *et al.* (2019) emphasized the different levels of biological organization between which eco-evolutionary feedbacks can take place, and the need to consider more natural settings of multiple species, interactions and sites. Both of these frameworks work with the concept of feedback between two processes. On the other hand, Lowe *et al.* (2017) consider the eco-evolutionary process as not separable into ecology and evolution, focusing at the population level. The first two frameworks are conceptual, while the third discusses integrating mathematical formalisms from population genetics with demography.

While mathematically formalized theories are superior over conceptual frameworks in predictive power, there is a trade-off between the comparative and organizing roles of a framework and the predictive role of a theory or model. The predictive power of theories and models comes at the expense of additional assumptions. But having additional assumptions interferes with the comparison of theories with different sets of assumptions. The advantage in comparative and organizing roles is therefore why some conceptual frameworks, like Vellend's (2010, 2016) framework for community ecology, become widely used despite not being mathematical and predictive.

In this paper I build on the previous efforts, but offer a new perspective. I suggest that the underexplored individual level may be particularly useful for a common eco-evolutionary framework because of its ability to naturally link processes at higher levels of organization (populations, communities). I present such a conceptual framework that integrates existing population genetic and community ecology frameworks. I show how the new simple framework allows: i) systematically comparing, organizing, and relating existing theoretical concepts from ecology and evolutionary biology to one another (Table 1) to help ecologists and evolutionary biologists think about the other discipline as an integral part of theirs, ii) comparing and organizing eco-evolutionary theories and models (Table 2), iii) framing of empirical studies and models in a way that is accessible to all organismal biologists, and iv) connections between processes in biology across temporal scales and levels of biological organization. The framework can be used in two modes – as an environment for integrating concepts across entire ecology and evolutionary biology (encompassing both same-scale eco-evolutionary dynamics as well as theories and models which assume separation of scales), or in a more restricted sense for eco-evolutionary dynamics studies only. Organismal biology is very broad and there are many cases where one might prefer to address a problem using more restricted, purely ecological or evolutionary frameworks. The eco-evolutionary framework presented here should be seen as an alternative, rather than a replacement, of these traditional frameworks.

Synthesis

Theoretical concepts in ecology are disconnected and a widely accepted “general theory of ecology” does not exist (Sober, 2000; Vellend, 2016). In contrast, evolutionary theory is viewed as a largely homogeneous integration of current knowledge from different fields that is referred to as the modern evolutionary synthesis (Fisher, 1930; Huxley, 1942; Mayr, 1993), notwithstanding some continuing debates (e.g., Laland et al., 2014). This difference is partly due to different views of the same patterns and processes (Sober, 2000; Vellend, 2016). While ecology traditionally focuses on the *causes* of fitness differences between species and populations which are likely to be numerous and system-specific (e.g. temperature, nutrition, competition, social interactions, species interactions), evolutionary theory focuses on the *consequences* of fitness differences which are likely to be fewer in number and more general (e.g. directional, stabilizing or disruptive selection) (Vellend, 2016). Yet, Vellend (2010, 2016) demonstrated that it is possible to develop a general theory that focuses on *consequences* for community ecology, a subfield of ecology. He took inspiration from the practical framework of four basic processes used in population genetics and applied it analogically to ecological communities, one level of biological organization above populations. In doing so, he also shifted the focus of the theory from genes to organisms: basic processes became ecological, and evolution became one of the possible *causes*.

Focusing on *consequences* therefore seems important for building a general framework. Since *consequences* are more traditionally the focus of evolutionary theory, it makes the modern evolutionary synthesis a suitable backbone for a common eco-evolutionary framework (Schoener, 2011). At the core of the modern evolutionary synthesis lies population genetics with a widely used conceptual framework of four key processes (natural selection, genetic drift, gene flow, and mutation). The modern evolutionary synthesis already includes many aspects of ecology (see overlap section in Figure 1), although some important aspects are better developed in individual ecological theories. Such areas of well-developed ecological theory include species interactions, food webs, and community ecology in general (Johnson et al., 2015; Segar et al., 2020; Toju et al., 2017), spatial considerations like metapopulation and metacommunity theory (Leibold & Chase, 2018; Urban et al., 2020; M. Urban et al., 2008), and metabolic theory (Burger et al., 2019; Martinez, 2020) (Fig. 1).

