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An ecological and evolutionary perspective on species coexistence under global change

Adam M Siepielski, Adam Z Hasik and Brittany H Ousterhout[1]

Whether assemblages of insect species locally coexist or are only being slowly lost from communities remains an enduring question. Addressing this question is especially critical in the wake of global change, which is expected to reshuffle biological communities and create novel interspecific interactions. In reviewing studies of putative insect species coexistence, we find that few have demonstrated necessary criteria to conclude that species coexist. We also find that few integrate ecological and evolutionary perspectives towards understanding coexistence. Yet, both micro-evolutionary and macroevolutionary processes can play a critical role in shaping species coexistence mechanisms, especially in response to global change. We suggest that understanding how global change may affect the makeup of communities can be best achieved by developing a research program focused on the joint contribution of ecological and evolutionary processes.

Address
Department of Biological Sciences, University of Arkansas, Fayetteville, AR 72701, USA

Corresponding author: Siepielski, Adam M (amsiepie@uark.edu)
[1] Present address: National Great Rivers Research and Education Center, East Alton, IL 62024, USA.

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Introduction

Huxley's quip on an 'inordinate fondness' for beetles and Hutchinson's observations of water boatmen (Corixidae) [1] set the stage for a now vast series of inquiries focused on uncovering astounding levels of species diversity. Hundreds if not thousands of Coleoptera [2] and Hymenoptera species [3], and equally impressive numbers of butterfly species [4], can all be found together in small areas (i.e., a single plant). Examples such as these abound in the literature. This leads to a fundamental question at the interface of ecology and evolutionary biology — how (or do) all of these species coexist?

Addressing this question is important because global climate change is causing the disassembly of existing communities and assembly of novel communities as species distributions shift [5–9,10•]. Similarly, anthropogenic changes such as urbanization are altering community composition, particularly among insects [11]. Such shifts in community composition can result in both novel direct and indirect species interactions [10•,12–14]. These altered interactions, along with the direct effects of climate change, will affect not only the ecological factors underlying the abilities of species to coexist [10•,15,16], but will also influence evolutionary processes [17,18]. Indeed, although some species may migrate and undergo range shifts to avoid climate-induced extinction [9], an alternative is adaptive evolution in response to selection imposed by climate change [17,18]. Such adaptive evolution, or lack thereof, to the local biotic and abiotic environment may therefore play a role in shaping community structure [19,20,21••,22••].

Thus, to understand if communities will be resilient to global change and successfully re-assemble in new locations there is an important need to determine (1) whether species are truly coexisting or not, and (2) to incorporate the role of evolutionary processes. Yet, there is presently a limited understanding of how ecological and evolutionary processes combine to shape coexistence in insect assemblages. Many studies have focused on identifying ecological processes, such as the role of competition or predation, in promoting niche differences that structure communities [23]. Similarly, numerous evolutionary studies have focused on understanding how microevolutionary processes shape individual taxa and the macroevolutionary relationships among them. However, few studies combine these efforts in a framework aimed at incorporating feedbacks between ecological and evolutionary processes in a community context (Figure 1) [24••,25•,26••,27].

In this review, we discuss how a research program focused on combining ecological and evolutionary perspectives can advance our understanding of species coexistence. Our goal is to demonstrate that incorporating this eco-evolutionary perspective will be insightful for understanding how biological communities may respond to global change. To achieve this goal, we first present an overview of modern coexistence theory, outlining the requirements for species coexistence. Although coexistence mechanisms can operate over various spatial scales [28] we focus on local coexistence, in which species interact with each other and the local environment. We then evaluate studies where this framework has been

