

Opportunities to advance the synthesis of ecology and evolution

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Despite growing interactions between ecology and evolution, there still remain opportunities to further integrate the two disciplines, especially when considering multispecies systems. Here, we discuss two such opportunities. First, we suggest to relax the focus on the distinction between evolutionary and ecological processes. This focus is particularly unhelpful in the study of microbial communities, where the very notion of species is hard to define. Second, we propose that key processes of evolutionary theory such as adaptation should be exported to hierarchical levels higher than populations to make sense of biodiversity dynamics. Together, we argue that broadening our perspective of eco-evolutionary dynamics to be more inclusive of all biodiversity, both phylogenetically and hierarchically, will open up fertile new research directions and help us to address one the major scientific challenges of our time, i.e. to understand and predict changes in biodiversity in the face of rapid environmental change.

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Abstract

Despite growing interactions between ecology and evolution, there still remain opportunities to further integrate the two disciplines, especially when considering multispecies systems. Here, we discuss two such

opportunities. First, we suggest to relax the focus on the distinction between evolutionary and ecological processes. This focus is particularly unhelpful in the study of microbial communities, where the very notion of species is hard to define. Second, we propose that key processes of evolutionary theory such as adaptation should be exported to hierarchical levels higher than populations to make sense of biodiversity dynamics. Together, we argue that broadening our perspective of eco-evolutionary dynamics to be more inclusive of all biodiversity, both phylogenetically and hierarchically, will open up fertile new research directions and help us to address one the major scientific challenges of our time, i.e. to understand and predict changes in biodiversity in the face of rapid environmental change.

Although Darwin, the father of modern evolutionary biology, had a strong interest in ecological issues, ecology and evolution developed historically as separate scientific disciplines, each with its own set of concepts, methods and study objects (Futuyma 1986). While ecology is broadly concerned with the interactions between living organisms and their biotic and abiotic environment, evolutionary biology focuses on changes in the intrinsic characteristics, or traits, of these organisms through time under changing environments. As a result of this focus, evolutionary biology built a coherent body of theory that gave rise to the so-called “modern synthesis”. This synthesis integrated knowledge from genetics, palaeontology, systematics and morphology, but ecology played a relatively small role, even though the influence of ecological processes on evolution was recognised (Huneman 2019). By contrast, ecology developed a wide range of perspectives, from the dynamics of a single population to the functioning of the entire biosphere, but it is arguably still searching for a general synthesis that includes evolutionary thinking at all scales (Loreau 2010).

A number of attempts have been made to bring ecology and evolution together over the past 70 years (e.g. Pimentel 1961; Antonovics 1976). In particular, the recent emergence of the field of eco-evolutionary dynamics has greatly contributed to this effort by revealing how ecology affects evolution and, conversely, how evolution affects ecology (Fussmann *et al.* 2007; Schoener 2011; Hendry 2017; Govaert *et al.* 2019). We now know that emergent properties of communities and ecosystems, such as material cycling, functional complementarity between species and community stability, have the potential to affect evolutionary processes, just as evolution can affect ecosystem functioning (Loreau 2010; Borrelli *et al.* 2015; Calcagno *et al.* 2017; Aubree *et al.* 2020). Other advances that strengthen the links between ecology and evolution include consideration of concepts that could be relevant across the hierarchy of life from genes to ecosystems, such as heritability above the individual level (Shuster *et al.* 2006) and the role of trait-based intraspecific variability in community dynamics (Violle *et al.* 2012). Despite growing recognition of the interactions between ecological and evolutionary processes, however, there still remain opportunities to further integrate ecology and evolution, especially when considering multispecies ecological systems.

Here, we discuss two such opportunities. First, we suggest to relax the focus on the distinction between evolutionary and ecological processes. This focus is particularly unhelpful in the study of microbial communities, where the very notion of species is much harder to define than for macroorganisms. Second, we propose that key processes of evolutionary theory such as adaptation should be exported to hierarchical levels higher than populations to make sense of biodiversity dynamics. Together, broadening our perspective of eco-evolutionary dynamics to be more inclusive of all biodiversity, both phylogenetically and hierarchically, will open up fertile new research directions.

