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Received: 21 October 2022 | Revised: 27 March 2023 | Accepted: 29 March 2023

DOI: 10.1111/ele.14222

PERSPECTIVE

ECOLOGY LETTERS cnrs WILEY

Eco-evolution from deep time to contemporary dynamics: The role of timescales and rate modulators

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Funding information
Agence Nationale de la Recherche, Grant/Award Number: ANR-19-CE02-0015; Centre National de la Recherche Scientifique

Editor: Ulrich Brose

Abstract

Eco-evolutionary dynamics, or eco-evolution for short, are often thought to involve rapid demography (ecology) and equally rapid heritable phenotypic changes (evolution) leading to novel, emergent system behaviours. We argue that this focus on contemporary dynamics is too narrow: Eco-evolution should be extended, first, beyond pure demography to include all environmental dimensions and, second, to include slow eco-evolution which unfolds over thousands or millions of years. This extension allows us to conceptualise biological systems as occupying a two-dimensional time space along axes that capture the speed of ecology and evolution. Using Hutchinson's analogy: Time is the 'theatre' in which ecology and evolution are two interacting 'players'. Eco-evolutionary systems are therefore dynamic: We identify modulators of ecological and evolutionary rates, like temperature or sensitivity to mutation, which can change the speed of ecology and evolution, and hence impact eco-evolution. Environmental change may synchronise the speed of ecology and evolution via these rate modulators, increasing the occurrence of eco-evolution and emergent system behaviours. This represents substantial challenges for prediction, especially in the context of global change. Our perspective attempts to integrate ecology and evolution across disciplines, from gene-regulatory networks to geomorphology and across timescales, from today to deep time.

KEYWORDS
contemporary evolution, eco-evolutionary feedback, ecological opportunity, ecosystem genetics, emergence, geomorphology, global change, key innovation, multilayer networks, speciation

INTRODUCTION

That evolutionary and ecological change can happen on similar timescales has been known since the mid of the 20th century (Antonovics, 1976; Chitty, 1967; Hutchinson, 1965; Pimentel, 1961). Interestingly, this 'old' idea has only recently been revived thanks to conceptual advances (e.g. the genotype–phenotype map), long-term studies and advances in mathematical modelling which have made it operational (Huneman, 2019). Starting in the early 2000s, eco-evolutionary dynamics and feedbacks, or eco-evolution for short, have experienced an important hype (Bassar et al., 2021). Accordingly, reviews, perspectives (Fussmann et al., 2007; Kokko &

López-Sepulcre, 2007; Lion, 2018; Pelletier et al., 2009; Post & Palkovacs, 2009), special issues (BES special issue 'Eco-evolutionary dynamics across scales' 2019) and entire books (Hendry, 2017; McPeek, 2017) have been written on the topic.

In his book, Hendry (2017) defines five categories of eco-evolution: for the first two, an ecological (evolutionary) change influences an evolutionary (ecological) change, but not the other way around. The third and fourth category are 'broad sense feedbacks' where an ecological (evolutionary) change influences an evolutionary (ecological) change but the starting and end points of the feedback need not be identical. Fifth, the core or 'narrow sense' eco-evolutionary feedback *sensu* Hendry involves identical starting and end-points. For instance, plant seeds could exhibit morphological traits that protect them from avian seed predation. This could lead to the evolution of new beak morphologies in the birds, which may ultimately feedback on plant seed evolution. Bassar et al. (2021) argue that the most correct and useful definition of eco-evolution is restricted to Hendry's broad and narrow sense feedbacks with an emphasis on there being 'no separation in time between ecological and evolutionary dynamics', because this situation of synchronised timescales leads to novel and emergent phenomena (Box 1) which cannot be understood in a purely ecological or evolutionary context.

Today, most of the work in eco-evolution has a strong background in evolutionary biology. As a consequence, ecology is often understood as, or reduced to, pure demography and influences from community ecology and even more so from ecosystem ecology remain weak. This perspective dates back to the foundational works of Pimentel (1961) and Chitty (1967), and is today apparent in Hendry (2017)'s book, for example. While this missing synthesis has already been noted over a decade ago (Matthews et al., 2011), limited progress seems to have been made (for exceptions, see Bassar et al., 2010; El-Sabaawi et al., 2014; Kylafis & Loreau, 2008; Matthews et al., 2016). Most often, ecology, that is, relationships of organisms with their environment, serves as a 'theatre' for the gene-centred 'evolutionary play' (Hutchinson, 1965) because ecology and evolution have experienced little crosstalk since the Modern Synthesis, with notable exceptions including the examples discussed above (Futuyma, 1986; Huneman, 2019; Loreau, 2010; Vellend, 2010).

Very much in parallel to the literature focusing on simultaneously fast ecological and evolutionary dynamics, eco-evolutionary interactions have also been studied when both ecological and evolutionary dynamics are slow (for a recent review see Pausas & Bond, 2022). Here, the ecological dynamics occur at much longer timescales than demography because they are defined by slow geological and geomorphological settings that impact abiotic ecosystem properties. The evolutionary answers to these selection pressures often involve speciation and

BOX 1 Emergence

In the scientific literature 'emergence' is often used rather loosely implying only the appearance of a pattern of some kind. Strictly speaking, emergence refers to a particular class of phenomena or processes, which feature either (i) underivability from their components, or (ii) unpredictability from the laws that govern basic phenomena, or (iii) irreducibility to lower-level processes. Emergent properties have to be differentiated from collective or aggregative properties (Wimsatt, 1997), such as the species diversity of a community (for a discussion, see Salt, 1979).

As Sartenaer (2013) and Bedau (2008) summarised it, emergence always denotes the conjunction of a requisite of ontological dependence between two kinds of things (parts and wholes or low-level and higher-level phenomena), and a requisite of autonomy from the behaviour or properties of one from the other. The current conceptual discussions led by philosophers aim at reconciling these two requisites.

Many accounts have been given, including alternative views that focus on the lack of analytical derivability of the focal pattern from the initial state (Bedau, 2008; Huneman, 2008b) and equate emergence to the property of computational incompressibility. This kind of emergence is said to be 'weak' in comparison to emergence defined in more ontological terms, and represents a specific relation between multiple levels of organisation. Weak emergent structures possess autonomous characteristics that can be used for macroscopic descriptions, but the actual and ultimate causal processes reside at the lowest level of organisation. Most strictly physical and chemical self-organising phenomena fall under weak emergence. Weak emergence in the form of such 'computational emergence' clearly occurs in multilevel ecological settings: Grantham (2007) showed that, according to such a 'computational account' of emergence, some biogeographical dynamics are indeed emerging from regional ecological processes. In some cases, feedback phenomena between the higher and lower level may occur, which constitutes a stronger form of emergence. Therefore, 'strong' emergence refers to a situation where the whole system has an influence on its parts. A full discussion of emergence is beyond the scope of our work, but the interested reader will find a discussion in an evolutionary context in Huneman (2008a) and a broader discussion in Corradini and O'Connor (2010).

evolutionary radiations of new taxa that may in turn act as long-term geomorphic agents, for example, through bioturbation, biostabilisation or bioconstruction (Corenblit et al., 2011). In general, this literature links macroevolution and macroecology (Butterfield, 2007; Judson, 2017; Vermeij, 2017) and an integration of concepts with fast eco-evolution has not happened.

