Breaking down the wall between ecology and evolution

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Abstract

Despite their close links, ecology and evolution have remained separate disciplines to this day. Breaking down the wall between the two disciplines is essential for at least two reasons. First, this wall is an obstacle to the study of most microorganisms, which constitute a large part of the Earth's biodiversity. Asexual reproduction, gene transfer and the lack of a clear definition of the species taxonomic level blur the distinction between ecological changes in species abundances and evolutionary changes in genotype frequencies in microbes. Second, a key question that biodiversity science will have to address in the coming decades is how ecological systems will cope with rapid environmental change. Generalising the concept of adaptation across multiple timescales and levels of organisation would provide an integrative framework for studying the combined ecological and evolutionary responses to environmental change, and thus help us to address one the major scientific challenges of our time.

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Abstract

Despite their close links, ecology and evolution have remained separate disciplines to this day. Breaking down the wall between the two disciplines is essential for at least two reasons. First, this wall is an obstacle to the study of most microorganisms, which constitute a large part of the Earth's biodiversity. Asexual

reproduction, gene transfer and the lack of a clear definition of the species taxonomic level blur the distinction between ecological changes in species abundances and evolutionary changes in genotype frequencies in microbes. Second, a key question that biodiversity science will have to address in the coming decades is how ecological systems will cope with rapid environmental change. Generalising the concept of adaptation across multiple timescales and levels of organisation would provide an integrative framework for studying the combined ecological and evolutionary responses to environmental change, and thus help us to address one the major scientific challenges of our time.

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, although 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 (Loreau 2010). Despite the close links between ecological and evolutionary processes, ecology and evolution have remained separate disciplines to this day.

The traditional separation between ecology and evolution assumes that the timescales of ecological and evolutionary processes differ, evolution being slower than ecological dynamics. This assumption has been challenged by recent studies showing that evolution can be rapid, leading to an interplay of ecological and evolutionary dynamics known as "eco-evolutionary dynamics" (Fussmann *et al.* 2007; Schoener 2011; Hendry 2020). The field of eco-evolutionary dynamics has greatly contributed to strengthening the links between ecology and evolution by revealing how ecology affects evolution and, conversely, how evolution affects ecology, leading to potential eco-evolutionary feedbacks. 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). Despite growing awareness of the interactions between ecological and evolutionary processes, however, there remains a wide gap between ecology and evolution, both in terms of concepts and study objects. Even in eco-evolutionary dynamics, ecology is often reduced to changes in the abundance of species or phenotypes, while ecosystem processes and abiotic factors are more background than genuine actors.

Here we argue that breaking down the wall between the two disciplines is essential for at least two major reasons: (1) this wall is an obstacle to the study of most microorganisms, which constitute a large part of the Earth's biodiversity; (2) understanding and predicting the response of biodiversity and ecosystems to environmental change requires a more integrative view of ecological and evolutionary processes. In the current context of accelerating environmental change, we discuss why microorganisms are ideal systems for revisiting the deep links between ecology and evolution. We also discuss how some concepts such as adaptation could serve as tools for a fruitful dialogue in the convergence between the two disciplines.

The separation between ecology and evolution implicitly assumes not only that the timescales considered differ, but also, more fundamentally, that within-species evolutionary processes can be neatly separated from between-species ecological processes. While these distinctions in timescales and levels of biological organisation 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 and thus the distinction between ecological and evolutionary processes is blurred. Although asexual reproduction and gene transfer do not preclude a taxonomic classification of microbes as microbial traits are phylogenetically conserved in a hierarchical fashion (Martiny *et al.* 2015), the species level in this hierarchy is ill-defined and largely arbitrary. 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 evolution. 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 the key factor explaining the maintenance of biodiversity (Chesson 2000). Widespread gene transfer is another aspect that makes the distinction between ecology and evolution much more blurred in microbes than in macroorganisms. Given the enormous abundance, phylogenetic diversity and functional importance of microbes, they should be considered more than a curiosity in evolutionary biology or an exceptional model for experimental evolution (Lenski 2017). Microbes invite us to rethink the boundaries and interactions between ecology and evolution, and we feel this invitation should be seen as a great opportunity rather than a problem.

