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VIEWPOINT

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Opportunities to advance the synthesis of ecology and evolution

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Abstract

Despite decades of research on the interactions between ecology and evolution, opportunities still remain to further integrate the two disciplines, especially when considering multispecies systems. Here, we discuss two such opportunities. First, the traditional emphasis on the distinction between evolutionary and ecological processes should be further relaxed as it is particularly unhelpful in the study of microbial communities, where the very notion of species is hard to define. Second, 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 of the major scientific challenges of our time, that is, to understand and predict changes in biodiversity in the face of rapid environmental change.

KEYWORDS

abrupt ecological change, adaptation, concepts, eco-evolutionary dynamics, ecology, evolution, levels of biological organisation, microbes, rapid environmental change, synthesis

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 closer together over the past 60 years or so (e.g., Antonovics, 1976; Hutchinson, 1965; Pimentel, 1961). The recent emergence of the field of eco-evolutionary dynamics has further contributed to this effort by revealing how the reciprocal interactions between ecology and evolution generate eco-evolutionary feedbacks (Fussmann et al., 2007; Govaert et al., 2019; Hendry, 2017; Schoener, 2011). These feedbacks are particularly important when ecological and evolutionary processes are running at the same pace (Hendry, 2017). 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 (Aubree et al., 2020; Borrelli et al., 2015; Calcagno et al., 2017; Loreau, 2010). 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 these advances, 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 add our voice to suggestions 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 macro-organisms. Second, we echo proposals 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 (Falkowski et al., 2008; Whitman et al., 1998). 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, it is 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 macro-organisms (Fraser et al., 2009; Rosselló-Mora & Amann, 2001). 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, that is, 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 intraspecific 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). Furthermore, 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 6 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. Vellend (2016) proposed that community ecology should be rethought in terms of the same overarching processes as population genetics. His innovative view suggested that the two disciplines might proceed in parallel, as they deal with different levels of biological organisation. Microbes invite us to breakdown this distinction further and rethink what ecology is and what evolution is (see also West et al., 2006 for how social evolution could be considered in microbes). We believe this invitation should be seen as a great opportunity rather than a problem—specifically, an opportunity to develop a conceptual framework that accounts for the intertwining of ecological and evolutionary processes more generally.

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 (Gardner, 2017;

Williams, 1966), 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 controversial issue (Eldakar & Wilson, 2011; Goodnight, 2015; West et al., 2021).

It would be particularly useful to further 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). Quantitative approaches based on the Price equation can be used to integrate and partition some of these responses (Collins & Gardner, 2009; Govaert et al., 2016). This theory could be further extended to include evolutionary, ecological and social changes that reduce the vulnerability of social and ecological systems to environmental change (Moore & Schindler, 2022), as well as interactions between processes that occur at different scales and levels of organisation (Leibold et al., 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 (Goodnight, 2015; Swenson et al., 2000; West et al., 2006; Wilson, 1980). Defining and measuring fitness is associated with several, though not insurmountable, difficulties. First, fitness should be defined 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, that is, they are characterised by a maturity function that systematically increases over time, as well as community-level selection in space, that is, 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.

Improved 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, that is, 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.

AUTHOR CONTRIBUTIONS

ML wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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