Here, we bring these fields together by conceptualising eco-evolution within a two-dimensional time space (Figure 1) expanding the scope of existing research in eco-evolution. Building on Hutchinson's theatre analogy, time is now the 'theatre' in which ecology and evolution are two interacting players (see also Reznick, 2016). In its extremes, this time space includes: (a) fast eco-evolution *sensu* Bassar et al. (2021) where evolution is fast enough to impact fast ecology (demography) and (d) slow eco-evolution, such as when geomorphological conditions provide an ecological opportunity for new species to emerge and impact geomorphology in a feedback loop (Butterfield, 2017; Corenblit et al., 2011; Pausas & Bond, 2022). Two additional extreme cases with mismatching timescales exist: (b) classical ecosystem ecology where evolution is too slow to immediately impact fast ecological dynamics (ecology is the main player) and (c) evolution is faster than ecology which could imply rapid adaptation to relatively slower environmental changes and, ultimately, neutral evolutionary dynamics (evolution is the main player).

Our representation of eco-evolution in a two-dimensional time space (Figure 1) immediately raises the question of whether and how systems can change between states or move along the axes, given that timescales are continuous and the four cases mentioned in Figure 1 only represent extremes along a continuum. These changes may synchronise or desynchronise ecological and evolutionary dynamics, whether overall slow or fast, which is especially relevant to understand since this potentially implies moving into or leaving eco-evolution states with emergent phenomena (Box 1) as discussed by Bassar et al. (2021).

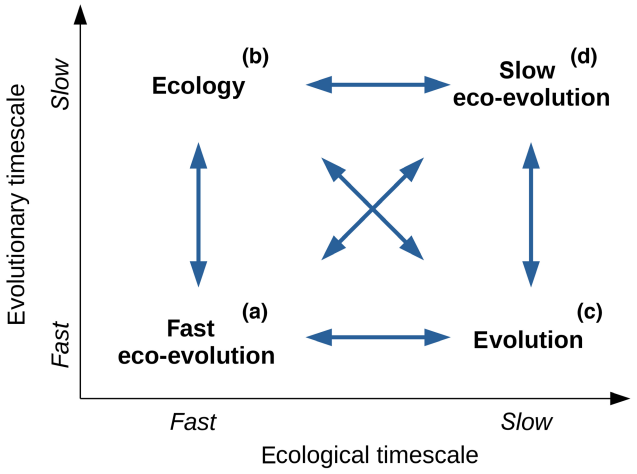

FIGURE 1 Eco-evolutionary system states describing extremes along continuous variation of matching or mismatching ecological and evolutionary timescales. Transitions in and out of states and between states are possible via the action of modulators of ecological and evolutionary rates which slow down or speed up ecology or evolution, respectively. Using Hutchinson's theatre analogy, time space is here the 'theatre' in which ecology and evolution are two players that may or may not interact.

Therefore, we here synthesise eco-evolution across slow and fast timescales. Our framework allows us to ask one central question: How is it possible to move between states, or, in other words, are there modulators that speed up or slow down ecological and evolutionary dynamics (or both)? We first briefly discuss the paces of ecology and evolution more generally, before focusing on modulators of ecological and evolutionary rates and their interaction, highlighting the connection between environmental factors, demography and evolutionary processes. We discuss rate modulators in the context of environmental change, since global change drivers, such as temperature, may act as rate modulators (for a discussion of the effects of stress on predators-prey eco-evolution, see Theodosiou et al., 2019).

The general objective of our work is to build an eco-evolution framework that can be used across timescales in order to help derive predictions in times of environmental change. We highlight the continuity of ecological and evolutionary processes and their interdependence across timescales as well as resulting emergent phenomena. Our framework therefore includes not only eco-evolution, but provides a roadmap for a broader synthesis of ecology and evolution.

THE PACES OF ECOLOGY AND EVOLUTION

Fast eco-evolution

The awareness of eco-evolution happening in contemporary time (a in Figure 1) has led to a large number of studies examining the conditions promoting rapid evolution, such as the genetic architecture of the traits involved (Rudman et al., 2017; Yamamichi, 2022). Questions to how relatively important such rapid trait evolution is in comparison to ecological factors has motivated the design of eco-evolutionary partitioning approaches (Collins & Gardner, 2009; Govaert et al., 2016; Hairston et al., 2005; Stoks et al., 2015). Quantification of evolutionary rates showed that these rates tend to be higher than one used to think, especially if measured on short timescales (Hendry & Kinnison, 1999). All rates can be projected onto the same generation-to-generation rates if analysed correctly, and evolution only seems slow on long timescales (Gingerich, 2001, 2009). Most recently, DeLong et al. (2016) quantitatively showed, using a dataset encompassing a wide array of organisms from protozoans to humans, that evolution, defined as the rate

of phenotypic change, can be fast, but is usually slightly slower (by a factor <10) than ecological dynamics (rate of population change). While timescales are traditionally divided into ecological, which comprises time in the 10s of generations, versus evolutionary, which lies more in the 100,000s of generations (Slobodkin, 1961), these studies therefore all indicate that fast eco-evolution with matching fast timescales may be more common than traditionally assumed.

One of the most classical examples of fast eco-evolution with novel dynamics emerging dates back to the foundational work of Pimentel (1961, 1968) and has been shown to be rather widespread (Hiltunen et al., 2014): cycling predator–prey dynamics, which are characterised by a quarter-phase lag between prey and predator cycles, select for (costly) defence mechanisms in the prey. As predation pressure increases with increasing numbers of predators, the prey evolves a defence mechanism, while, due to the associated costs, the undefended prey will start dominating when predator numbers are low again. This oscillation between defended and undefended prey (evolutionary change) is as fast as the demography of the predator–prey system (ecological change) which leads to an eco-evolutionary feedback in the narrow sense (eco-evolution) and a novel, emergent, system property *sensu* Bassar et al. (2021): the predator–prey system now does not oscillate with a quarter-phase lag any more but it shows anti-phase dynamics. This was first reported by Yoshida et al. (2003) for rotifers and alga, and shown to be a relatively common but overlooked feature of a lot of predator–prey time-series, from bacteria-phage systems to insects and their parasitoids, hinting at the ubiquity of eco-evolution (Hiltunen et al., 2014). Due to the similar timescales, Bassar et al. (2021) conclude that there is a very specific domain of applicability of eco-evolution: strong selection (large mutational effects; Lion, 2018), non-negligible phenotypic variances and large genetic effects on ecological variables.

Work on the Trinidadian guppy system (reviewed by El-Sabaawi et al., 2014; Reznick & Travis, 2019) goes beyond a pure focus on demography and includes ecosystem-level processes in the form of nutrient recycling. This body of work shows that in low predation conditions guppy population density is higher than under high predation (Reznick, 1982), which leads to modifications in the ecosystem through grazing, affecting algae and invertebrates, and excretion rates, which in turn imposes selection on guppy traits (Bassar et al., 2010, 2012; Reznick & Travis, 2019).

