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► **To cite this version:**

Philippe Jarne, Gilles Pinay. Towards closer integration between ecology and evolution. *Ecology Letters*, 2023, 26 (Suppl. 1), pp.S5-S10. <10.1111/ele.14298>. <hal-04252326>

HAL Id: hal-04252326

<https://hal.science/hal-04252326v1>

Submitted on 20 Oct 2023

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EXECUTIVE SUMMARY

Towards closer integration between ecology and evolution

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Funding Information

Université de Montpellier

Keywords: biodiversity levels, concepts, deep-time eco-evolution, eco-evolutionary dynamics, environmental change, fast/slow processes, integrative models, overlooked variability, plasticity, tree of life

DEEPENING LINKS BETWEEN ECOLOGY AND EVOLUTION

Developing deeper links between ecology and evolution is not a new idea and has been advocating since at least the 1950s (Futuyma, 1986), but most 20th-century attempts can be considered more as rapprochement than actual integration (Huneman, 2019 for a detailed historical review). However, based on early isolated insights (e.g. Antonovics, 1976; Pimentel, 1961), the idea has been revived over the last two decades, around the concepts of eco-evolutionary dynamics and feedbacks (Hendry, 2017). Significant efforts have indeed been made to percolate concepts and ideas between the two fields, especially across biodiversity levels (e.g. Hendry, 2017; Leibold & Chase, 2017; Loreau, 2010; Vellend, 2016), even if (i) more has been done at the population to community level than for higher levels of ecological organization (e.g. including ecosystem functioning) and (ii) analyses of reciprocal feedbacks remain rare compared to mainstream research in either field.

The number of studies claiming to be ‘eco–evo’ has risen sharply (Bassar et al., 2021), even if most of these studies actually represent classical ‘eco’ or ‘evo’ approaches, raising the question of what eco–evo really is. The definition proposed by Bassar et al. (2021; see also Hendry, 2017, chapter 1) may serve as a baseline, built on the assumption that ecological and evolutionary processes occur at the same timescales because this allows for true eco-evolutionary dynamics (EED) and

feedbacks. Fast global change (e.g. temperature increase; IPCC, 2023) leading to enhanced selective pressure is certainly a good reason for considering such EED, highlighting the fact that fast evolutionary dynamics can match fast environmental change (and fast biodiversity loss; Diaz & Malhi, 2022). From this definition, the debate can (and must) develop to integrate concepts, ideas and practices of ecology and evolution into EED, and this is what is proposed in this *special issue* (general outline in Figure 1), revivifying this debate by considering several themes: the first relies on biodiversity itself, with the idea of including all biodiversity levels (from molecule to biomes), all branches of the tree of life, and some overlooked aspects of variability. The other themes are concerned with extending the temporal (and implicitly spatial) frame in which biodiversity unfolds, considering the full range of forces and processes acting on biodiversity, and lastly revisiting concepts and extending models.

Rather than commenting sequentially on each paper in this *special issue*, we have chosen a summary to gather the ideas and suggestions presented around these themes—all the more so as several articles contribute to multiple themes (Figure 1). They are not presented in order of importance, although some papers offer more general perspectives than others. Of course, this *special issue* does not exhaust the field of possibilities. Each paper suggests several avenues for further research, and we also mention (Conclusion) some additional research directions that are not considered here, but worth exploring.