The individual scale

Synthesis at individual level is underexplored but focus at this level may be particularly useful for a common eco-evolutionary framework. This is because higher levels of organization can be mechanistically linked by considering how patterns and processes perceived at population or community levels stem from an individual-based process. Likewise, individual scale can link ecology and evolutionary biology. In evolutionary theory, natural selection was originally defined as acting on individuals by Darwin and Wallace (1858), although different views exist on whether the individual level is the only or primary level of selection (see e.g., multilevel selection) (Kramer & Meunier, 2016). In ecological theory, individuals interact with conspecifics, heterospecifics, and the environment (Barker & Odling-Smee, 2014; Coulson, 2021; Nakazawa, 2020). It may be practically difficult to identify individuals in certain types of organisms (e.g., in grasses or endosymbiotic organisms, see Box 1), but most population and community theories work with individuals in one way or another (e.g., as population size), so these practical limits are not unique to an individual-level eco-evolutionary framework. An individual comprises the physical organism (the phenotype) and its genes (the genotype).

Developing the framework

Individuals are born, grow, move, interact with each other and the environment, reproduce, and die. This individual-based eco-evolutionary process of life is extremely complex and to understand it, biologists subdivide it into basic processes. Four basic processes (natural selection, genetic drift, gene flow, and mutation) are widely used in population genetics (Hartl & Clark, 1997; Lowe et al., 2017) and Vellend (2010, 2016) showed that an analogous framework of four basic processes can be used in community ecology (selection, ecological drift, dispersal, and speciation). This raises the possibility of moving from the analogy towards integration of these frameworks (Fig. 2). If the current population genetics and community ecology theories are comprehensive when considered together, eco-evolutionary dynamics can be fully described using eight basic processes – four at the population level and four at the community level (Fig. 2A). Recently, Govaert *et al.* (2021) developed an eco-evolutionary framework along this line of thought, taking the four population level and four community level processes and examining all 16 pairwise interactions between them.

Here I was interested if the synthesis could go further, asking if any of the eight processes are redundant for describing eco-evolutionary dynamics. This is likely to be the case given that the four community processes were developed as an analogy of the four population processes and because processes perceived at community level already include processes happening in populations of the component species, indicating internal redundancy. Indeed, some of these processes are fundamentally equivalent when viewed as stemming from an individual-based process (Fig. 2B). Stochastic individual demographics results in both genetic drift (random changes in allele frequencies in a population) and ecological drift (random changes in community composition). Thus, there is only a single underlying process of stochastic demography (called “drift” here), and population genetics primarily focuses on the genetic consequences, while community ecology focuses on the organismal consequences. Natural selection likewise acts on individuals (Darwin & Wallace, 1858). Selection within a community, defined by Vellend (2016) as “the deterministic fitness difference between individuals of different species”, is therefore only a summation of natural selection for a given species (net outcome of selection integrated across all individuals within each species’ population), and not a separate process.

Merging the remaining processes (gene flow, mutation, dispersal, and speciation) is not as direct (Fig. 2B). Aspects of gene flow caused by movement can be merged with dispersal because they both result from the same process: movements of individuals. When an individual moves into a community, population genetics perceives this as a change in genetic composition of the population of that species, while community ecology perceives this as a change in community structure based on the species identity and traits of the individual. However, gene flow within populations also includes consequences from gene transfer between individuals. Gene transfer cannot be directly merged with the community level processes and I therefore propose to treat it separately. Speciation (evolution of reproductive isolation) is treated phenomenologically by Vellend (2010, 2016) and therefore cannot be directly merged with one of the population genetic processes. Vellend (2010, 2016) treats speciation as the appearance of new variants at the community level (i.e. species) as an analogy to mutation which results in appearance of new variants at the population level (i.e. genotypes). In the new framework described here, speciation is treated mechanistically as a step in the individual-based eco-evolutionary process. Specifically, speciation results from the interaction of some or all the five basic processes (e.g., disruptive selection, lack of dispersal, or incompatibility caused by drift, non-random gene-transfer or mutation). Finally, mutation does not have a direct mechanistic counterpart among community level processes. Thus, all dynamics of organismal life can be described using interactions of only five basic processes: natural selection, drift, dispersal, gene transfer, and mutation (Fig. 2C). These basic processes interact with each other to produce the eco-evolutionary process.