Indeed, a functional ecosystem perspective, which extends ecology beyond pure demography to include fluxes of matter and energy, may not be at odds with fast eco-evolution. Using the meta-ecosystem ecology framework, Gounand, Little, et al. (2018) have summarised available information on carbon fluxes, and show that, although fluxes vary widely, often, timescales are within years, implying that ecosystem dynamics and demographic rates are comparable, and might even be intrinsically linked. Interestingly, spatial flows of matter and energy are often mediated by spatial behaviour of organisms (movement, foraging, seasonal migrations, dispersal; Gounand, Harvey, et al., 2018) which provides a mechanistic link between metacommunity and metaecosystem ecology (Loreau et al., 2003; Massol, Gravel, et al., 2011). This behavioural link is especially true for taxonomically similar ecosystems (e.g. two lake ecosystems) that are more linked by dispersal than ecosystems that are biotically dissimilar (e.g. terrestrial–aquatic linkages) which may be more linked by flows of resources (Gounand, Harvey, et al., 2018). Of course, different organisms within an ecosystem may experience different timescales, such as bacteria versus large mammals, which is certainly an important issue but beyond the scope of the current article (see Loreau et al., 2023, for a discussion on hierarchies).

Slow eco-evolution

Stereotypically, slow eco-evolution (system state d in Figure 1) will imply that slow ecosystem-level processes (e.g. via physico-chemical conditions, leaching of nutrients, fluxes and organisation of mineral matter) linked to the abiotic compartment act as a 'pacemaker' for ecology. Geology and geomorphology provide the environmental matrix in which (meta)ecosystem dynamics play out (Phillips, 2021). Evolutionary answers to these selection pressures are equally slow or rare such as in key innovations (Hunter, 1998; Wagner, 2011), which might require more fundamental changes in metabolic pathways or the body plan, and occur less frequently, especially if historical contingencies are involved (Blount et al., 2008). Slow evolutionary processes may include major transitions (Maynard Smith & Szathmáry, 1995; Szathmáry & Maynard Smith, 1995) and adaptive radiations leading to the occupation of new ecological opportunities after extinctions (Stroud & Losos, 2016; Vermeij, 2017).

Going far back in time, the dynamics of oxygen on Earth provide a good example (Judson, 2017), especially two major oxidation events: the 'Great Oxidation Event' slightly more than 2 Ga ago and the phase just before the Cambrian (Holland, 2006). The 'Great Oxidation Event' is most likely due to cyanobacteria evolving oxygenic photosynthesis as a key innovation which raised oxygen levels in the atmosphere (Judson, 2017). This new ecological opportunity eventually led to wide-sense slow eco-evolution and permitted the emergence of eukaryotes and land plants (for a more detailed discussion see Judson, 2017; but see Mills et al. (2022) for a recent argument decoupling eukaryogenesis and oxygen levels).

The increase in oxygen probably set the conditions for the explosion of animal body plans and the rise of wasteful species (i.e. species that are energetically more efficient when using resources, but are releasing more

waste; Vermeij, 2017). The new life forms enlarged interaction networks (e.g. food chains and webs, see Butterfield, 2007) and exhibited adaptations to predatory lifestyles which had a major impact on the environment via bioturbation (Johnson, 2002; Meysman et al., 2006). Bioturbation is known to have driven slow eco-evolution in the oceans and on land by influencing key geomorphological and physicochemical components (Butterfield, 2017; Johnson, 2002; Meysman et al., 2006; Murray et al., 2008; Phillips, 2015).

Other examples involve riparian ecosystems which we discuss in detail in Box 2, the building of past and actual reefs (Kiessling et al., 1999), creating new geological carbonate structures in the ocean, that have subsequently served as substrate for life and the development of new ecosystems over millions of years (bioherms). Of course, reef building is a lot more complex and varied than what we can discuss here (Kiessling et al., 1999).

Mismatching timescales

Moving away from the a–d diagonal in Figure 1 desynchronises timescales and makes either ecology or evolution become the focal point of interest (in Hutchinson's words, the 'play') because the other is too slow. In the extreme of b in Figure 1, evolution does not play any role and we may be speaking of classical ecosystem ecology as envisioned, for example, by Odum (see Futuyma, 1986, for a historical discussion). In this upper left triangle of state space we may situate functional ecology *sensu* Orians (1962) with a focus on proximate explanations of ecological patterns. While ecological dynamics could be the result of past evolutionary changes (evolution may form the 'theatre'), the timescales do not match, which, following Bassar et al. (2021) prevents emergent phenomena (Box 1). Of course, modern functional ecology has included an evolutionary perspective, based, for instance, on the notion of response and effect traits (Violle et al., 2007) or on biodiversity and ecosystem functioning relationships (Loreau, 2010).

In the lower right triangle of Figure 1, ecological dynamics become slow relative to evolution and, therefore, the evolutionary play becomes a point of focus. In this sense, the lower triangle of Figure 1 also includes evolutionary ecology as described by Hutchinson (1965)'s ecological 'theatre' and evolutionary 'play'. More precisely, evolutionary ecology may form an area on both sides of the eco-evolution diagonal. Such quick evolutionary responses may include rapid adaptation to relatively slower environmental changes without eco-evolutionary feedbacks (rapid adaptation to anthropogenic disturbance Chakravarti & van Oppen, 2018; Lagerstrom et al., 2022) and, ultimately, neutral evolutionary dynamics. Evolutionary biology as envisioned by the Modern Synthesis is certainly situated in this lower triangle.

Importantly, Figure 1 highlights that a strict separation is meaningless because timescales are continuous. While a comprehensive treatment of the relationships between ecology and evolution is beyond the scope of this paper, the separations mentioned above are mainly historical (Futuyma, 1986; Huneman, 2019) which has already been recognised in the 1960s (Orians, 1962). Separations can also be used for reasons of tractability and simplicity, as when adaptive dynamics approaches assume a separation of timescales between ecology and evolution but investigate eco-evolutionary questions (Govaert et al., 2019; Lion, 2018). Even the fast eco-evolution literature likes to separate 'eco-to-evo' and 'evo-to-eco' causal pathways in order to explain feedback loops (Hendry, 2017).

CHANGE OF SYSTEM STATES: WHAT MODULATES ECOLOGICAL AND EVOLUTIONARY RATES?

Given the continuous nature of eco-evolutionary systems, we can expect transitions between states or at least movement along the axes when ecological and evolutionary rates change. In addition to the 'pacemakers' introduced above, which globally define whether systems are on fast or slow timescales, we will refer to the factors responsible for changes in the ecological or evolutionary rates as 'rate modulators' (Figure 2). While certain processes may modulate both, ecological and evolutionary rates, we will first discuss them separately (Figure 2) and focus on interactions later. We here do not provide an exhaustive list of all potential rate modulators, but rather want to illustrate the role of rate modulation for eco-evolution.

Modulators of ecological rates: Changing the speed of ecology

Ecological rate modulators (Figure 2; captured by the horizontal axis in Figure 1) are well known, and involve classical stressors and global change drivers such as temperature, pH, salinity, precipitation and other environmental factors. For example, Theodosiou et al. (2019) have discussed factors that reduce population fitness for predator–prey eco-evolutionary dynamics. Importantly, the form of a modulator's effect on biological rates can vary broadly, from linear, monotonic to unimodal or u-shaped. If effects are extremely non-linear, these have usually been described as tipping points implying alternative stable states (Drake et al., 2020; Scheffer et al., 2001). We start with discussing what modulates demographic rates and then focus on modulation via the abiotic environment (Figure 2).