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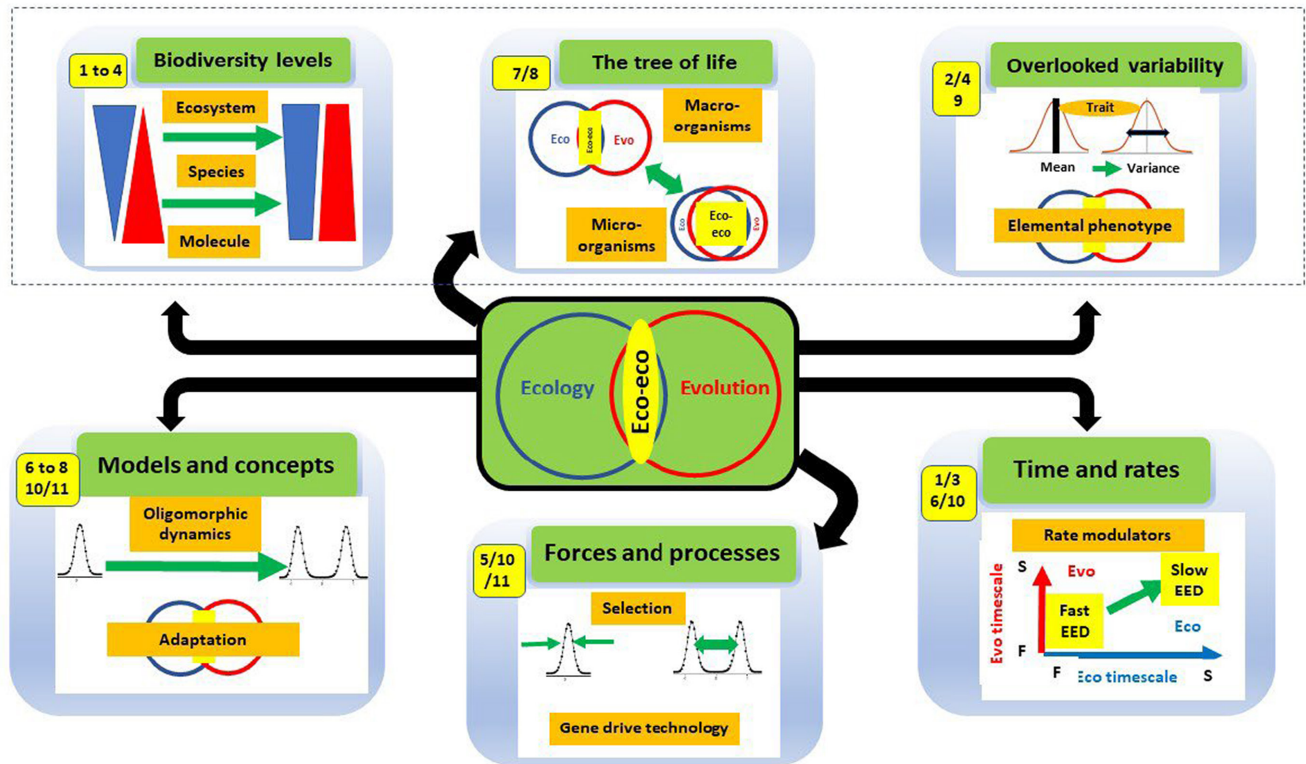


FIGURE 1 Schematic representation of the main contributions of papers in this *special issue* to the extension of the eco-evolutionary framework. The central box represents the current situation (ecology in blue and evolution in red), and black arrows point to the analysed themes (indicated at the top of each box). The top part (biodiversity levels, the tree of life and overlooked variability) corresponds to the ‘biodiversity in itself’ section in the text. Triangles (top left box) indicate the amount of ecology (blue) and evolution (red) from molecule to ecosystems, now (left) and in the desired future (right). In the top central box, ecology and evolution are much harder to distinguish in micro-organisms than in macro-organisms. In the top right box, both the importance of trait variance (not only mean) and of ‘elemental phenotype’ are highlighted. The right bottom box (‘Times and rates’) represents eco and evo timescales and suggests to move studies from fast to slow eco-evolutionary dynamics (EED), considering EED rate modulators (F=fast; S=slow). The central bottom box (‘Forces and processes’) suggests to move from directional to disruptive selection on phenotypes and to consider artificial introduction of genetically manipulated organisms (gene drive). The left bottom box (‘Model and concepts’) introduces a new integrative modelling framework (oligomorphic dynamics) and calls for using ‘adaptation’ across the whole range of EED. The papers contributing to each theme are indicated by a number (small yellow box). 1. Calcagno et al. (2023), 2. El-Sabaawi et al. (2023), 3. Fronhofer et al. (2023), 4. Gómez et al. (2023), 5. Kim et al. (2023), 6. Lion et al. (2023), 7. Loreau et al. (2023), 8. Martiny et al. (2023), 9. Sanderson et al. (2023), 10. Yamamichi, Ellner, and Hairston (2023), 11. Yamamichi, Letten, and Schreiber (2023).

