

An ecological and evolutionary perspective on species coexistence under global change

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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.

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Introduction

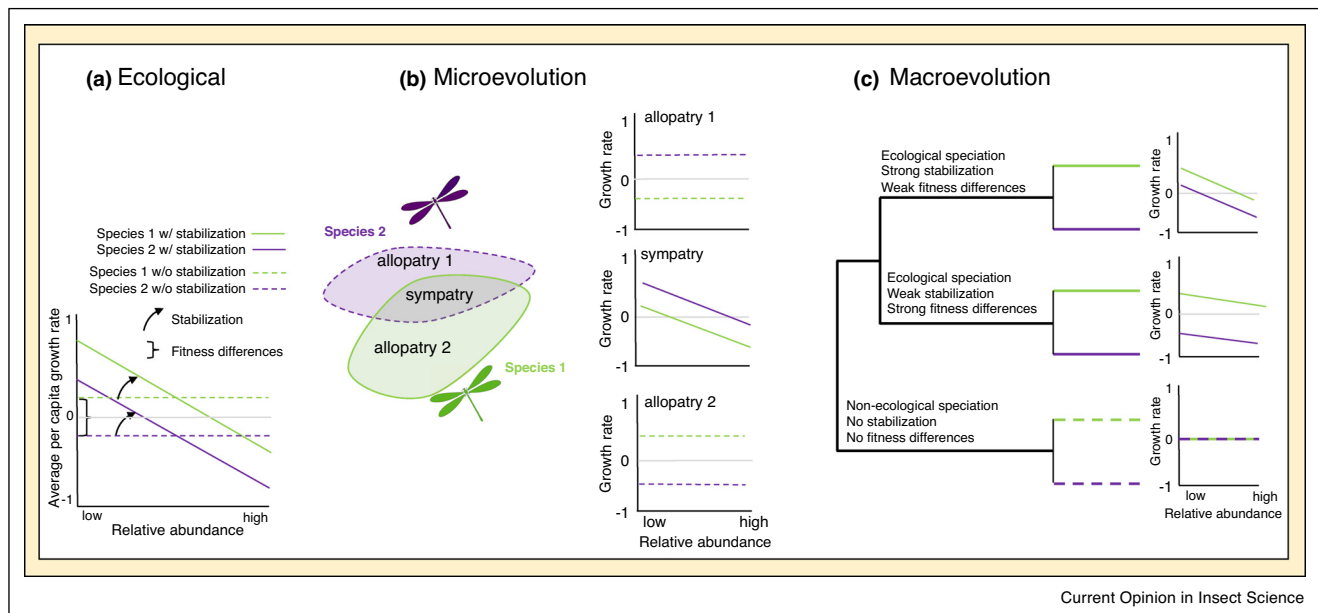
Huxley's quip on an 'inordinate fondness' for beetles and Hutchinson's observations of water boatmen (Corixidae) [1] set the stage for a now vast series of inquiries focused on uncovering astounding levels of species diversity. Hundreds if not thousands of Coleoptera [2] and Hymenoptera species [3], 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

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 [31], 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

simply co-occurring, for example, are neutral species, then for that set of taxa they are essentially replaceable in an ecological community. That is, the diversity *per se* does not matter. But if they are coexisting, the unique ecological properties of those species may critically underlie their abilities to coexist in those communities.

Evidence for coexistence in insects

To evaluate our understanding of insect species coexistence in local communities using Chesson's (2000) coexistence framework, we examined recent studies that focused on coexistence in insect assemblages. We completed a non-exhaustive literature review of studies among insect groups citing key references that have recently spurred the hunt for species coexistence [30,31,33,34].

The results from this exercise were striking: although studies of stabilizing niche differences that could promote coexistence in insect assemblages abound [35], only a single study provided evidence of local species coexistence by demonstrating invasibility [22**]. Using an experimental lab approach, [22**] found that two species of *Callosbruchus* bean beetles exhibited mutual invasibility. Although demonstrating invasibility is the benchmark for coexistence, other approaches are also useful. For instance, [36] estimated competitive zero-growth isoclines with three different genera of grass-eating grasshoppers. Results from this experiment demonstrated intersecting zero-growth isoclines, implying mutual invasibility and indicating that coexistence is achievable under field conditions [36].