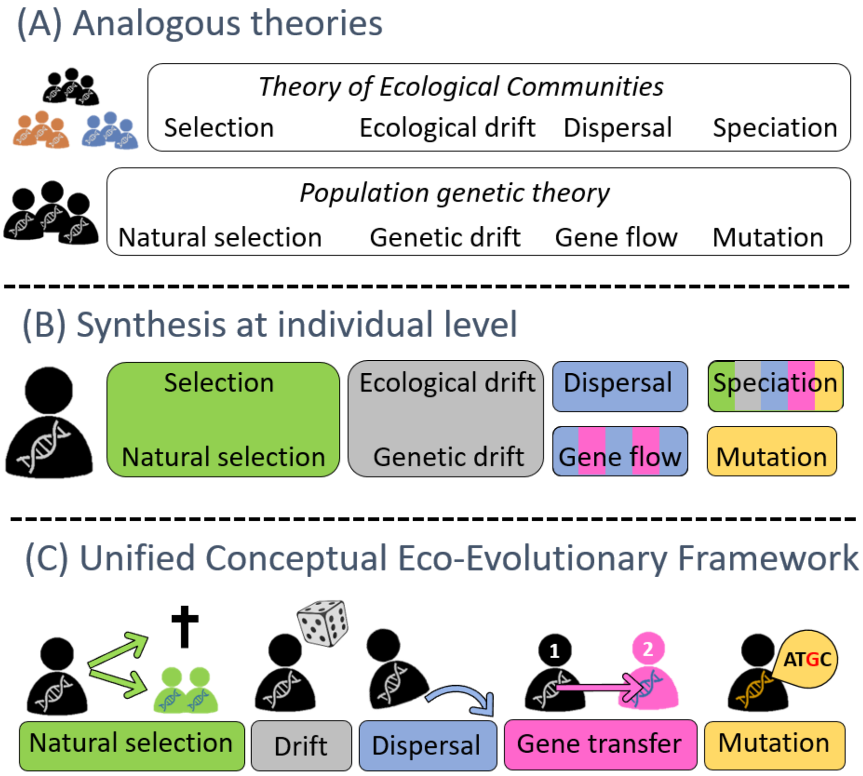

Fig. 2. Development of the framework. *(A) Basic processes specified in the Theory of Ecological Communities (Vellend, 2016) and population genetics theory (Hartl & Clark, 1997). (B) Pairs of community and population level processes that are redundant between the two theories when considered to be a consequence of the same individual-based process are colored the same. Gene flow at the population level is the product of up to two basic processes: movement of individuals and gene transfer between individuals. Speciation is a step in the eco-evolutionary process and thus results from up to all the five basic processes. (C) Overview of the new unified conceptual eco-evolutionary framework that incorporates five individual-based basic processes to sufficiently and fully describe the dynamics of organismal life.*

From the viewpoint of evolutionary theory, the new framework might be seen as a minor tweak to population genetic framework (shifting focus to the individual level and splitting one process). This is encouraging, because it means that it is possible to integrate ecological and evolutionary theory with a simple framework. It shows how close ecology and evolutionary biology really are. Yet, the focus on individual level is important because it allows a mechanistic integration of processes at population and community levels, as well as ecological and evolutionary views. The framework therefore goes beyond a semantic and phenomenological integration that would only use more general terms for similar processes operating at different levels (e.g., by calling both "genetic drift" and "ecological drift" generally just "drift" without mechanistically integrating them). Rather, the new framework shows that both aspects of drift result from the same process of stochastic individual-level demographics. Further, the split of gene flow into dispersal and gene transfer allows the integration of ecological theories (which often consider dispersal but never gene transfer) with modern evolutionary synthesis.

In the following section I redefine the processes at individual level to clarify their meaning within the new framework. Only in the case of natural selection this is not necessary because it has already been defined at individual level.

Defining the five basic processes at the individual level:

Natural selection maintains its original meaning in the proposed framework and is defined at the individual level by Darwin and Wallace (Darwin & Wallace, 1858). Natural selection is the differential survival and reproduction of individuals as a result of their traits, and consequently represents deterministic demography. Natural selection is a very broad process, encompassing interactions of individuals with the environment, as well as all types of interactions (trophic, competitive, mutualistic, and cooperative) with conspecifics and heterospecifics. Natural selection usually results from multiple selection pressures acting simultaneously on multiple phenotypic traits of an individual (Toju et al., 2017).

Drift is defined here as the stochastic survival and reproduction of individuals that concurrently results in genetic drift (stochastic changes in allele frequencies) and ecological drift (stochastic changes in community composition). A stochastic death of an individual can thus lead to a loss of an allele from a population but also potentially to a loss of entire species from a community. Drift is particularly important in small, isolated populations and communities that are thus also often endangered. Drift is the stochastic counterpart of deterministic natural selection and plays an important role in understanding neutral dynamics and stochasticity (Hubbell, 2001; Kimura, 1983; Nosil et al., 2020). See Box 2 for discussion on alternative treatments of drift within the framework.