BOX 2 Niche construction and slow eco-evolution in riparian ecosystems

A well-documented example of slow eco-evolution involves riparian ecosystems which cover large areas in almost all terrestrial biomes (Corenblit et al., 2015). Plants establishing in riparian areas are subject to strong selection pressures related to flooding, drought, sediment erosion, transport and burial (Gurnell, 2014). At the same time, plants have an important impact on river morphodynamics via the stabilisation of the substrate by their belowground organs (rhizomes, roots) and the modulation of water flow properties and sediment dynamics by their aboveground organs (Gurnell, 2014). As a consequence, plant traits and assemblages, on the one side, and river morphology on the other, impact each other in a feedback loop (Corenblit et al., 2015). More specifically, plant colonisation of the continents began in the late Ordovician and early Silurian (444–416 Ma), with small tracheophytes colonising coastal areas (Bashforth et al., 2011). Initially, plants evolved traits that allowed them to live in intertidal areas, followed by traits related to the new hydrodynamic, geomorphological and physiological constraints they encountered while spreading into river corridors (Bashforth et al., 2011). The gradual evolution of riparian plant traits in the face of disturbances and stresses inherent to the coastal and fluvial environment led in turn to drastic and irreversible changes in river morphodynamics across continents throughout the Palaeozoic Era (Bashforth et al., 2011; Davies et al., 2021; Davies & Gibling, 2011; Gibling et al., 2014). Palaeozoic changes in fluvial morphodynamics led to the development of fluvial landforms that were rare or absent in the Cambrian or before, such as elevated, muddy floodplains incorporating confined sinuous channels showing at their margins steles of levees and crevasse splays (Gibling et al., 2014). It was during this pivotal period in the evolution of the biosphere that meandering and anastomosing geomorphological fluvial patterns first developed in close relation to the evolution of riparian trees with robust and deep root systems. The stabilising and constructing effect of riparian vegetation on the floodplains fed back and caused major changes in riparian ecosystem structure and function (Falcon-Lang et al., 2011; Gibling & Davies, 2012). The meandering and anastomosing fluvial patterns in particular provided new opportunities for plants and animals to evolve in a variety of patchy habitats such as main and side channels, oxbows, and to move from wet coastal to dry upland conditions, ultimately leading to the spread of seed plants and animals on hillslopes during the Carboniferous period (Davies & Gibling, 2013; Greb et al., 2006). The fossil record indicates that the Devonian period (419 to 359 Ma ago) already encompassed numerous non-vertebrates, vertebrates and plant communities forming complex ecosystems (DiMichele et al., 2005; Kennedy et al., 2012; Labandeira, 1998; Wilson et al., 2020).

This and all main text examples imply that the biotic compartment impacts the abiotic compartment. This impact is often referred to as 'niche construction', which directly connects (ecosystem) ecology and evolution. Erwin (2008), for example, discusses how niche construction may impact macroevolution and biodiversity. Labelled 'ecosystem engineering' by ecologists (e.g. Jones et al., 1994), this interaction across generations changes selective pressures exerted upon the niche-constructing species and therefore induces evolution (Odling-Smee et al., 2003). More precisely, ecosystem engineering is related to the effect of a species on the structure and function of the ecosystem through modification of the physical environment without an evolutionary feedback. The latter is described by the concept of niche construction. Debates are raging about the specificity of niche construction, and its reducibility to the ordinary selective process where an allele affects the environmental parameters of the focal species (Laland et al., 1999; Lehmann, 2007). According to the latter view, niche construction would just be a form of extended phenotype (Dawkins, 1982) which has led to notable debates (Dawkins, 2004; Laland, 2004; Laland et al., 2016).

The concepts of ecosystem engineering and niche construction can also be found in the Earth System Sciences literature (Butterfield, 2011) since ecosystems can be seen as complex adaptive systems (Levin, 1998; Solé & Levin, 2022). A more detailed discussion of the relationship between evolutionary biology, ecology and Earth sciences is unfortunately beyond the scope of this paper.

Modulation of birth and death rates

Temperature is a well-known ecological rate modulator that regulates the metabolism of organisms, and hence can alter birth and death rates (Brown et al., 2004; Gillooly et al., 2001). Biological rates may scale exponentially within a certain range of temperature, but will globally scale with a unimodal relationship (Kingsolver, 2009).

Global change-induced rises in temperature may speed up or slow down ecological processes, depending on whether environmental conditions are above or below the focal organism's thermal optimum. For example, in consumer-resource systems, both foraging rate and

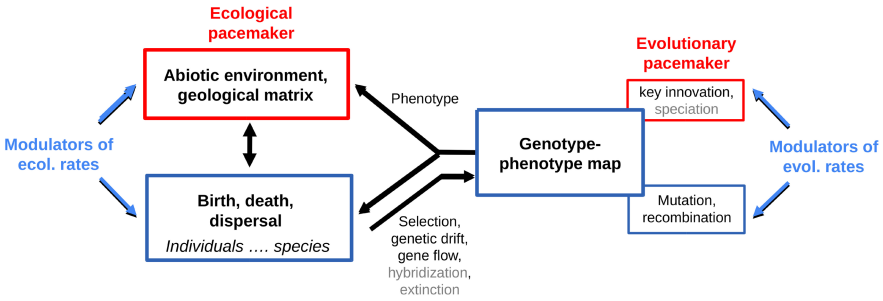

FIGURE 2 Eco-evolutionary feedback loop (left: ecology; right: evolution) with pacemakers (red) and modulators of ecological and evolutionary rates (blue). Pacemakers will define whether the fundamental dynamics are overall slow or fast. For instance, if slow geological processes, such as nutrient leaching, determine the pace of ecology, ecology will be overall slow. The analogous is true for evolutionary responses: if the focal evolutionary response is, for instance, linked to key innovations and speciation, this process may be overall slow. These broadly defined paces can be modulated by rate modulators. Some of these are external, like temperature, or internal such as mutation rate evolution or changes in the genotype–phenotype map. Note that the feedback loop depicted here highlights the importance of the individual level and of basic processes, such as birth, death and dispersal for ecology which then lead to higher-level patterns including demography, as well as to evolutionary processes (selection, gene flow). We have added some emergent features such as speciation, hybridisation or extinctions (grey) for clarity. While we do not intend to wade into a discussion on the link between processes that are classically understood as microevolutionary and processes labelled as macroevolutionary, we here assume that species-level patterns, such as speciation are driven by underlying processes such as (the lack of) gene flow, for example. Figure adapted from Govaert et al. (2019).

consumer-resource interaction strength depends on temperature (Dell et al., 2014; Gilbert et al., 2014; Hamann et al., 2020; Synodinos et al., 2021). If higher temperatures speed up birth rates of prey or predator species, this could lead to fast eco-evolution or, on the contrary, disrupt fast eco-evolution, depending on the rate of evolution. More generally, if a system already has matching ecological and evolutionary rates (the a–d diagonal in Figure 1), the consequence will be a reduction of the potential for eco-evolution because ecological timescales will become faster or slower than evolutionary ones.

