Organisms as complex structures wrapped in a complex web of life

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Abstract

A pressing issue is to understand how biological complexity impacts the persistence and adaptation of populations. Natural environments are under unprecedented pressure, due to climate change and land-use change which makes biological populations and ecological communities vulnerable. Evolution by natural selection, i.e. genetic change in response to selection, is one important way species can cope with such changes. Selection often operates on complex traits and much of selection is due to ecological interactions which, in turn, often form complex networks of species. In this sense, ecological interactions play a dual role: ecological interactions are essential to guarantee the resilience of communities and the functioning of ecosystem services and they are a source of selection that shapes complex traits. The development of a new integrative framework combining the complexity of selected traits with the complexity of interaction patterns is essential to address potential cascading effects and extinctions. Unfortunately, studies that focus on those two levels of complexity, both using theoretical or empirical approaches, are still scarce. In this special feature, we bring together articles that contribute to bridging this gap in the study of species coevolution and evolution of complex traits.

Resumo

A compreensão de como a complexidade biológica influencia a persistência e adaptação das populações é uma questão premente. Os ambientes naturais estão sofrendo pressões em níveis sem precedentes, devido às mudanças climáticas e mudanças no uso da terra, o que faz com que as populações biológicas e as comunidades ecológicas se tornem vulneráveis. Evolução por seleção natural, ou seja, a mudança genética em resposta à seleção, é uma forma importante das espécies lidarem com essas mudanças. A seleção geralmente atua em características complexas e grande parte da seleção se deve a interações ecológicas que, por sua vez, formam redes complexas de espécies. Nesse sentido, as interações ecológicas desempenham um papel duplo: as interações ecológicas são essenciais para garantir a resiliência das comunidades e o funcionamento dos serviços ecossistêmicos e são uma fonte de seleção que molda traços complexos nas diferentes populações. O desenvolvimento de um mapa conceitual que aborde de forma integrativa a complexidade das características sob seleção e a complexidade dos padrões de interação é essencial para compreendermos efeitos-dominó e extinções potenciais. Infelizmente, ainda são escassos os estudos que focam nesses dois níveis de complexidade, tanto com abordagens teóricas quanto empíricas. Nessa edição especial, reunimos artigos que contribuem para começar a preencher essa lacuna no estudo da coevolução de espécies e evolução de características complexas.

Introduction

Understanding the natural world is a daunting task. How can we understand the consequences of all the interactions connecting millions of individuals of hundreds of species that ultimately affect the organization and resilience of a given ecological community? How to properly quantify the effects of each interaction and the intrinsic features of organisms that may shape and be shaped by ecological and evolutionary cascading effects? This task is even more pressing in this ever-changing world where climate and land-use change are driving species and communities to rapid extinction (Barnosky et al. 2011; Dirzo et al. 2014). In this special feature, we highlight articles that, by merging tools from different disciplines, advance how to deal with the complexity of the evolution of large communities of interacting species and its relationship with within-species genetic variation. Our hope is that this collection of studies, by providing novel insights in the interface of the evolution of complex traits and the consequences of complex patterns of interaction, might contribute to novel pathways of research on the architecture of diversity at different levels of biological organization, from genes to ecosystems.

At finer scales, complexity plays a fundamental role in shaping the outcome of the evolutionary process. Evolution by natural selection is intrinsically a high dimensional phenomenon (Melo et al. 2016), and to fully understand it we need to take into account the multidimensionality of both selection and inheritance. Multiple traits are often correlated due to widespread pleiotropy, implying they often respond in non-independent ways to selection. Moreover, multiple traits influence fitness simultaneously and are therefore under potentially conflicting selective pressures, leading to constraints that can impact evolutionary change both at a micro and macroevolutionary scales (Kruuk et al. 2008; Pujol et al. 2018; Machado 2020). To the complexity of non-independent multiple traits responding to selection adds the fact much of selection arises from ecological interactions (Thompson 2005).

The patterns of how individuals from different species interact in a community influences selection, evolutionary outcomes, and as a side-effect the pattern and function of ecological communities. In this special feature, two papers deal directly with how the community context of populations can influence both selection (Campbell et al. 2022) and phenotypes (Eisen et al. 2022). Campbell et al. (2022) look at how different episodes of selection from two different types of ecological interactions, mutualism from pollinators and antagonism by seed predators, shape the selective pressures of multiple floral traits. They showed evidence that both episodes of selection exerted directional and stabilizing selection in the traits analyzed. The strength of selection, however, varies across interactions, with pollination exerting stronger selection. Their results support the notion that the combined effects of selective pressures are distinct from the simple sum of the parts. Rather, ecological interactions exerted correlational selection between suites of traits, favoring a certain combination of traits, highlighting the complexity of understanding selection resulting from multiple ecological interactions.

Eisen et al (2022) investigated whether the community context influenced multivariate chemical traits in two different plant species from *Clarkia* genus. They presented evidence that community context leads to multivariate character displacement. The role of community context to evolutionary biology has been argued for some time as important in the definition of patterns of morphological evolution. The contribution of Eisen et al (this special feature) highlights the ways in which the community context influences species phenotypes, and selective pressures (Eisen et al. 2020). Their work is a good example of using multivariate approaches to tackle the complexity of communities and phenotypes, and how this can bring novel insights about the evolution and ecology of communities. Both papers illustrate the role of the community context in influencing multivariate selection and evolution in a set of traits of a focal species, highlighting the necessity of incorporating the holistic view of ecological interactions to understand evolution. In this sense, because the selective consequences of ecological interactions depend, at least partially, on the structure of interactions, exploring the community-level of organization of ecological interactions may provide insights on (co)evolutionary dynamics in species-rich systems.