EXPLORED THEMES AND SUGGESTED EXTENSIONS IN ECO-EVOLUTION

Biodiversity in itself

Biodiversity is classically considered hierarchically from molecules to ecosystems (or even biomes). While somewhat of a caricature, there is some truth in the view that the penetrance of evolutionary theory is much stronger at the level of the smallest entities (genes, populations), while ecological theories are generally more concerned with more complex entities (communities, ecosystems) (see the top left part in Figure 1). However, biodiversity levels are connected by multifarious links (e.g. selection, predation, variable environments), and EED can play a role at all levels with feedback between levels (Hendry, 2017; Loreau, 2010). This is a strong incentive to consider these dynamics across biodiversity levels. A first entry is proposed in this *special issue* by Yamamichi, Letten, and Schreiber (2023) who conduct

an analysis of models in population genetics and community ecology following the general approach advocated by Vellend (2016): there are indeed clear parallels between, for example, selection and competition or gene flow and dispersal. They focus on the critical role of temporally fluctuating environments in maintaining variation both within and among species through fast EED. Drawing on Chesson (2000)’s theory of coexistence, they begin from a simple lottery model used in both fields to explore how the temporal storage effect affects both genetic and species diversity, incrementally complexifying this model to account for ‘reality’. This pedagogic approach may certainly be open beyond the storage effect to consider for example the respective role of genetic and ecological drift (Yamamichi, Letten, & Schreiber, 2023). The second entry, proposed by Calcagno et al. (2023), is to consider several biodiversity levels simultaneously through trophic chains. What constrains their complexity, and especially their length, is a central issue in ecology (Calcagno et al., 2011) and can be envisaged as a tension between top-down (e.g. predation)

and habitat-selection effects in a metacommunity context, space being critical to account for their maintenance (Calcagno et al., 2011). Calcagno et al. (2023) introduce an ounce of evolution in this perspective, considering that dispersal rates can evolve under mutation pressure; this leads in general to longer food chains, depending on, for example, the competition-colonization trade-off among species. However, the benefit of evolution decreases when considering increasingly higher levels in food chains. Here, only dispersal evolves, and Calcagno et al. (2023) consider several worthy perspectives, such as for instance more complex descriptions of individual phenotypes than mean trait value. How dispersal evolution itself may affect the perturbation regime may also be worth taking into account for EED.

A second aspect is to reconsider how the tree of life is dealt with in EED studies as well as in both ecology and evolution in general (Figure 1). To put it bluntly, microbes are overlooked, although they represent the bulk of biodiversity, and most studies are conducted on multicellular organisms (Loreau et al., 2023; Martiny et al., 2023). The point is not just that this is 'unfair', but that looking at the world from a microbial perspective drastically changes the meaning of eco-evolutionary dynamics. Indeed, let us imagine what the theories of ecology and evolution would have been if they had been written before the rise of multicellular organisms: disentangling ecology from evolution is difficult in the microbial realm if it even has any meaning. Indeed, the species concept poorly applies, and horizontal gene transfers are common, even if microbial Operational Taxonomic Units within communities are separated by much larger distances than in macro-organisms (Martiny et al., 2023). The fundamental differences made in macro-organisms between changes in species abundance and in genotype frequencies are therefore blurred. Microbes, no less than macro-organisms, can respond to environmental change with solutions going from rapid evolution to broad-scale community shifts, going up to those biogeochemical processes governing ecosystem functioning and dynamics, which implies a strong potential to lead to EED (Martiny et al., 2023). However, they are not indistinct players collectively expressing functional redundancy, and we should now dig deeper into their ecology and evolution in natural environments to fully make sense of their role. Recent work has shown that it is for example possible to quantify dispersal and evaluate its impact on decomposition processes in soils (Martiny et al., 2023).