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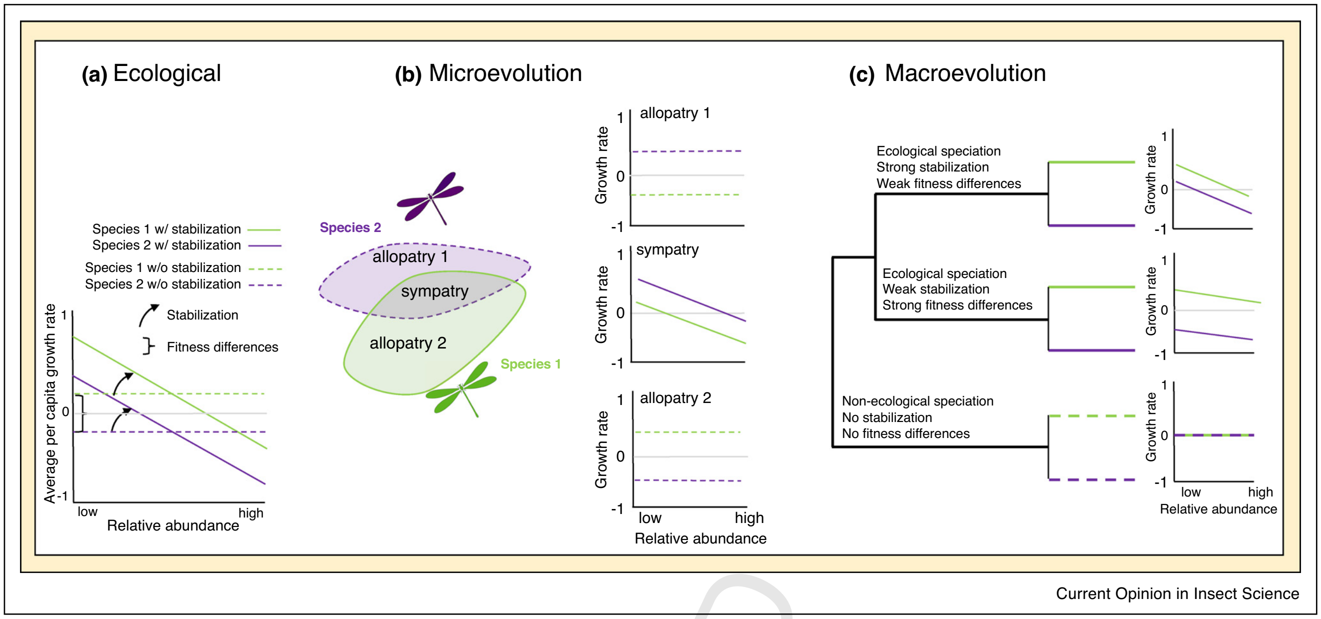
Figure 1



Mechanisms of species coexistence across ecological and evolutionary scales. **(a)** The immediate, ecological time scale of stabilizing effects and fitness differences. Different colored lines represent two species. The solid lines depict stabilizing effects, with the small arrow showing the demographic advantage gained when rare, and the slope indicating the strength of stabilization. Dashed lines show species per capita population growth rates in the absence of stabilizing effects (i.e., fitness differences). Modified from Ref. [17]. **(b)** A depiction of the geographic distributions of two species, and expectations of how microevolutionary processes may affect the strength of fitness differences and stabilizing effects when species' populations have not coevolved with each other (allopatric scenarios; showing no stabilizing effects and strong fitness differences with greater fitness for the locally adapted species) to reduce competition, and when they have (the sympatric scenario; showing how local coevolution can generate stabilizing effects promoting local coexistence even if fitness differences remain). **(c)** Different macroevolutionary speciation dynamics involving ecological and non-ecological speciation generating species pairs with different combinations of stabilizing effects and fitness differences. The scenario depicted in the top panel would result in coexistence, the middle panel competitive exclusion of the purple taxa, and the bottom panel would eventually result in one species coming to dominate by random chance.

applied in insects. Finally, we discuss how micro-evolutionary and macro-evolutionary processes may shape the potential for species coexistence [19,21••,26••,29], and how this may be impacted under global change.

Species coexistence and co-occurrence are not the same

Defining coexistence

Simply because two or more species can be found in a location co-occurring with one another does not mean they coexist [30]. Co-occurrence simply indicates that any two species are found living together [30]. Coexistence, or more specifically stable coexistence, requires that every species meets the invasibility criterion [31,32]: each species can increase when rare ('invade') and the other species (the 'residents') are at their single species equilibrium (or long-term abundances) when the invader is absent. Few studies have directly tested for invasibility [30], which is necessary to understand if species can indeed re-assemble in communities that have been perturbed in response to global change. As explained by Chesson (2000), the potential for competitor coexistence is a consequence of two components: (i) stabilizing niche effects that reduce interspecific competition and intensify intraspecific competition, and (ii) competitive fitness differences, which predict which species would go locally extinct without stabilizing effects (Figure 1). The balance between stabilizing effects and fitness differences determines whether or not species coexist [31].

The difference between co-occurrence and coexistence is not a matter of semantics. The issue is that an assemblage of species in a community may be composed of any combination of species that are coexisting (satisfy the invasibility criterion), neutral (ecologically equivalent; *sensu* [33]), walking dead (undergoing slow extinction via interactions with the environment), and sink (maintained locally because of immigration) [26••]. Across the landscape the same sets of species may vary in their assignment to each of these species types. Therefore, it is impossible to simply conclude that a group of taxa found co-occurring in a location are coexisting without rigorous empirical testing.

The distinction between co-occurrence and coexistence also matters for developing a framework on how biological communities may respond to global change. If species are

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