Studies of coexistence typically reach the conclusion that an assemblage consists of either niche or neutral species. Yet, there is no reason that any assemblage cannot contain both [26**,37]. Studies of damselfly (Odonata, Zygoptera) diversity demonstrate the need for plurality [35,38,39]. Experimental and observational studies have shown that although stabilizing effects are not operating among *Enallagma* damselfly species assemblages [38], they are operating among three genera of damselflies that co-occur (*Enallagma*, *Ischnura*, and *Lestes*). Thus, multiple types of 'species' can occur in a single system [35,38,39].

Why evolution matters for species coexistence

The study of species coexistence, like many ecological problems, has often ignored or only subtly considered the contribution of evolutionary processes [29]. However, evolution undoubtedly plays an important role [19,21**,24**,26**,29], and may affect the ability for species to coexist in biological communities as species respond to global change. Indeed, evolutionary processes have increasingly been used as part of an emerging framework for developing ideas in community ecology, and coexistence in particular [26**,29,40–43]. Here we

consider microevolution as a focus on shorter-term evolutionary dynamics occurring within populations (e.g., mainly adaptive evolution), and macroevolution as a focus on speciation and extinction dynamics [44]. The contribution of evolutionary processes to Chesson's framework can be applied over varied time scales, as both ongoing micro-evolutionary processes and historical macro-evolutionary processes can shape stabilizing effects and fitness differences (Figure 1).

Microevolutionary contributions towards coexistence

One way that microevolution, particularly local adaptation, might affect coexistence is through character displacement — competitor coevolution to reduce resource competition [21**,29,45–48]. By reducing resource use overlap, character displacement should cause species to experience stronger intraspecific competition relative to interspecific competition, and thereby strengthen stabilizing effects [21**,29,49]. Alternatively, if species evolve towards niche convergence and competitive similarity rather than character displacement, local adaptation may simultaneously affect fitness differences and stabilizing effects [26**,50,51] (Figure 1b). Or there may be no effect of coevolution on coexistence. In the above noted study by [22**] of bean beetles, there were no differences in invasibility between allopatric (e.g., where coevolution could not occur) and sympatric (e.g., where coevolution could occur) evolving populations. Thus, the common perception that competitor coevolution will necessarily promote species coexistence may not necessarily be so [43]. Such studies merging character displacement theory and coexistence theory are exceedingly rare, but are a promising approach for understanding how microevolutionary dynamics may affect local species coexistence [20,21**].

Short-term mutual invasibility experiments may also not predict the long-term outcome of competition when competitive interactions can evolve [50,52]. For instance, evolution can cause species to become more intense competitors [52]. In a lab experiment, houseflies (*Musca domestica*) were initially competitively superior to blowflies (*Phaenicia sericata*). However, in only a few generations, blowflies evolved to become competitively superior and exclude houseflies, demonstrating that fitness differences can rapidly evolve. Thus, although studies are limited, there is no consensus on what rapid evolution does to the ability for species to coexist.

Studies of frequency-dependent selection in polymorphic traits are also illustrative of how ongoing evolutionary processes might shape coexistence. For example, stick insects (*Timema cristinae*) can be striped or unstriped, allowing these insects to be camouflaged from predators on different hosts plants. Using an 18-year data set [53] found that the frequency of striped morphs would increase and then decrease through time — a pattern

consistent with negative frequency dependent selection. These different morphs are in the early stage of ecological speciation; they are ‘incipient species’ [54]. Thus, the ecological and evolutionary dynamics leading to divergent selection on these different morphs and maintaining them in local populations are essentially the early stages of species-level stabilizing effects evolving.

