# 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 suggest 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 reveals relationships between existing theories and models, provides simple means to discuss complex dynamics, and outlines 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) (Slobodkin 1961; Holt 2005). 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 (Hiltunen *et al.* 2018; Ramos & Schiestl 2019; Campbell-Staton *et al.* 2021; Rudman *et al.* 2022). Evolution can therefore be entangled with ecological processes in complex eco-evolutionary dynamics (Hairston *et al.* 2005; Post & Palkovacs 2009; Hendry 2017; Hart *et al.* 2019; Evans *et al.* 2020; Ives *et al.* 2020; Urban *et al.* 2020; Bassar *et al.* 2021; Rudman *et al.* 2022)**.** 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 (Segar *et al.* 2020; Sigmund & Holt 2021; Barbour *et al.* 2022; Nosil & Gompert 2022) to address pressing challenges like managing diseases, invasions and pests (Johnson *et al.* 2015; Lion & Metz 2018; Karlson Green *et al.* 2020; Latombe *et al.* 2021), mitigating impacts of global environmental change (Urban *et al.* 2016; Lasky 2019; Faillace *et al.* 2021), 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; Violle *et al.* 2012; Des Roches *et al.* 2018). 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 modelling approaches (e.g. eco-evolutionary feedback, integral projection matrices, evolutionarily stable strategies; Hairston *et al.* 2005; Hendry 2017; Lion 2018; Govaert *et al.* 2019), 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.

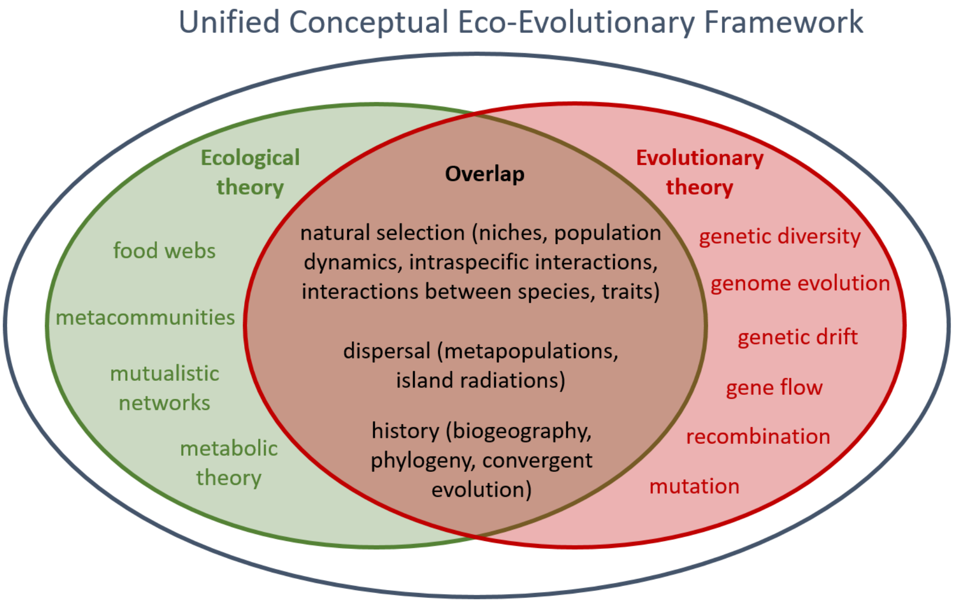


***Fig. 1. Ecological and evolutionary theory largely overlap, although each field has developed unique aspects.*** *The emphasis in ecology is on interactions of organisms with their environment and between themselves, while the emphasis of evolutionary biology is on modification of genetic components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

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 (Hairston *et al.* 2005; Post & Palkovacs 2009; Govaert *et al.* 2019). While this is a powerful modelling approach, such partitioning framework leads to emphasizing differences over commonalities and precludes the integration of ecological and evolutionary concepts. I argue here that a transition from conceptualizing eco-evolutionary dynamics as feedback between two separate processes towards a holistic framework of a single eco-evolutionary process can present an important step in integrating ecology and evolutionary biology.

In this paper, I suggest that underexplored individual level may be particularly useful for a common eco-evolutionary framework. I present one such framework that integrates existing population genetic and community ecology frameworks. I show how the new framework can be used to: i) relate 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) compare eco-evolutionary theories and models (Table 2), iii) frame empirical studies and models in a way that is accessible to all organismal biologists, and iv) connect 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, or in a more restricted sense for eco-evolutionary dynamics studies only. These two modes partly reflect whether same-scale eco-evolutionary dynamics is assumed to be the rule in organismal biology, or the exception. Further, organismal biology is very broad and there are many cases where one might prefer to address a problem using a more restricted ecological or evolutionary framework. The eco-evolutionary framework presented here should be seen as an alternative, rather than a replacement, of these more 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; Toju *et al.* 2017; Segar *et al.* 2020), spatial considerations like metapopulation and metacommunity theory (Urban *et al.* 2008, 2020; Leibold & Chase 2018), and metabolic theory (Burger *et al.* 2019; Martinez 2020) (Fig. 1).