Dispersal is defined here as the movement of individual organisms which concurrently results in change in genetic diversity at the population level and in species composition at the community level. Dispersal is closely associated with landscape structure, and the extent of dispersal results in complex consequences for eco-evolutionary dynamics (Urban et al., 2020). The importance of spatially explicit treatments of organismal dynamics is emphasized in metapopulation and metacommunity ecology (Leibold & Chase, 2018; M. Urban et al., 2008) and geographic mosaic theory (Thompson, 2005; Toju et al., 2017).

Gene transfer is defined here as the transfer of genetic information from one individual to another and can occur both vertically and horizontally. Vertical gene transfer through heredity from parent to offspring is tied with reproduction (a component of natural selection). Practically, it makes sense to discuss gene transfer as a separate process when offspring genome is different from parent, i.e. when reproduction is not clonal. Horizontal gene transfer is separate from reproduction and is most relevant in microorganisms where it can lead to transfer of genetic information between individuals (Thomas & Nielsen, 2005) and thus to spread of an important trait such as antibiotic resistance in a population or community. Differences in gene transfer mechanisms are key for understanding speciation among different taxa and largely determine how well-defined units are formed by organisms (e.g., species, varieties, and strains).

Mutation is defined here as the change in the genome of an individual and therefore can be regarded as an individual-based process with population and community level consequences. The range of possible mutation types is very broad and can include single nucleotide changes, structural changes comprising insertions, deletions, gene duplications, and chromosomal rearrangements, in addition to whole genome duplications and epigenetic changes (e.g., DNA methylation). Mutations are typically heritable, but not in all instances. For example, mutations in somatic cells of multicellular organisms with germ line (e.g., animals) are not heritable.

Many aspects of eco-evolutionary dynamics result from interactions among multiple basic processes. For example, sexual reproduction and sexual selection arise from the interactions between natural selection and gene transfer processes. Similarly, gamete movement (e.g., pollen dispersal) results from the interaction of dispersal and gene transfer processes. Further, selection in a metacommunity involves interactions between natural selection and dispersal processes.

Applying the framework

The new framework described here integrates ecological and evolutionary theories through focus on a single underlying individual-based eco-evolutionary process. The framework thus: i) allows comparison of ecological, evolutionary and eco-evolutionary concepts, ii) facilitates the design and increases reach of empirical studies and mathematical models, iii) connects processes in biology across scales and levels of biological organization, and iv) fosters a holistic perspective of ecology & evolution.

The new framework takes inspiration from Vellend’s (2010, 2016) framework which proved to be useful in improving communication and comparing theories within community ecology. The exact number of the basic processes in the framework is arbitrary to some extent, but I chose to focus on integrating the processes which are already widely considered at the population and community levels (Fig. 2). Like Vellend’s (2010, 2016) framework, the framework presented here is not predictive – it is a tool for discussing, comparing, organizing, clarifying and developing concepts, and for communicating research. Just the scope of the new framework is much wider, encompassing ecology and evolutionary biology. The new framework only assumes that population and community level processes result from an underlying individual-based process. Vellend (2010, 2016) specified his framework for horizontal communities (i.e. one trophic level), but the framework presented here does not have this restriction and can be applied to interactions between multiple trophic levels, which are an important aspect of eco-evolutionary dynamics.

Comparison of concepts

The proposed framework allows, for the first time, comparison of all theories and models across ecology and evolutionary biology using five basic eco-evolutionary processes, thereby making explicit how existing concepts relate to one another. A first step in this synthesis is the comparison of the basic processes considered in existing theories and models. In Table 1, I illustrate such a comparison for an arbitrary selection of ecological, evolutionary, and eco-evolutionary theories and models, but others could be easily added. From the comparison it appears that ecological theories tend to include fewer basic processes, but in greater detail. In contrast, existing evolutionary theory includes all five basic processes, but with a less comprehensive treatment of interaction networks (a component of natural selection) and spatial considerations (a component of dispersal). Most eco-evolutionary theories and models include most basic processes, at least in simple forms, although some do not consider gene transfer. A second step in the synthesis is a comparison of how each basic process is considered in theories and models and how individuals are considered. A detailed comparison of selected eco-evolutionary theories and models is presented in Table 2. For example, more general theories consider natural selection as multiple types of interactions acting on multiple traits of an individual (Coulson, 2021; Thompson, 2005), while specific models typically consider natural selection acting on a single trait like competitive ability (Rosindell et al., 2015). Dispersal is implemented in models with varying complexity from one dimensional gradient (Pontarp et al., 2019) to spatially explicit metacommunities (Toju et al., 2017). In theories, dispersal is given a varying degree of focus, ranging from brief consideration (Coulson, 2021) to a strong emphasis

(Thompson, 2005). Models generally focus on the organismal characteristics of individuals (Pontarp et al., 2019; Rosindell et al., 2015), their genetics (Quilodrán et al., 2020), or both (Coulson, 2021).