Similar to temperature, other physico-chemical stressors and global change drivers (e.g. pH, salinity, humidity, pollution) that have linear or non-linear relationships with demographic rates may shift eco-evolutionary system states (see also Theodosiou et al., 2019). Importantly, even with monotonic response curves, whether such stressors speed up or slow down ecological rates may depend on whether the stressor acts via decreasing birth rates (slowing down ecology by reducing turnover of individuals if death rates are fixed) or increasing death rates (speeding up ecology by increasing turnover of individuals if birth rates are fixed; see also Boyce et al., 2006, Lawson et al., 2015). Overall, this calls for detailed analyses of the effect of environmental variation on demographic rates first, and then on evolutionary rates.

Stressors may of course exist outside of the global change context. Especially gradients of stress, such as large scale, latitudinal or altitudinal temperature gradients may be responsible for determining species ranges exactly via ecological rate modulation. For instance, the 'Species-Interactions Abiotic-Stress Hypothesis' (SIASH, reviewed by Louthan et al., 2015) states that stressful range edges are defined by abiotic forces and that non-stressful edges are more defined by species interactions (for a focus on facilitative interactions see the 'Stress Gradient Hypothesis' by Bertness & Callaway, 1994 which has somewhat opposing predictions). One potential mechanism for the SIASH is the reduction of inter-individual interactions at stressful margins via reduced densities, which leads to a spatial gradient in ecological rates (analogous to moving along the horizontal axis in Figure 1 for a given evolutionary timescale). As a consequence, such large-scale gradients may lead to geographical hot- and cold-spots of eco-evolution (crossing of the a–d diagonal in Figure 1). Patterns can of course be complexified due to dispersal, for instance.

Beyond the abiotic environment, biotic interactions themselves may act as rate modulators (Figure 2; see also Lagerstrom et al., 2022). For example, the presence of predators may induce variation in morphological and life-history traits, as shown by studies on the effect of crayfish on maturation age in freshwater snails (Covich, 2010; Hoverman et al., 2005). More generally, predator defence mechanisms or competitive ability may be linked to demographic rates directly (via density regulation in the case of competition; see e.g. Fronhofer et al., 2020, Siepielski et al., 2020) or indirectly (via costs of anti-predator mechanisms, for example; Urban, 2007) and modulate eco-evolutionary rates. New biotic interactions may arise from the immigration of new species, as has been largely studied in the field of bioinvasions (see, e.g. Davis, 2009), highlighting the role of the third demographic rate: dispersal.

Modulation of dispersal

External factors may also impact dispersal, the third demographic rate. Fragmentation, for instance, and loss of habitat in general, may reduce effective dispersal rates

and thereby reduce the speed of ecological dynamics (Legrand et al., 2017). Conversely, the rewiring of dispersal networks (Bullock et al., 2018) may facilitate dispersal and speed up ecological dynamics. Dispersal may also be modulated via biotic interactions. Theory indicates that dispersal should globally increase with intra and interspecific competition (Metz & Gyllenberg, 2001; Poethke & Hovestadt, 2002). Empirical evidence indicates that, in a food-web context, both bottom-up and top-down effects will determine dispersal rates (Cote et al., 2022; Fronhofer et al., 2018).

If ecological dynamics are overall fast and linked to demography (which is usually slightly faster than evolution; DeLong et al., 2016), ecological rate modulators, whether acting via dispersal or birth and death rates, that slow down ecological dynamics may lead to an increased likelihood of eco-evolution and, therefore, emergent system properties (moving towards the a–d diagonal in Figure 1).

Modulation via the abiotic environment

In the sections above, we have discussed demographic rates and the abiotic factors modulating them with a focus on globally fast ecological dynamics and opportunities for fast eco-evolution. In the realm of slow eco-evolution, slow ecological processes will modulate ecological rates, and we here propose to differentiate three categories: First, slow ecological processes with external slow forcing, such as, large scale glaciations that occurred over the last three million years in relation with Milankovitch cycles which are at the basis of long-term climatic variations that deeply impact biomes. Here, external forcing happened via astronomical parameters that extensively affected environmental parameters, like temperature, on the long term. These factors changed slowly, potentially allowing organisms to track climatic zones geographically according to their niches and to occupy 'refuges'. The slowness of these ecological processes likely prevented eco-evolution (system to the right of the a–d diagonal in Figure 1), while local adaptation to refuges, as a relatively fast evolutionary response, may have been possible. Another example is the colonisation of land ca. 500 Ma ago where the abiotic environment was defined by available space, which led to ecological opportunities and subsequent major key innovations (Vermeij, 2017) leading to slow eco-evolution (movement towards d in Figure 1).

Second, slow ecological processes with internal (biological) slow forcing which includes the great oxidation events discussed earlier. The rise in oxygen availability was due to internal forcing with bacterial activity slowly rising and coinciding with the rate of key innovations which implies slow eco-evolution. Interestingly, oxygen is a rate modulator that is produced and consumed by organisms, which may hint at complex feedbacks.

Third, slow ecological processes following catastrophic events (e.g. asteroid impacts, volcanic activity). These include long-term volcanic activity, for example, the formation of Deccan Traps and their potential role in the massive extinction of non-avian dinosaurs and many other taxonomic groups at the Cretaceous – Paleogene boundary, leaving room for birds and mammals (Longrich et al., 2012). Similarly to the internal forcing example, here, ecological opportunities arise paving the way for key innovations and slow eco-evolution.

Modulators of evolutionary rates: Changing the speed of evolution

In general, the rate of an evolutionary response is contingent on the amount of heritable phenotypic variation that aligns with the optimum that is selected for, potentially determined by ecological change (Schluter, 1996) and the ability of a biological system to show an adaptive response. On short timescales, evolvability (Pigliucci, 2008; Riederer et al., 2022) is defined as standing genetic variation (Houle, 1992). If such variation is already present, then rapid evolution can be expected in response to rapidly changing ecological conditions (see, e.g. Lee & Coop, 2017; Reid et al., 2016). At intermediate timescales, mechanisms that generate standing genetic variation, termed variability (potential to vary; Wagner & Altenberg, 1996), contribute to evolvability. The potential to generate variation depends not only on mutation rates but also on how these mutation rates impact fitness (Riederer et al., 2022). Thus, mechanisms that generate, deplete or maintain variation are critical to understanding how evolutionary rates are modulated (Payne & Wagner, 2019). We will discuss modulators of evolutionary rates in two sections, first focusing on external modulators, such as temperature or other stressors and, second, highlighting internal modulators, for instance, related to genetic architecture. We do not discuss epigenetic variation in any detail but some of the reasoning below may also apply.

Internal modulation

Modulation of evolutionary rates may, however, be a lot more complex. Specifically, evolution of mutation rates, as well as changes in the structure of the genotype–phenotype map, can change evolutionary rates.

Mutation rates are subject to evolution with, for example, selection favouring overall low mutation rates in stable environments for well-adapted populations (movement towards b in Figure 1) because the majority of mutations will have harmful effects (see also Wielgoss et al., 2012, for hypermutator fates in *E. coli*). Evolution of mutation rates might be regulated by the physiological cost of maintaining mutations at low level or by genetic

drift (Lynch et al., 2016; Sniegowski et al., 2000) and is probably rather to be expected on longer timescales or in alternating bouts of high and low mutation rates (Giraud, 2001). This is not the case for recombination and hybridisation which may modulate rates on both short and long timescales impacting adaptation rates but also potentially leading to fast innovation. Of course, the effect of mutations will depend on their effect size, with large effect mutations having the potential to lead to innovations.