*The individual scale*

I suggest that synthesis at individual level is underexplored and 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; Nakazawa 2020; Coulson 2021). 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 with a similar motivation to this study, examining all 16 pairwise interactions between each of the four population level and four community level processes.

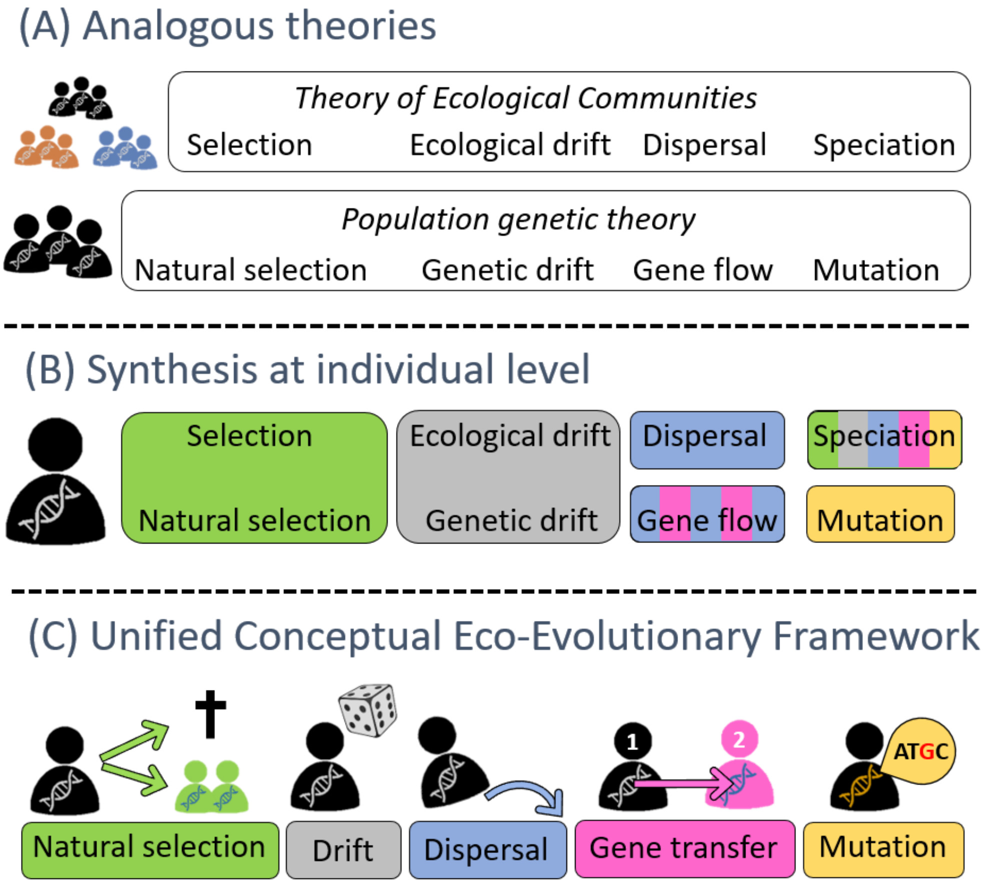


***Fig. 2. Development of the framework.*** *(A) Basic processes specified in the Theory of Ecological Communities (Vellend 2016) and population genetics theory (Hartl & Clark 1997). (B) Pairs of community and population level processes that are redundant between the two theories when considered to be 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.*

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 result 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.

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. 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 (Kimura 1983; Hubbell 2001; 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

(Urban *et al.* 2008; Leibold & Chase 2018) 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) fosters a holistic perspective of ecology & evolution, ii) allows comparison of ecological, evolutionary and eco-evolutionary concepts, iii) facilitates the design and increases reach of empirical studies and mathematical models, and iv) connects processes in biology across scales and levels of biological organization.

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 to some extent arbitrary, but I chose to focus on integrating the processes which are already widely considered on population and community level (Fig. 2). Like Vellend's (2010, 2016) framework, the framework presented here is not predictive – it is a tool for discussing, organizing, comparing, 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. Predictive power of theories comes at the expense of additional assumptions and there is therefore a trade-off between the organizing role of a framework and the predictive role of a theory. Note also that 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.