The last aspect regarding biodiversity is some facets of variability, within and among species, that have been overlooked in EED (Figure 1). Variability is needed for evolution to proceed, and its maintenance is a central issue in both evolution and ecology, in particular as a resilience mechanism under unpredictable environmental conditions. Variance is certainly a key concept in ecological studies above the species level but has been essentially considered among species (Villette et al., 2012). Yet, we are not short of studies analysing trait variance within species in population biology. However, studies assessing rates of phenotypic change

focus on population mean trait values, while their variance might be as significant for EED. Contributing to filling this gap is the goal of Sanderson et al. (2023), based on a compilation of both trait means and variances measured in context of environmental changes. Means and variances are globally positively correlated, and the distribution of genetic and phenotypic variances is also very similar. No general patterns for phenotypic variance emerge among different types of environmental changes, or traits, rendering prediction of future phenotypic trends difficult. Sanderson et al. (2023) conclude that much has still to be done to build more ambitious datasets on a wide range of organisms, but also to link this variance to environmental variance, a pre-requisite to EED studies.

Part of this variance is due to phenotypic plasticity, and here again, a plethora of studies have been conducted (Pfennig, 2021). However, how phenotypic plasticity can contribute to EED through propagating effects in ecological networks remains to be evaluated. Gómez et al. (2023) explore more specifically in this *special issue* how plasticity contributes to expand or shift the interaction niche, or even cause the colonization of new niches. This may lead to the topology of ecological networks being rewired, an aspect that is open to empirical evaluation through metrics such as nestedness or modularity. That individual plasticity may percolate to affect various key characteristics of networks confronted with environmental perturbations, such as resistance to invasions, is an interesting perspective (Gómez et al., 2023). Whether plasticity may be defined at network scale and submitted to selection is more contentious. A full analysis should also specify how plasticity may drive EED in actual cases.

Perhaps, more ambitious is the idea of considering stoichiometry as a key part of variability (El-Sabaawi et al., 2023)—ecological stoichiometry studies how the relative supply and demand of essential elements, such as carbon, nitrogen and phosphorus, influence biological interactions (Elser et al., 2000). It contributed largely to our understanding of ecosystem functioning (Van de Waal et al., 2018), but not so much to EED. Here, El-Sabaawi et al. (2023) propose to develop organismal stoichiometry to access an understudied aspect of the phenotype. This 'elemental phenotype' integrates body elemental content, and how these elements are acquired, assimilated, allocated or released and exhibits much intraspecific variation, leading to selective pressures. Beyond providing a direct link between population biology and fluxes of matter in ecosystems, this idea opens connections to the notion of functional traits (Loranger et al. 2016), also considered integrators between ecological and evolutionary processes (Hendry, 2017), as well as to a whole body of evolutionary theory on resource allocation (Charnov, 1993; Stearns, 1992). The 'elemental phenotype' perspective includes connections with species interactions as well, and therefore, a wide range of ecological processes through cascading effects in trophic chains.

Eco–evo and the time issue

Bassar et al. (2021) argued that genuine eco-evo dynamics can only unfold when ecology and evolution proceed at the same timescale. However, they implicitly assumed that both were fast because they focused on ongoing processes. Fronhofer et al. (2023) enlarge the picture by extending the idea to any timescale and considering the dynamics of biological systems in a two-dimensional space—the two axes representing respectively the speed of ecology and evolution (Figure 1). In this framework, ecology and evolution *sensu stricto* can be redefined by their relative speed with regard to evolution and ecology respectively (Figure 1). More importantly, this means that change of states in Figure 1 can occur whenever modulators modify ecological and evolutionary rates—such modulators can be factors external to the biological systems (e.g. environmental temperature) or internal to them (e.g. new genetic variation, itself influenced by external factors). EED may therefore emerge when rate modulators synchronize the speed of ecology and evolution. This framework also extends Hutchinson (1965)'s analogy (the ecological theatre and the evolutionary play): time is the theatre in which ecology and evolution are two interacting players.