Recombination rate may evolve under stressful environmental conditions, most notably in species with flexible sexuality including transition from asexual to sexual reproduction (Burke & Bonduriansky, 2017; Gerber et al., 2018; Moerman et al., 2020). Of course, asexuality can also be triggered by demographic conditions such as low density, for example, and not because of selection. In addition, hybridisation processes (i.e. interspecific gene flow) can speed up evolutionary rates (movement towards a and c in Figure 1), which is illustrated by the Gulf killifish. This species rapidly adapted to the extremely polluted environment of the Houston harbour thanks to an adaptive introgression by the Atlantic killifish. This introgression occurred because of secondary contact between the two killifish species most probably due to human-assisted transport (Oziolor et al., 2019).

Ultimately, the fitness impact of mutations depends on the structure of the genotype-to-phenotype map, which includes mutation effects, pleiotropy and epistasis. The structure and properties of this map (Nichol et al., 2019) are thus relevant to defining evolutionary rates at varying timescales (Figure 2). Since in realistic maps multiple genotypes can correspond to one phenotype, robustness to mutation can emerge. While the potential to generate more variation might lead to rapid evolutionary responses at short timescales (Deshpande & Fronhofer, 2022), on longer timescales, robustness to mutation (genetic canalisation) can lead to large leaps in evolution and innovations (Wagner & Altenberg, 1996). This is because mutationally robust genotypes can neutrally explore genotypic space without any changes in the phenotype (see Ciliberti et al., 2007). Hence, robustness on short timescales allows for evolvability on longer timescales (Wagner, 2011). Mutational robustness therefore acts not only as an evolutionary rate modulator but also as a pacemaker (covering the extremes of the vertical axis in Figure 1). Of course, phenotypic plasticity can also modulate evolutionary rates (genetic assimilation or the accumulation of cryptic genetic variation; e.g. Van Gestel & Weissing, 2016), but this is beyond our focus.

External modulation

External modulation of evolutionary rates may be due to processes very similar to those discussed above for ecological modulators. Focusing on variability, temperature, for instance, has been shown to impact spontaneous mutation rates in a u-shaped manner (back-and-forth movement along the vertical axis in Figure 1), with increased mutation rates at both low and high temperatures (Waldvogel & Pfenninger, 2021). Other stressors and global change drivers, such as UV or chemical contaminants, are also well known to impact mutation rates (see e.g. Bickham, 2011; López-Barea & Pueyo, 1998; Saaristo et al., 2018; Somers et al., 2002).

In analogy to ecological rate modulation and focusing on variation, influx of novel genes or genotypes via gene flow will be modulated negatively by fragmentation and positively by rewiring of dispersal networks (Bullock et al., 2018). Gene flow may not only bring new alleles, but also lead to new allelic combinations through hybridisation and introgression. However, the question is whether such inflow will increase or decrease the rate of evolution. Isolation may indeed promote local adaptation, while high gene flow may reduce local adaptation and could slow down evolutionary responses (Laroche et al., 2016; Massol, Duputié, et al., 2011).

Finally, in the context of slow eco-evolution, ecological opportunities, which may often be provided by previous (mass) extinction events, can promote key innovations, diversification and speciation (moving a system towards state d in Figure 1). Therefore, such extinction events may also be seen as external modulators of evolutionary rates. Large-scale latitudinal gradients of speciation rates as reported by Weir and Schluter (2007) or Rabosky et al. (2018), for instance, also provide examples of evolutionary rate modulation, potentially driven by associated major environmental factors.

Interactions between ecological and evolutionary rate modulators

A majority of the above-mentioned evolutionary rate modulators allow to speed up the pace of evolution (movement towards a and c in Figure 1). Since evolution seems to be slightly slower than ecology (DeLong et al., 2016, implying that most systems are in the upper triangle of Figure 1), these processes may bias dynamics towards fast eco-evolution. Yet, the action of rate modulators is likely more complex, in particular because they may simultaneously impact ecological and evolutionary change (Figure 2).

One example is again temperature which we have discussed in both ecological and evolutionary contexts. Interestingly, temperature will modulate ecological rates globally following a concave relationship (classical hump-shaped thermal performance curve) while the evolutionary modulation of mutation rates may be convex (u-shaped; Waldvogel & Pfenninger, 2021; for recombination see Morgan et al., 2017) as discussed above (see Figure 3). Considering that evolutionary rates are on average smaller than ecological ones, (DeLong et al., 2016) this leads to

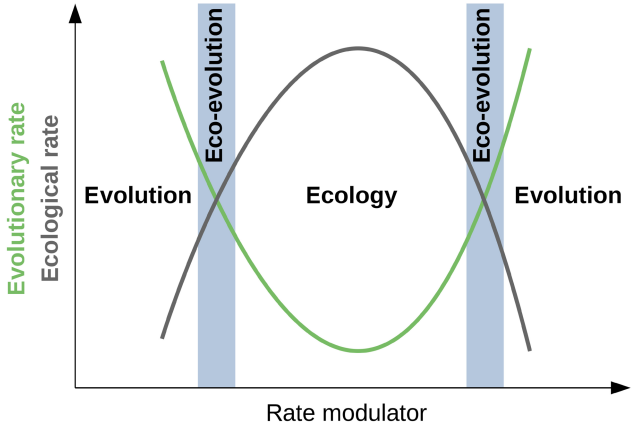

FIGURE 3 Possible interactions between modulators of ecological and evolutionary rates leading to changes in system states from evolution to eco-evolution via ecology back to eco-evolution and evolution (from left to right). Concretely, the rate modulator here is temperature which increases, for example, due to anthropogenic activities from left to right (alternatively, this could also be a latitudinal gradient). The rate modulator has a concave (convex) effect on the ecological (evolutionary) rates. For temperature, the grey (ecological) curve represents a thermal performance curve and temperature effects on population growth rates, while the green curve represents the impact of temperature on mutation rates, for example. Crossing lines indicate similar rates which implies that emergent, eco-evolutionary phenomena become possible. Of course, rate-modulator relationships can take different forms which will determine in which state the ecological system is (see Figure 1). Note that the example mentioned here is overall in the fast eco-evolution realm, but analogous patterns in the slow eco-evolution case are also possible.

a transition from slow ecology with fast evolution at low and high temperatures (system below the a–d diagonal in Figure 1) to fast ecology and slow evolution at intermediate temperatures (system above the a–d diagonal in Figure 1), close to the optimal temperature. Strong eco-evolution can therefore be predicted to occur at the intersection of these curves, namely to the left and the right of the mode of the thermal performance curve (Figure 3). In a climate change context, with extreme warming and temperatures beyond an organism's optimum, we can therefore predict the increased occurrence of eco-evolution.