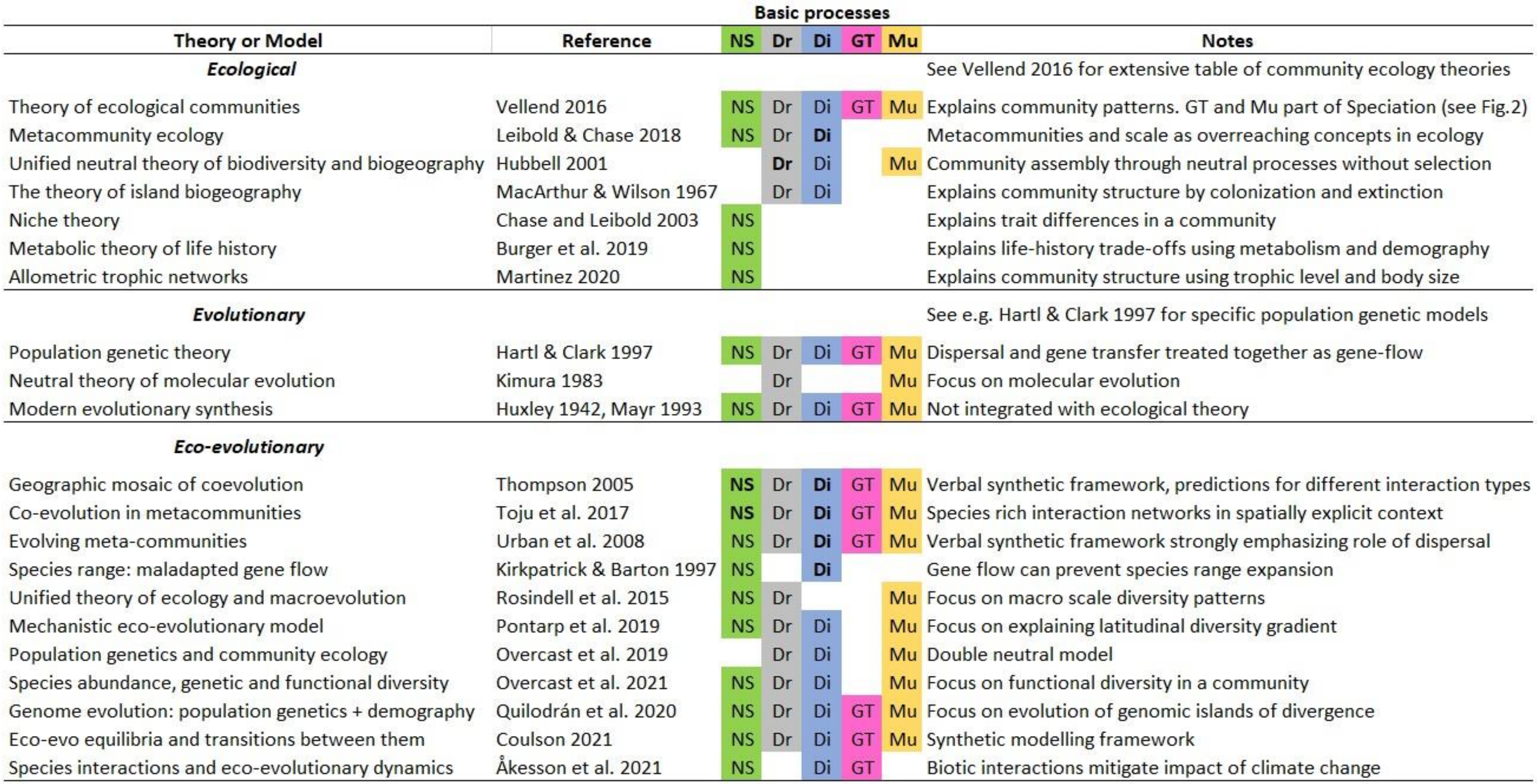
### *A holistic approach to ecology & evolution*

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 (Des Roches *et al.* 2018; Raffard *et al.* 2019; Theodoridis *et al.* 2020; Smee *et al.* 2021; Cannon & Lerdau 2022). 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, releasing the full power of the combined approach.

Ecology can also 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.

### *Comparison of concepts*

The proposed framework allows comparison and discussion 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 comparison for an arbitrary selection of ecological, evolutionary, and eco-evolutionary theories and models. A much broader range of theories and models could easily be added (see e.g., Hartl & Clark 1997; Vellend 2016). From this 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 the comparison of how each basic process is considered in theories and models and how individuals are considered. Such detailed comparison of eco-evolutionary theories and models is presented in Table 2. For example, more general theories consider natural selection as multiple interaction types acting on multiple traits of an individual (Thompson 2005; Coulson 2021), 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 treated variably from brief consideration (Coulson 2021) to strong emphasis (Thompson 2005). Models generally focus on the organismal characteristics of individuals (Rosindell *et al.* 2015; Pontarp *et al.* 2019), genetics (Quilodrán *et al.* 2020), or both (Coulson 2021). 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. The framework also presents 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. 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 framework that lists all the basic processes available, as it helps to identify which processes and in what detail should be considered in a given study.

*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, mathematical models of eco-evolutionary dynamics can be developed and described with the help of the framework, considering the 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). Considering interactions between all levels of organisation is necessary in eco-evolutionary dynamics (De Meester *et al.* 2019), and focus on individual level allows this by mechanistically linking population and community processes.

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. 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).

## 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 (as outlined in Comparison of Concepts section). 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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**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), but 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 + demogra | 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) |