Microbes constitute a large part of the Earth’s biodiversity, displaying enormous abundance, phylogenetic diversity and functional importance (Whitman *et al.* 1998; Falkowski *et al.* 2008). One important aspect of their biology is that within-species evolutionary processes cannot be neatly separated from between-species ecological processes. While this distinction may generally make sense for large, complex, sexually reproducing multicellular eukaryotes, they are far less relevant for bacteria, archaea and other microbes, where asexual reproduction and gene transfer are widespread (Doolittle 1999). Although asexual reproduction and gene transfer do not preclude a taxonomic classification of microbes as their traits are phylogenetically conserved in a hierarchical fashion (Martiny *et al.* 2015), the species level in this hierarchy is ill-defined and differs from that used for most macroorganisms (Rossello-Mora & Amann 2001; Fraser *et al.* 2009). Therefore, there is no fundamental difference between changes in the abundance of different microbial “species” through time

— the traditional focus of community ecology — and changes in the relative frequency of different microbial “genotypes” — the traditional focus of evolutionary biology. Indeed, some classic examples of eco-evolutionary dynamics, such as Yoshida *et al.*’s (2003) predator-prey cycles driven by the “rapid evolution” of clonal algae, could be easily reinterpreted as simple ecological dynamics in which the abundance of different algal “species” changes. A similar issue arises in clonal multicellular organisms (e.g. parthenogenetic freshwater snails: Facon *et al.* 2008). Changes in species abundances and changes in phenotype frequencies generate the same type of effect, i.e. changes in mean trait values. Whether these changes in mean trait values take place at the population or community level is largely irrelevant in the case of microbes, as the two hierarchical levels cannot be distinguished unambiguously. Note that this also challenges the distinction between intra- and interspecific competition, which is widely regarded as a key factor explaining the maintenance of biodiversity (Chesson 2000).

Many studies have considered microbial evolution in the laboratory, where particular strains can be examined for new mutations and their effects on fitness (Lenski 2017). Under natural conditions in diverse communities, however, it is much more difficult to define what a microbial species is, and almost impossible to distinguish between standing genetic variation and new mutations. Recent advances in sequencing have revealed that natural microbial communities are not unstructured swarms of genotypes, but rather assemblages of coexisting, genetically distinct lineages (Arevalo *et al.* 2019; Chase *et al.* 2019). Further, the genetic differences between such lineages yield hypotheses about the ecological distinctions between them (Arevalo *et al.* 2019). It is even possible now to detect evolution of free-living microbes in the wild. For instance, a strain of *Curtobacterium*, dominant in the surface soil, was inoculated into microbial “cages” and transplanted into five sites across a temperature and precipitation gradient (Chase *et al.* 2021). After just six months in the field, the strain accumulated genomic mutations, and some mutations occurred in parallel across sites, indicating that some mutations were likely adaptive to the new conditions. Together, these advances reveal a previously unknown structure of fine-scale diversity in microbial communities, while clarifying the absence of a distinct species boundary, which makes it difficult to apply classic evolutionary principles.

To overcome this difficulty, we suggest that more attention should be paid in both ecology and evolution to the general fact that evolutionary and ecological dynamics can have similar effects, to the point of being sometimes indistinguishable in microbes. This could contribute to the development of a more integrative conceptual framework that crosses the traditional disciplinary boundaries. Microbes invite us to rethink what ecology is and what evolution is (see also West *et al.* 2006), and we feel this invitation should be seen as a great opportunity rather than a problem.