Moving beyond temperature, Goehlich et al. (2022) could show that epidemics in a bacteria-phage system can be altered due to salinity stress via reduced host growth and resistance evolution. More generally, ecological rate modulators will also impact evolution, depending on whether they primarily act on birth or on death rates (we have seen above the importance of distinguishing between the two demographic effects). If stressors mainly act via a decrease in birth rates (see e.g. Aulsebrook et al., 2020) evolutionary rates will also be decreased because less births imply less input of novel mutations. By contrast, an effect on death rates (e.g. Pardo et al., 2017) may have no impact or increase the strength of selection. Dynamics may get even more complex if one thinks about processes like senescence, that will increase selection early on in the life-cycle (Rose, 1991), or trade-offs and trait correlation such as the competition-colonisation trade-off (Cadotte, 2007; Cadotte et al., 2006), for example. The effect of ecological rate modulators on evolution may also be more indirect. It has for instance been shown that mutation rates can depend on population density (Krašovec et al., 2017). Therefore, any ecological rate modulator that changes population densities also immediately has the potential to impact mutation rates, and thus the potential for evolution.

Regardless of which demographic rate is impacted by the modulators, selection pressures will be changed. One example is the variability of selection pressures due to frequency-dependent selection. In this case, an ecological rate modulator may imply a feedback on evolutionary change that decreases the intensity of selection, which, in turn, impacts ecological change, slowing it down. This eventually lets evolutionary change occur in a more constant ecological setting.

Beyond these specific examples, the intrinsic linkage of ecological and evolutionary rate modulators becomes clear when one realises that selection pressures, gene flow (including across species through hybridisation and subsequent introgression) and drift are the evolutionary forces that are most likely directly defined by ecology (Figure 2). Note that this is not completely true as discussed, for example, by Futuyma (2010) who points out that selection may also be 'internal' via developmental effects. In Figure 2 this may be captured by the genotype–phenotype map.

At the intersection between ecological and evolutionary rate modulators, dispersal and its drivers may become especially prominent. Clearly dispersal can be a key player in eco-evolution (Govaert et al., 2019): it is itself an ecological rate, it defines gene flow and therefore the pace of evolution and, finally, it has a genetic basis (Saastamoinen et al., 2018) and can itself be subject to evolution (Bowler & Benton, 2005; Ronce, 2007). This combination of roles may lead to complex eco-evolutionary feedbacks (for a discussion of temperature and fragmentation effects on eco-evolution, see Faillace et al., 2021).

Last, we would like to mention that all rates and modulators mentioned above may be context-dependent, such as dependent on body sizes or complexities of the ecosystem and therefore exhibit plasticity. While certainly interesting, these complexities are beyond the scope of this work. In conclusion, changes in ecological and evolutionary rates are highly coupled, and causation is not always easy to disentangle, calling for detailed analyses of the mechanisms involved in eco-evolution and their respective strength (Figures 2 and 3).

DISCUSSION

We have here revisited the definition of eco-evolution given by Bassar et al. (2021) and argue that, for emergence

to happen, similar timescales are enough, and fast ecological and evolutionary dynamics are not necessary (Figure 1). We show that eco-evolution can very well embrace the ecosystem level as well as geology and geomorphology while keeping its focus on emergence. Indeed, slow eco-evolution allows us to understand emergent phenomena over longer timescales, such as the trajectories of ecosystems in which abiotic components are coupled to the biological activities of ecosystem engineers. In these systems, adaptive changes of organisms to the environment participate in the formation of emerging patterns and ecosystem self-organisation.

This expansion of the eco-evolution framework across timescales, allows us to highlight a point of central importance: biological systems do not need to be associated with a specific timescale forever. Ecological and evolutionary rates that determine eco-evolution can be modulated (Figure 2), that is, can be sped up or slowed down by what we term 'rate modulators'. Rate modulators thereby move biological systems across eco-evolutionary time–space in Figure 1. The dynamical nature of eco-evolutionary systems, especially in combination with possible emergent behaviours, is not only interesting from a fundamental research point of view, but also relevant in the current context of ongoing global changes, in which temperatures, for example, are expected to rise quickly and globally (IPCC, 2021; Perkins-Kirkpatrick & Lewis, 2020). Systems may be pushed into alternative eco-evolutionary states by changing ecological and evolutionary rates as has been discussed by Theodosiou et al. (2019) for predator–prey systems. While we could not provide a comprehensive list of such modulators, the main point we would like to underline is the dynamical nature of eco-evolutionary systems. Our perspective highlights that focusing on extreme system states (Figure 1) in isolation may not always be productive. Timescales are continuous and most rate modulators, as mentioned above, may impact ecological and evolutionary rates simultaneously, which highlights the long-established intrinsic interdependencies between ecology and evolution (Levins & Lewontin, 1985; MacArthur & Wilson, 1967; Mallet, 2012). In this sense, the eco-evolution space in Figure 1 with its poles (a, b, c, d) may be a new, more integrative 'theatre' where the action of rate modulators define the eco-evolutionary 'play'.

Above, we have not explicitly considered stochasticity, although it plays a key role in both evolution (Lenormand et al., 2009), hotly discussed in the wake of Gould (1989)'s 'replaying the tape of life' idea, and ecology (Shoemaker et al., 2020) and presumably also for eco-evolution. At the same time, stochasticity is likely to increase with global change (IPCC, 2021; Perkins-Kirkpatrick & Lewis, 2020). While a comprehensive treatment is beyond the scope of this article we provide some insights in Box 3.

Of course, reciprocal feedbacks can also occur across different timescales (e.g. Govaert et al., 2019; Lion, 2018; Figure 1) and interesting phenomena can be studied in that context. We here do not argue that these lines of research are not valuable, on the contrary, we would like to call for a broader integration of ecosystem ecology, geology, palaeontology and evolutionary biology. Such an integrative approach can help us to not only understand past and current dynamics of biodiversity, but also tackle the challenges of the future associated with massive urbanisation and global change. Understanding where natural systems are situated in the eco-evolution time–space, and how they move within this space, may help inform management strategies for global change mitigation.

Finally, it is important to keep in mind that eco-evolution may not be immediately visible: As McShea and Brandon (2010) have argued, the null expectation for a biological system is continuous change rather than permanence. Variation keeps occurring, so that permanence, like the continued existence of some taxa for millions of years, is something worth explaining and may require stabilising natural selection as a cause. Therefore, we should understand 'change' in its most general sense that also includes permanence, that is, zero change, as a special case. This special case has been termed 'cryptic' eco-evolution by Hendry (2019).

Perspectives

Our work highlights two main challenges: (1) understanding eco-evolution across time–space scales requires bridging across disciplines studying ecology and evolution, regardless of whether they focus on the present or on the past, which (2) leads to an important challenge for prediction. As a consequence, future eco-evolutionary work has to be more integrative, including levels of complexity from gene networks to networks of ecosystems (Melián et al., 2018) at various time–space scales. This is certainly a major issue for empirical studies, especially for field studies, which will require analyses over many generations and the integration of various environmental stressors.