Fronhofer et al. (2023)'s proposal undermines the usual 'slow evolution/fast ecology' wisdom that served for decades as a 'good reason' for not considering ecology and evolution together. It also calls for reconsidering the 'time-scale separation' classically used in EED models based, for example, on the adaptive dynamics approach (see Calcagno et al., 2023). This approach considers weak selection on traits and assumes that evolution is much slower than ecology in order to facilitate model analysis (Calcagno et al., 2023; Lion et al., 2023; Yamamichi, Letten, & Schreiber, 2023). The new approach to trait modelling—oligomorphic dynamics—by Lion et al. (2023, detailed below) is a way of overcoming this problem while addressing the question of eco–evo prediction at temporal scales beyond the few generations that quantitative genetics can offer. A significant contribution, no doubt, to predicting EED under a regime of rapid environmental change.

Broadening the set of studied forces and processes

Yamamichi, Ellner, and Hairston (2023) argue that evolution in EED studies has too often focused on a reduced set of forces (i.e. strong selection, negligible phenotypic variances, large genetic effects on ecological variables; see Bassar et al., 2021). They discuss several aspects that should be deepened, insisting on the role of mutation and genetic drift. For example, we know that deleterious mutations can drive populations to extinction (mutational meltdown; Lynch et al., 1995), but the role of genetic

drift remains to be sorted out to fully understand how 'evolution may save' populations when environmental variation drives down demography (evolutionary rescue). Yamamichi, Ellner, and Hairston (2023) also point out that too much emphasis has been put on directional and balancing selection (Figure 1), and not enough on disruptive selection (see also Lion et al., 2023). Assuming similar speeds for evolution and ecology, an open question is how lineage diversification (or even fusing after diversification) is affected by disruptive selection, both in the short- and long-term, providing a link between microevolution and macroevolution (see also Fronhofer et al., 2023). As mentioned above, temporal variation (and the storage effect; Yamamichi, Letten, & Schreiber, 2023) and phenotypic plasticity (Gómez et al., 2023) are also critical processes to be considered. The modulators of ecological and evolutionary rates introduced by Fronhofer et al. (2023) provide a general umbrella term to account for the fact that we should consider not only those forces and processes but also the speed at which they may change.

In this approach to EED through forces and processes (Figure 1), Kim et al. (2023) propose another, more applied, angle of attack, based on an arguably contentious issue, that is, the use of gene drive technology to introduce genes of interest into natural populations. The argument is simple: the spread of genes should be so fast that it can occur over timescales similar to many ecological processes, as in situations where there is strong selection. Kim et al. (2023) describe the key forces and processes that should be accounted for in future studies, for example, population structure or the rise of gene drive in other species on the evolutionary side and environmental variation on the ecological side. The strong economic pressure to release these technologies from the laboratory into the field certainly calls for an EED approach to better understand and manage the associated risks.

Extending models and revisiting concepts

Considering other forces and processes in the previous section (Yamamichi, Ellner, & Hairston, 2023) is certainly a call to develop new models of EED. We already saw the conceptual gain derived from considering the possibility that the colonization rate can evolve in models of food-chain length (Calcagno et al., 2023), and how models can be derived from analogous forces at both the population and community levels to account for the temporal storage effect (Yamamichi, Letten, & Schreiber, 2023). What Lion et al. (2023) propose is perhaps even more ambitious by opening a door to integrate the two major theoretical approaches used to model traits and their evolution, namely adaptive dynamics (AD) and quantitative genetics (QG). In a simplified presentation, QG assumes that traits have a normal distribution, and AD often results in bivariate distributions. To get rid of the