Ecological interactions often form complex network-like structures at the community level. Recent years have seen a burst in the study of ecological networks. Ecological networks is an approach that seeks to obtain insights into the dynamical implications of interactions by quantifying the patterns of interaction among different actors in an ecological community (Pascual and Dunne 2006). Actors here can refer to any hierarchical entity since those networks can be described in the level of individual-individual, individual-species, species-species, or even higher taxonomic and functional groups (Guimarães 2020). This approach can give us information on the resilience of communities (Memmott et al. 2004), and on the ecological impacts of changes in the structure of interactions, for example (Bastolla et al. 2009; Allesina and Tang 2012). From a coevolutionary perspective, the fact that populations are evolving in communities of interacting species leads to the potential for indirect effects to occur that cascade through the network and impact not only the phenotypes but the degree of adaptation of the different species in the community (Assis et al. 2020).

In this issue, (Benadi et al. 2022), deals with the important issue of how to estimate interaction frequencies in ecological networks. Specifically, they tackle one of the main challenges for models of ecological networks, namely, the non-independence of ecological interactions. Classical network models often assume that interactions between agents are independently drawn from a distribution, as in the classical Erdös-Rényi random graph. To explore the non-independence of ecological interactions, Benadi et al. (2002) introduce an approach that essentially incorporates the complex patterns of association across interactions in an ecological community. Their approach combines both the outcome of evolutionary process (traits), information on macroevolutionary patterns (phylogeny), and fundamental ecological drivers (abundances) to estimate interaction strengths. By using the method proposed by Benadi (2022) one can investigate how invasions or extinction will impact the interaction patterns in ecological networks, leading to better predictions of the resilience of ecological networks and coevolutionary cascades. Their approach has the advantage of being able to be used with suites of traits measured for each species in the network, but also it can be used by creating latent traits (based on the phylogenetic relationship across species) that improve the estimation of interaction strengths in the ecological network. The accurate estimation of interaction strengths is essential to the advance of the coevolutionary effects of interaction for the whole community, as interaction strengths is important for our understanding of how species interactions exert selective pressures and the importance of the interactions for ecosystem services. Indeed, Dehling et al. (2022) in this feature shows that interaction frequencies on its own can modulate niche overlapping between species in mutualistic networks, and might be an important mechanism of how species avoid competition and can coexist in hyperdiverse ecological networks. Specifically, they used seven highly diverse frugivory networks from the tropical Andes and showed that niche packing was driven in most part due to changes in the frequency of resource use, instead of niche contraction. By doing so, their manuscript sheds light on the possible ways the feedback between network organization, trait evolution, and diversification may operate. A next step that emerges from Dehling et al. (2022) is the need to explore how the network-trait-diversification feedback changes when one incorporates the role of complex genetic associations among traits in shaping evolutionary dynamics.

Finally, Nuismer et al. (2022) describe the theoretical and empirical challenges of investigating coevolution from a community perspective. Their perspective piece makes a good summary of the state-of-the-art tools available to the study of community coevolution and brings a good discussion of the necessary theoretical advances. One exciting venue they highlight is the use of model-based statistical methods in the study of coevolution. This approach needs only easily collected trait data for species in the community and has the potential to greatly increase our understanding of how coevolution involving multiple species operates in biological communities. A promising outcome of such an approach would be to tackle the role of "cryptic coevolution", a phenomenon we should expect to occur in real, species-rich communities since these systems are characterized by a multitude of indirect pathways connecting species in ecological networks (Guimarães et al. 2017). One potential future avenue would be to extend similar analyses to multiple traits, especially when correlations among traits create non-independence on the coevolutionary dynamics.

Even though the field is progressing through large steps, there is still a lot of theoretical and empirical advances needed. We think that data constraints are vanishing rapidly, as it is easier and easier to gather data in this big data world. The challenge ahead would involve finding ways to simplify and aggregate such astonishing amounts of information (Levin 1992) on the cross-talk between complex trait evolution and patterns and processes in ecological communities in such a way that we can understand at least some of its fundamental principles. Thus, the understanding of coevolution in a community context will depend on a highly interdisciplinary research program that combines approaches derived from evolutionary biology, quantitative genetics, community ecology, and network science. The papers highlighted in this special feature are great examples of how this interdisciplinary view can increase our knowledge and bridge this gap. We are excited to see how the field will progress in the next few years, and how much we will all learn by considering this integrated multivariate perspective.

Acknowledgments

We would like to thank all the authors and reviewers that contributed to this special feature. We are extremely grateful to Dan Bolnick, Owen Cook, and Patricia Morse for all the editorial help. It was an honor and a pleasure for us to work with all of you on this issue, which was a beautiful collaboration amid the challenges that the world pandemics imposed on all of us. This work was supported by funds from FAPESP (2016/14277-2 and 2018/14809-0), CNPq (307134/2017-2), Royal Society, London (CHL/R1/180156), and CAPES.

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