The second aspect we wish to highlight is that, to achieve greater integration of ecology and evolution, many concepts used in either discipline could be profitably generalised to the other — they would serve as ‘boundary objects’ (Star & Griesemer 1989) in their conceptual unification. Nosil *et al.* (2021) provided an example when applying the concepts of stability and resilience, imported from ecology, to evolutionary biology. Here we propose to go in the other direction by extending the concept of adaptation from evolution to ecology. In evolutionary biology, ‘adaptation’ *sensu stricto* is generally considered as a process leading to higher fitness as a result of natural selection (Williams 1966; Gardner 2017), while ‘adaptedness’ denotes the state of being adapted, but the distinction is not always so clear (Lewens 2016). Moreover, adaptation is traditionally assumed to take place at the individual or genotype level. Even such a strong proponent of individual-level selection as Williams (1966), however, distinguished between ‘organic adaptations’ and ‘biotic adaptations’, which help perpetuate a group or population and open up the possibility of clade selection, a very controversial issue (Eldakar & Wilson 2011; Goodnight 2015; West *et al.* 2021).

It would be particularly useful to extend and generalise the concept of adaptation to wider ecological contexts. For example, soil microbial ecologists use this concept at the community level to describe an increase in overall microbial activity as temperature changes, an approach that integrates across the mechanisms and timescales involved (Bradford 2013; Nottingham *et al.* 2021). This extension of the adaptation concept is fully consistent with that formally proposed by hierarchical adaptability theory (Conrad 1983; Lekevičius &

Loreau 2012). Hierarchical adaptability theory generalises adaptation to any process that results in improved performance in response to environmental change in a multilevel hierarchical perspective, from molecules to ecosystems. These responses range from differential gene activity (molecular-level mechanism), through phenotypic plasticity (individual-level mechanism) and differential reproduction of genotypes (population-level mechanism), to changes in species abundance (community- or ecosystem-level mechanism). This theory could be further extended to include the evolutionary, ecological, and social changes that reduce the vulnerability of social and ecological systems to environmental change (Moore & Schindler 2022).

These extensions, of course, raise the question of how to measure performance below or above the hierarchical level of the individual organism. In evolutionary theory, performance is encapsulated in the concept of fitness, which is traditionally defined at the individual or genotype level, although theory has long been proposed to apply it to higher levels of organisation (Wilson 1980; Swenson *et al.* 2000; West *et al.* 2006; Goodnight 2015). Defining and measuring fitness is associated with several, though not insurmountable, difficulties. First, fitness should be defined fitness as a propensity, not a realised property, if it is to have any explanatory power (Mills & Beatty 1979; Orr 2009), a criterion that should apply to any performance indicator at any biological level. Second, many ecosystem processes, such as resource uptake, primary production, secondary production and material cycling efficiency, are closely linked (Loreau 2010), so that different measures of ecosystem performance may often provide broadly consistent results when assessing the response of an ecosystem to abrupt environmental changes. Third, current environmental changes are likely to shed new empirical light on this issue in the near future by pushing ecosystems beyond critical thresholds, leading to major, readily observable changes in ecosystem structure and functioning. Interestingly, recent ecological theory predicts that simple competitive communities with high variance in species interaction strength produce coalitions of strong and weak interactors that behave somewhat like superorganisms along environmental gradients, with abrupt species turnover and sharp boundaries between communities, despite the absence of strong functional integration (Liautaud *et al.* 2019). Furthermore, these communities can exhibit directional dynamics in time, i.e., they are characterised by a maturity function that systematically increases over time, as well as community-level selection in space, i.e. they expand across space by replacing other communities with copies of themselves (Bunin 2021). Thus, we may soon have access to performance measures that will allow us to rigorously define adaptation at the community and ecosystem levels in changing environments.

Successful integration of ecology and evolution is likely to require a great deal of theoretical and empirical effort to examine how the various ecological and evolutionary processes operate, interact and combine at multiple scales of time, space and biological levels. But this effort is well worth it, as it would bring enormous benefits. In particular, it would help us to address one the major scientific challenges of our time, i.e. to understand and predict changes in biodiversity in the face of rapid environmental change. The ongoing anthropogenic environmental changes are so widespread, rapid and profound that the historically inherited distinction between ecology and evolution might soon become an obstacle to our understanding of the many consequences of these changes. To meet this challenge, ecology and evolution should join forces and build a broader synthesis adapted to our time.

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