The comparison in Tables 1 and 2 reveals that theories and models often don’t consider the same processes, or consider processes differently. Such a comparison makes assumptions clearer; when a theory or model does not consider a process, it assumes that this process is not important for the resulting dynamics. Thus, a comparison of concepts through the lens of the five basic processes can help researchers from different backgrounds and subfields better understand results from other subfields where different theories are likely used to present results. The framework also provides an accessible point of entry into organismal biology for students and researchers in other disciplines by clarifying the relationships between existing concepts.

		Basic processes					
Theory or Model	**Reference**	**NS**	**Dr**	**Di**	**GT**	**Mu**	**Notes**
Ecological							See Vellend 2016 for extensive table of community ecology theories
Theory of ecological communities	Vellend 2016	NS	Dr	Di	GT	Mu	Explains community patterns. GT and Mu part of Speciation (see Fig.2)
Metacommunity ecology	Leibold & Chase 2018	NS	Dr	**Di**			Metacommunities and scale as overreaching concepts in ecology
Unified neutral theory of biodiversity and biogeography	Hubbell 2001		**Dr**	Di		Mu	Community assembly through neutral processes without selection
The theory of island biogeography	MacArthur & Wilson 1967		Dr	Di			Explains community structure by colonization and extinction
Niche theory	Chase and Leibold 2003	NS					Explains trait differences in a community
Metabolic theory of life history	Burger et al. 2019	NS					Explains life-history trade-offs using metabolism and demography
Allometric trophic networks	Martinez 2020	NS					Explains community structure using trophic level and body size
Evolutionary							See e.g. Hartl & Clark 1997 for specific population genetic models
Population genetic theory	Hartl & Clark 1997	NS	Dr	Di	GT	Mu	Dispersal and gene transfer treated together as gene-flow
Neutral theory of molecular evolution	Kimura 1983		Dr			Mu	Focus on molecular evolution
Modern evolutionary synthesis	Huxley 1942, Mayr 1993	NS	Dr	Di	GT	Mu	Not integrated with ecological theory
Eco-evolutionary							
Geographic mosaic of coevolution	Thompson 2005	**NS**	Dr	**Di**	GT	Mu	Verbal synthetic framework, predictions for different interaction types
Co-evolution in metacommunities	Toju et al. 2017	**NS**	Dr	**Di**	GT	Mu	Species rich interaction networks in spatially explicit context
Evolving meta-communities	Urban et al. 2008	NS	Dr	**Di**	GT	Mu	Verbal synthetic framework strongly emphasizing role of dispersal
Species range: maladapted gene flow	Kirkpatrick & Barton 1997	NS		**Di**			Gene flow can prevent species range expansion
Unified theory of ecology and macroevolution	Rosindell et al. 2015	NS	Dr			Mu	Focus on macro scale diversity patterns
Mechanistic eco-evolutionary model	Pontarp et al. 2019	NS	Dr	Di		Mu	Focus on explaining latitudinal diversity gradient
Population genetics and community ecology	Overcast et al. 2019		Dr	Di		Mu	Double neutral model
Species abundance, genetic and functional diversity	Overcast et al. 2021	NS	Dr	Di		Mu	Focus on functional diversity in a community
Genome evolution: population genetics + demography	Quilodrán et al. 2020	NS	Dr	Di	GT	Mu	Focus on evolution of genomic islands of divergence
Eco-evo equilibria and transitions between them	Coulson 2021	NS	Dr	Di	GT	Mu	Synthetic modelling framework
Species interactions and eco-evolutionary dynamics	Åkesson et al. 2021	NS		Di	GT		Biotic interactions mitigate impact of climate change

Table 1. Overview of selected theories according to the basic processes that they consider. *Processes that are emphasized in a given theory are shown in bold. NS: Natural selection, Dr: Drift, Di: Dispersal, GT: Gene transfer, Mu: Mutation.*

Framing individual studies

Some researchers already comfortably embrace both ecological and evolutionary theory, but many do not yet do so. The new framework allows conveying ecological, evolutionary, and eco-evolutionary studies to all organismal biology researchers through the five basic processes. Adopting a general eco-evolutionary framework will thus make studies more widely accessible. Using basic processes for this purpose is intuitive, since they have long been applied in population genetics (Hartl & Clark, 1997) and following the publication of Vellend's (2010, 2016) framework commonly also in community ecology. As one example from hundreds of studies, Pontarp *et al.* (2019) used Vellend's framework to compare hypotheses about latitudinal gradient of diversity in communities. A similar study could now use the new framework presented here, taking the advantage of the fewer assumptions and more explicit link with population level processes. The entries in Tables 1 & 2 illustrate how the framework can be used to present a study: first, in general, in the terms of the basic processes considered (Table 1), and then more specifically, explaining how each process is considered (Table 2). When planning empirical studies, it is useful to have such a framework that lists all the basic processes, as it helps to identify which processes should be considered in a given study and at what level of detail.