With the increasing availability of large amounts of data and immense computing power, machine learning and artificial intelligence may help improve predictability in ecology and evolution (Peters et al., 2014; Rammer & Seidl, 2019). However, the increased occurrence of emergent phenomena under eco-evolution implies that these phenomenological approaches may reach their limits. As described in Box 1, emergent phenomena are by definition underivable from their components which represents important challenges for theory and modelling and for moving from a descriptive to a more predictive science of the environment (Houlahan et al., 2016; Mouquet et al., 2015; Urban et al., 2016; Wortel et al., 2023; Yates et al., 2018). It is currently debated what kinds of models are needed in such non-analogue,

BOX 3 Stochasticity

Stochasticity is a hallmark of living systems, it can be demographic or environmental, and we outline some of its impacts on eco-evolution below. Environmental stochasticity is perhaps, in our context, the most straightforward to consider since it affects both the evolutionary and ecological dynamics. Environments are often spatially heterogeneous, and may fluctuate in time in a more or less predictable fashion. Of importance here is that the abiotic side of environmental stochasticity may affect living entities, from genes to ecosystems, at various timescales on the fast to slow continuum of eco-evolution. For example, the occurrence of floods, storms and fires can be sources of stochasticity at short timescales. Of course, mitigating environmental stochasticity is part of the selective process at these timescales (Lenormand et al., 2009), for example through bet-hedging strategies. A less common source of stochasticity comes from rare large-scale events, such as volcanic eruptions with global effects or asteroid impacts (Hoffman et al., 1998), leading to extreme consequences on living beings, such as mass extinctions (Longrich et al., 2012; Raup & Sepkoski, 1982), and no less extreme evolutionary consequences such as radiations (Penny & Phillips, 2004).

Ecological rate modulators and changing demographic rates will also directly impact demographic stochasticity. Even if the equilibrium density is not impacted, higher underlying birth and death rates will increase demographic stochasticity due to increased turnover at population equilibrium. Even more extreme, increasing demographic rates are known in discrete-time systems to lead to deterministic chaos (Hassell, 1975; Hassell et al., 1976, for an experimental demonstration of chaos see Becks et al., 2005).

Besides these direct impacts on variance in population dynamics, ecological rate modulators can also have indirect impacts on demographic stochasticity, via effects on (equilibrium) population sizes. For instance, equilibrium population sizes have been shown to decrease with increasing temperature (Bernhardt et al., 2018), which implies that demographic stochasticity will become relatively more important with increasing temperature, for example.

Beyond obvious consequences for stability, risk of extinction and predictability of systems, these ecological effects also impact evolution via increased genetic drift, if population sizes are small enough. We know that drift may play a (non-directed) positive role in evolution (Lenormand et al., 2009), for example by purging deleterious mutations under specific conditions (Glémin, 2003) or by impacting mutation rates (Lynch et al., 2016). Over much longer timescales, drift may shape genome evolution with differential effects depending on organism size (effective size; Lynch, 2007). Similarly, genetic diversity in animals seems to be strongly linked to a slow–fast continuum of life-history strategies, such that demography and drift might also be at play here (Romiguier et al., 2014). Clearly, at larger scales, founder effects may play important roles in (island) biogeography, for example. Especially when coupled with rare, long-distance dispersal such events can shape biogeographic patterns (Gillespie et al., 2012).

Genetic drift may also be relevant in a spatial context via its spatial analogue, gene surfing. Gene surfing is a process by which neutral or even deleterious alleles can increase in frequency at expanding range fronts thanks to sequential founder events (for a review see Miller et al., 2020).

that is, new, conditions (Yates et al., 2018). Urban et al. (2016) argue that mechanistic models including species interactions, dispersal, demography, physiology, environment and evolution are promising. Network-based approaches can represent a productive way forward in this context. As Melián et al. (2018) highlight, multilayer networks (Pilosof et al., 2017) can be used to capture eco-evolution from gene-networks (Deshpande & Fronhofer, 2022) to networks of ecosystems. Hierarchy theory and its combination with networks ('heterarchy'; Cumming, 2016) and especially approaches proposed by Wu and Loucks (1995) in the context of Hierarchical Patch Dynamics Theory could be transposed to include an eco-evolutionary perspective. Importantly, the latter body of theory also provides tools for understanding emergent properties (Box 1) using a multi-level triadic approach: In order to explain the emergent properties of a specific level of organisation, the adjacent lower and higher levels should be considered simultaneously with the focal level of interest. Of course, global change drivers and stressors have to be included as rate modulators (Theodosiou et al., 2019; van Moorsel et al., 2023).

Our work raises the question: Is eco-evolution likely, is it an (evolutionary) repellor or maybe an attractor? Where are real biological systems in the diagram of states represented in Figure 1? Addressing the second question, at least for globally fast ecological dynamics, DeLong et al. (2016) suggest that most systems will be above the a–d diagonal in Figure 1. While we can only speculate about the answer to the first question,

we would like to highlight a few important takeaways. Global change, such as increased temperature, landscape fragmentation, sea-level rise, species transports and invasions beyond their natural range, has the potential to impact biological systems and move them in or out of their current eco-evolution state. Specifically, temperature increases above an optimum have the potential to slow down ecology and speed up evolution, thereby moving systems towards the a–d diagonal in Figure 1 and, therefore, rendering eco-evolution and emergent phenomena more likely. At the same time, many other environmental changes are becoming stronger (e.g. land use change, urbanisation, pollution). While many ecologists may assume that these pressures are occurring too fast and are too strong for evolution to be relevant, these strong environmental changes actually can exert strong selection pressures on organisms, prompting fast evolutionary responses (Colton et al., 2022; Reid et al., 2016). Together with evolutionary rate modulators, such as the capacity of genetic architecture to speed up evolutionary responses via decanalisation, strong environmental pressures may be exactly creating the context that moves biological systems into the eco-evolution realm (the a–d diagonal in Figure 1). In combination with decreasing population sizes and increasing stochasticity (Box 3), this represents an important challenge for predicting the future of ecosystems. Clearly, without an eco-evolutionary perspective, our capacity to understand system behaviour may be severely limited. On a more speculative note, slow eco-evolution may be relevant when trying to envision changes over the very long term, such as the future of the Earth including (or not) humankind after a sixth mass extinction and potential novel adaptations including radiations of new biological groups.

AUTHOR CONTRIBUTIONS

Conceptualisation: Emanuel A. Fronhofer, Philippe Jarne, Sara Puijalon, Dov Corenblit, Frédérique Viard; Visualisation: Emanuel A. Fronhofer, Philippe Jarne, Lynn Govaert, Dov Corenblit; Writing—original draft: Emanuel A. Fronhofer, Philippe Jarne, Jhelam N. Deshpande, Philippe Huneman, Dov Corenblit, Sara Puijalon; Writing—review & editing: all authors.

ACKNOWLEDGEMENTS

We thank the editor and three anonymous referees for their constructive feedback as well as Pierre-Olivier Antoine and Olivia Judson for valuable comments on a previous manuscript version. P.J., E.A.F., S.P., D.C. and F.V. are supported by the CNRS Institute for Ecology and Environment. This work was supported by a grant from the Agence Nationale de la Recherche (No.: ANR-19-CE02-0015) to EAF. This is publication ISEM-2023-069 of the Institut des Sciences de l'Evolution — Montpellier.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14222.

DATA AVAILABILITY STATEMENT

No new data were used.

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How to cite this article: Fronhofer, E.A., Corenblit, D., Deshpande, J.N., Govaert, L., Huneman, P., Viard, F. et al. (2023) Eco-evolution from deep time to contemporary dynamics: The role of timescales and rate modulators. *Ecology Letters*, 26(Suppl. 1), S91–S108. Available from: https://doi.org/10.1111/ele.14222