Perhaps nowhere is cross-fertilisation between the two disciplines more important than in fostering a better understanding of current and future changes in biodiversity and ecosystems at a time when the impact of human activities on the biosphere is rapidly increasing. Climate change seems to have already acted as a catalyst for eco-evolutionary studies (Hendry 2020). The ongoing anthropogenic environmental changes are so widespread, rapid and profound that the historically inherited distinction between ecology and evolution might soon become at best irrelevant, at worst an obstacle to our understanding of the consequences of these changes. One of the main questions that biodiversity science will have to address in the coming decades is how ecological systems will cope with rapid environmental change: Which communities or ecosystems will adapt and persist, and which will collapse? What will be the characteristics of the new communities or ecosystems that emerge? Answering these questions in detail will require careful dissection of the various evolutionary and ecological mechanisms at work, but in many circumstances, this will not be possible due to limited time and resources. Again, microbes are a case in point. Although careful experimental studies can unravel the respective roles of demographic and evolutionary responses to environmental change in at least some bacteria (Chase *et al.* 2021), the microscopic spatial and temporal scales at which changes in microbial communities occur, the fact that many bacteria cannot be cultured, and the lack of a clear definition of the species concept in microbes make it unrealistic to expect to be able to clearly separate ecological and evolutionary responses to environmental change in most microbiomes.

In the face of these conceptual and technical obstacles, many concepts used in either ecology or evolution could be profitably applied in the other discipline, provided that their definition is generalised in a relevant and consistent way. In particular, adaptation is a concept that is mainly used in evolution, but is very relevant to ecology. In evolution, '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). Even in the writings of such a strong proponent of individual-level selection as Williams (1966), 'organic adaptations' could be distinguished from 'biotic adaptations', which help perpetuate a group or population. It would be particularly useful to extend and generalise the concept of adaptation to wider ecological contexts. Soil microbial ecologists have begun to 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 regards adaptation as a multilevel hierarchical process that involves a range of adaptive responses to environmental changes, from molecules to ecosystems. These responses include differential gene activity (molecular-level mechanism), phenotypic plasticity (individual-level mechanism), differential reproduction of genotypes (population-level mechanism), and changes in species abundances (community- or ecosystem-level mechanism). In this theory, the adaptation concept is generalised to refer to any process that results in improved performance in response to environmental change. The concept could be further extended to denote 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. Defining the performance of a community or ecosystem seems challenging because communities and ecosystems are not superorganisms (Loreau 2010). This difficulty, however, may not be as great as it first appears. First, the well-accepted fitness concept is also notoriously difficult to define and measure a priori in evolutionary theory. In particular, it is critical to define fitness as a potential, not a realised property, if it is to have any explanatory power (Brandon 1990; 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 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).

One might object that there is currently limited evidence for abrupt ecological responses to environmental changes (Hillebrand *et al.*2020). This empirical argument, however, may soon become obsolete. In particular, changes in plant and animal community composition are lagging behind current climate warming, generating a significant climatic debt (Bertrand *et al.* 2011). As climate warming is expected to accelerate during this century, this climatic debt is likely to increase, eventually leading to the collapse of existing communities before being possibly replaced by new ones. Other drivers of changes in biodiversity and ecosystems, such as habitat loss and fragmentation, invasive species, overharvesting and pollution, are likely to combine with climate change to form a 'deadly anthropogenic cocktail' (Travis 2003). Thus, it seems clear that most abrupt ecological changes are yet to come.

Successful integration of ecology and evolution requires a careful assessment of the scales and hierarchical levels at which the various ecological and evolutionary processes operate, and how they interact or combine. But the generalisation of basic concepts such as adaptation across scales and hierarchical levels would be a particularly useful effort — they would serve as 'boundary objects' (Star & Griesemer 1989) in the conceptual unification of ecology and evolution. Other concepts, such as stability, resilience and resistance, which are commonly used in ecology, could also be applied to evolutionary systems (Nosil *et al.* 2021), provided that their definitions are clear and consistent. The effort is well worth it, as breaking down the wall between ecology and evolution would bring enormous benefits. In particular, it would help us to address one the major scientific challenges of our time — to understand and predict changes in biodiversity in the face of rapid environmental change, especially in microbiomes, which play a key role in all biological and ecological processes, from the health of individual organisms to the functioning of the biosphere as a whole.

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