Mathematical models

The proposed framework is conceptual, which allows it to be based on a single assumption of an individual basis of eco-evolutionary processes. But, predictive mathematical models of eco-evolutionary dynamics can be developed and described with the help of the framework, considering which processes to include and in what form, along with justifying any additional assumptions. The framework can also easily accommodate models that have been previously described using the concept of eco-evolutionary feedbacks, as demonstrated by a comparison of selected eco-evolutionary theories and models in Table 2.

Linking scales and levels of organization

The framework is based on the assumption that all processes observed (perceived) at higher levels of organization (i.e., populations and communities) can be viewed as resulting from an individual-based eco-evolutionary process. Individual-based models consequently naturally fit the framework, and these modelling approaches are quickly becoming accessible as computational power increases. However, theories and models at the population (e.g., Åkesson et al., 2021) and community (e.g., Vellend, 2016) levels are equally useful when the underlying assumptions are carefully compared with expected individual-based processes. The framework further implies that all processes at large spatial and temporal scales result from an individual-based eco-evolutionary process. Any process perceived at the macro eco-evolutionary level (e.g., diversification) is consequently a summation of underlying micro eco-evolutionary processes that have occurred over long periods of time over large geographic areas (Kutschera & Niklas, 2004). Nevertheless, huge differences in scale lead to macroecology and macroevolution being mostly studied with species as the focal unit, and without a direct connection to micro-scale processes that operate at the level of populations and individuals (McGill et al., 2019). Indeed, the gap between studies of micro and macro-scale processes has been suggested to be larger than that between ecology and evolutionary biology (McGill et al., 2019). However, emerging models that explicitly incorporate micro-scale eco-evolutionary processes provide promising insights into patterns observed at larger scales, for example by explaining mechanisms that lead to the latitudinal diversity gradient (Pontarp et al., 2019).

The newly proposed framework connects organismal ecology and evolution with other biological disciplines. For example, processes operating below the individual level (e.g., at the organellar or cellular level) are intrinsically associated with the framework via their effects on fitness that are evaluated at the individual level. The framework can also be linked to developmental biology through trait changes of individuals during their development (see e.g. Smallegange, 2022). In addition, ecosystem and environmental sciences are connected with the framework through the individual-based eco-evolutionary process interacting with the environment, either through environmental influences or by modifying the environment (Barker & Odling-Smee, 2014; Matthews et al., 2014).

A holistic approach to ecology & evolution

Through the comparative and organizing function described above, the framework fosters a holistic approach to ecology & evolution. Diversity and stability are examples of fundamental topics which have typically been separately addressed in ecology and evolutionary biology, despite being mechanistically connected. This is because we lacked a framework clarifying the connection between the two fields. The framework presented here makes a first step towards integrating these concepts by linking ecological and evolutionary theory. Maintenance of diversity in communities and of phenotypic and genetic diversity in populations are mechanistically connected by eco-evolutionary dynamics in the short term, and by speciation in the long term. Therefore they should be considered together in a holistic view of biodiversity maintenance (Cannon & Lerdau, 2022; Des Roches et al., 2018; Raffard et al., 2019; Smee et al., 2021; Theodoridis et al., 2020). Similarly, the concepts of ecological stability (Kéfi et al., 2019) and evolutionarily stable strategies would benefit from integration that would concurrently consider changes in population sizes and trait evolution. The framework thus provides an environment for integrating concepts from the separate fields.

Ecology can contribute well-developed concepts to the proposed synthesis, including metabolic theory, interaction networks, and metacommunities. For example, the Metabolic Theory of Ecology, together with its extensions to life history (Burger et al., 2019) and trophic networks (Martinez, 2020) are predictive theories that currently only consider natural selection. Consequently, the theory could become more comprehensive if its assumptions of metabolic constraints were extended to all five basic eco-evolutionary processes identified above. The proposed framework thus provides an environment for formulating predictive verbal and mathematically formalized theories via additional assumptions, and could ultimately catalyze the merging of ecological and evolutionary theory. The proposed framework could also help connect general theory with more specialized disciplines like epidemiology (Grenfell, 2004; Lion & Metz, 2018) by considering interactions between very different organisms (e.g., between animals and microorganisms) within a single framework.