Gaussian straitjacket and drawing on Sasaki and Dieckmann (2011), Lion et al. (2023) introduce ‘oligomorphic dynamics’—the basic idea is to decompose a multimodal trait distribution into a sum of narrow unimodal distributions, each peak corresponding to a morph and being characterized by its frequency and statistical moments (Figure 1). This elegant approach, developed here using simple models, displays several advantages, among others the possibility to consider EED at much larger time-scale than QG or to account for the dynamical nature of genetic variance. It can also take into account population regulation through frequency- and density-dependent selection induced by environmental change (see also Yamamichi, Letten, & Schreiber, 2023). Lion et al. (2023) also suggest that this approach should facilitate a much tighter integration between eco-evolutionary theory and empirical data. Much exciting work in perspective!

Advances in the eco-evolutionary field could also come from the judicious extension of concepts from ecology and evolution. For example, Nosil et al. (2021) suggested that resilience, a concept borrowed from ecosystem studies (Holling, 1973), can fruitfully be used to analyse the stability of evolutionary systems. Here, Loreau et al. (2023) go the other way around by showing that adaptation, a concept typically associated with evolutionary theory, could be considered above the species level (Figure 1). The idea is to generalize adaptation to any process that results in improved performance as a response to environmental change in a multilevel hierarchical perspective. Loreau et al. (2023) consider facets of this certainly contentious idea, such as how to measure performance (fitness in evolutionary parlance) and its connection with group and multi-level selection. Perhaps, the idea might be even more relevant to unicellular organisms, given the blurred boundaries between their ecology and evolution (Loreau et al., 2023; Martiny et al., 2023).

FURTHER DIRECTIONS

The border between ecology and evolution is a vast domain, and this *special issue* of course did not explore it fully. Here, we sketch out a few further directions and themes that could fruitfully be pursued. First, technological tools (e.g. omics and environmental sensors/probes) used by evolutionary biologists and ecologists are serving as common objects for a dialogue between the two communities. Although they were not covered explicitly here, the idea runs through most papers of the *special issue*. Second, fitness is the currency used in evolutionary biology and energy that is used by the most functional parts of ecology. Rather abstract frameworks have been proposed to link fitness and energy (entropy) in evolutionary biology (e.g. Frank, 2009). The approach of Brown et al. (2018), connecting energy use, traits and environment, is open to empirical evaluation, and might be pursued for understanding EED. Third, micro-organisms

represent interactive interfaces between macro-organisms and their environment, which is encapsulated in the holobiont concept (Simon et al., 2019). Both evolutionary and ecological paradigms are required to make sense of holobiont dynamics with echoes here in the contributions of Loreau et al. (2010) and Martiny et al. (2023), for example, on the notion of transmission units. Last, but not least, biodiversity management in a world of very fast and deleterious environmental changes should harness an eco-evolutionary framework and perspective (Sarrazin & Leconte, 2016), not only to manage the current problems but also to offer some hope for the future.

AUTHOR CONTRIBUTIONS

Both authors drafted and wrote the manuscript.

ACKNOWLEDGEMENTS

The authors thank E. Fronhofer, M. Gessner, L. Govaert, P. Huneman, M. Leibold, M. Loreau, J. Martiny, S. Puijalón, P. Vandenkoornhuysen and F. Viard for stimulating discussions when framing this special issue, and P. Thrall for comments on the manuscript. Both authors' work is supported by the CNRS Institute of Ecology & Environment.

CONFLICT OF INTEREST STATEMENT

PJ has co-authored three papers in this *special issue* of *Ecology Letters*.

DATA AVAILABILITY STATEMENT

Irrelevant.

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How to cite this article: Jarne, P. & Pinay, G. (2023) Towards closer integration between ecology and evolution. *Ecology Letters*, 26(Suppl. 1), S5–S10. Available from: <https://doi.org/10.1111/ele.14298>