Conclusion

The new framework presented here brings a mechanistic link between population and community processes through the extension of the individual basis of natural selection (Darwin & Wallace, 1858) to all basic ecological and evolutionary processes. The framework clarifies relationships between existing theories (Tables 1 & 2) and allows simple descriptions and comparisons of naturally complex dynamics. A further unification of ecological and evolutionary biology will require updating important concepts within an eco-evolutionary framework. The arrangement of basic processes might also keep developing. Yet, even the demonstration that a single framework can be built for ecology and evolutionary biology encompassing all particular theories and models is in itself an important step towards better communication between the fields. The integrative approach is likely to become increasingly useful as genomic tools for non-model organisms will become even more widely accessible. Ultimately, combined insights from ecology and evolution will help us better understand and predict complex processes occurring in nature.

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Text boxes

Box 1: Individuals in symbiosis.

Defining individuals can be complicated when individuals are not physically separated from others and this situation is common in nature (e.g., endosymbiotic bacteria and viruses, parasites, lichens, endophytic fungi, and mycorhysis). Nevertheless, these symbioses only represent strong interactions between individual organisms and whether symbiotic individuals need to be treated as individual organisms or whether a simplified assumption of unity could be applied would depend on the specific research question. Indeed, these distinctions have always been necessary, although the new framework attracts attention to them by focusing at individual level processes. It is often useful to consider multiple organisms as a single individual when they are not physically separable, such as aphids and their obligate nutritional symbiotic bacteria. It should be noted that this simplification will not hold over time scales of millions of years, as even obligate symbionts could be eventually replaced by other symbionts (Bennett & Moran, 2015). Similarly, mitochondria were separate individuals 1.5–2 billion years ago (Martin et al., 2015), and most studies treat them as components of eukaryotic individuals. Yet, studies of eukaryotic taxa where some lineages have lost mitochondria (Karnkowska et al., 2016), or those that study conflicts between nuclear and mitochondrial genome could meaningfully treat mitochondria as separate individuals.

Box 2: Stochasticity.

In the main text, the meaning of drift close to common usage is maintained for easier comparison of existing theories and models (Table 1). However, it should be noted that the role of stochasticity in the dynamics of organismal life is wider and would perhaps merit a more comprehensive treatment. This is especially true because the importance of stochasticity is widely debated, including the degree to which perceived stochasticity is real or only the result of an incomplete understanding of deterministic processes (Nosil et al., 2020). Dispersal, gene transfer, and mutation all have deterministic and stochastic components (as described in more detail below). It could consequently be argued that each process warrants separation of deterministic and stochastic components into separate basic processes, as is the case with natural selection and drift. Such a treatment would result in eight basic processes including four deterministic processes (natural selection, dispersal, gene transfer, and mutation) and four stochastic processes (drift, stochastic dispersal, stochastic gene transfer, and stochastic mutation). Alternatively, all stochasticity could be represented by a single basic process, but this would require extension of the common meaning of drift to include stochastic aspects of dispersal, gene transfer, and mutation. A third option would be to treat drift as a stochastic part of natural selection. Natural selection would thus include both deterministic and stochastic processes like dispersal, gene transfer, and mutation currently do. The latter solution may be the most practical option because all demographics (i.e., birth, death, and reproduction) would then be included in a single basic process, in contrast to the current concept where deterministic demography is natural selection and stochastic demography is drift.

Dispersal is often assumed to apply to random individuals from the population, but can be biased, for example towards larger individuals (Jenkins et al., 2007). Dispersal commonly interacts with natural selection, like when locally fitter individuals migrate (Edelaar & Bolnick, 2012; Lowe & McPeek, 2014).

Gene transfer is often thought of as stochastic process (e.g., random recombination of alleles), but also has deterministic aspects (e.g., the preference of alleles in meiotic drive).

Mutation is primarily considered as stochastic process, but also has deterministic aspects, including differences between organisms (e.g., dependence on genome size and differences between bacterial and eukaryote cells (Lynch, 2010)) and between environments (e.g., radiation resulting in increased mutation rates).

Table 2. Detailed comparison of selected eco-evolutionary theories and models.

		Basic processes					Individual			Basic processes in detail					
Eco-evolutionary Theory or Model	Reference	NS	Dr	Di	GT	Mu	organismal aspect	genetic aspect	genotype-phenotype link	Natural selection	Drift	Dispersal	Gene transfer	Mutation	Further notes
Geographic mosaic of coevolution	Thompson 2005	**NS**	Dr	**Di**	GT	Mu	multiple traits	multiple genes	dependent on biotic and abiotic environment, often polygenic	multiple selection pressures, different between local communities and environments	considered	species are "collections of genetically differentiated populations", implying limited dispersal	interacts with dispersal to reinforce population differentiation	considered	
Co-evolution in metacommunities	Toju et al. 2017	**NS**	Dr	**Di**	GT	Mu	multiple traits	multiple genes	dependent on biotic and abiotic environment, often polygenic	natural selection takes place in a network of interactions	considered	explicit and discrete space - metacommunities; limited dispersal	considered	considered	focus on "Metacomunity hub" species for feasibility
Evolving meta-communities	Urban et al. 2008	NS	Dr	**Di**	GT	Mu	multiple traits	not detailed	not detailed	focus on how natural selection interacts with dispersal	considered	explicit and discrete space - metacommunities	briefly considered	considered	dispersal centered framework
Species range: maladapted gene flow	Kirkpatrick & Barton 1997	NS		Di			one trait	many loci of small effect	quantitative genetics	mortality caused by maladaptation and density dependence. Gradient of optimum phenotype across the habitat	not considered	stochastic dispersal. Continuous space	not considered	not considered	
Unified theory of ecology and macroevolution	Rosindell et al. 2015	NS	Dr			Mu	single trait - competitive fitness category	single locus	absolute	Probability of reproduction proportional to fitness category. Stength of selection set by parameter	random death of one individual per time step	not considered	not considered	mutation rate set by parameter - probability of changing fitness category	constant community size set by parameter. Speciation is phenomenological result of mutation (grouping individuals of similar trait value)
Mechanistic eco-evolutionary model	Pontarp et al. 2019	NS	Dr	Di		Mu	single trait - thermal optimum	single locus	absolute	thermal adaptation and competition	population size dependent extinction risk	probabilistic dispersal to nearest region. Environment explicit as one-dimensional gradient	not considered	mutation creates species with different thermal optimum value	processes modelled at the level of species. Speciation is phenomenological result of mutation.
Population genetics and community ecology	Overcast et al. 2019		Dr	Di		Mu	no traits (neutral model)	single gene	no link	not considered	random death of one individual per time step	colonization rate as a parameter. Environment is a single focal island and mainland	not considered	infinite-sites model assuming invertebrate mitochondrial divergence rate	focus on species abundance distributions and community genetic diversity. Combination of a forward time ecological model and backward time genetic coalescence model
Species abundance, genetic and functional diversi	Overcast et al. 2021	NS	Dr	Di		Mu	single trait - environmental filtering or competition	single gene to whole genome	ecological trait linked to single locus. Separately, genetic variation is neutral without link to phenotype	environmental filtering or competition. Strength of selection vs. neutral process set by parameter	random death according to parameter	multiple local communities within a metacommunity	not considered	point mutation	intraspecific variation not modelled. Fixed total metacommunity size. Speciation phenomenological
Genome evolution: population genetics + demogr	Quilodrán et al. 2020	NS	Dr	Di	GT	Mu	summary fitness phenotype, can extend to separate traits	diploid males and females, any number of loci	any genotype-phenotype map, taking into account the environment	fitness function based on phenotype and density dependence	stochastic demography in fitness function	two populations which may or may not be linked	any mating system (primarily sexual)	considered in appendix	individual based forward in time model. Accomodates both deterministic and stochastic environments
Eco-evo equilibria and transitions between them	Coulson 2021	NS	Dr	Di	GT	Mu	multiple "resource accrual" traits	diploid males and females, any number of loci	any genotype-phenotype map, taking into account the environment	selection optimizes resource accrual traits and energy utilisation depending on biotic and abiotic environment	not explicitly mentioned, but can result from stochasticity in survival or probability density functions	mentioned, but not detailed	sexual	considered	equilibria defined as showing no persistent temporal trends. Assumes usually one dominant cause of death in a population. Does not include speciation. Considers development. Body size as key trait
Species interactions and eco-evolutionary dynamics	Åkesson et al. 2021	NS		Di	GT		temperature optimum mean and variance	many loci	quantitative genetics; variance has genetic and environmental contribution	interactions within and between trophic levels. Temperature dependent fitness and interspecific competition	not considered	explicit and discrete space - latitudinal gradient	modelled as trait change from dispersal	not considered	does not include speciation. Mate choice not linked with trait of interest (thermal tolerance)