Macroevolutionary contributions towards coexistence

Climate has long been thought to be an important factor contributing to the macroevolutionary dynamics that shape species communities [55]. At the macroevolutionary level, speciation and extinction dynamics can influence coexistence mechanisms [42], in part, by defining the regional and local species pools [56,57]. At this scale, of particular interest is to determine how introducing a new species via speciation, or removal through extinction, causes stabilizing effects and fitness differences to change among the constituent species in the community.

Speciation is in some ways a grand experiment in invasibility. Once a new species has evolved, can it successfully invade a local community where the other species remain intact? Both stabilizing and equalizing processes might affect this. However, we posit that ecological speciation is more likely to lead, at least initially, to coexistence than non-ecological speciation.

With ecological speciation, where reproductive isolation evolves as a by-product of adaptation to different niches [46,58,59], such speciation may immediately produce strong stabilizing effects (e.g., incipient speciation in stick insects [53]) (Figure 1c). Alternatively, if niche differentiation is subtle, stabilizing effects might be weak, and if fitness differences are substantial the result is competitive exclusion (Figure 1c). Stabilizing effects could potentially be further strengthened by local coevolution with competitors [20,21^{**}]. However, this need not be the case. For instance, character displacement appears to have little role for explaining potential coexistence of *Anelosimus* spiders [60]. Instead, ecological differences among these species appear to have evolved in allopatry during speciation, followed by community assembly with no ensuing changes in traits mediating competitive interactions.

By contrast, non-ecological modes of speciation such as those produced through genomic incompatibilities, hybridization and polyploidization, sexual selection, and mate recognition [26^{**},61,62,63^{*},64] may produce species with little to no niche differentiation, and therefore no to weak stabilizing effects [26^{**},38] (Figure 1c). Such species may co-occur, but these speciation modes do not generate coexistence as a by-product. Diverse insect groups such as *Enallagma* damselflies, *Chrysoperla* lacewings, Hawaiian crickets, and *Drosophila* are thought to have speciated via reproductive character displacement [26^{**}]. These species appear to differ largely in mating

system features, not ecologically, and are candidates for neutral species.

Thus, differences in speciation modes might offer a framework for predicting the ability of species to coexist (Figure 1c). Ecological speciation may produce species that are immediately coexisting, whereas non-ecological speciation may produce non-niche differentiated taxa that only co-occur [26^{**}]. This is a tantalizing possibility, because rather than generating predictions of how stabilizing and fitness equalizing effects might vary based on how closely or distantly related taxa are [65–67], the macroevolutionary dynamics of speciation may be more informative. Of course, simply because speciation occurred ecologically or non-ecologically does not mean that populations of the resulting species cannot undergo niche divergence that might promote local coexistence, or by contrast convergence reducing niche and fitness differences (e.g., Figure 1b). Indeed, the ecology of species differences that promote niche differentiation are not necessarily the same as those driving speciation [62].

By contrast to speciation, how the macroevolutionary dynamics of extinction affect coexistence is less well understood and rarely considered [42]. Yet, the ramifications of extinction are multifarious and not always obvious. On the one hand, global or local extinction of one member of a pair of competing species has an overt equalizing effect, immediately removing any fitness differences. In the simplest case of pair-wise competition, this also means that the remaining species need not occupy a unique competitive niche to persist. However, this ‘simplest case’, and much of our thinking on competitor coexistence, is framed as a problem of pairwise competition [68,69^{**}], which is often an unrealistic caricature of communities.

Most communities have multiple species, and this diversity affords the opportunity for coexistence mechanisms where the effects of extinction may be key. In some cases, coexistence between two competitors is dependent on indirect interactions with other competitors, which can affect stabilizing mechanisms and fitness differences [69^{**}]. Under intransitive competition, for example, the indirect competitive effects that one species exerts on another are what allow another competitor to coexist. Thus, extinction of one species can cause an extinction cascade [69^{**},70]. However, only recently has an invasibility criteria been developed for intransitive competition [68] and quantifying intransitivity is challenging [71]. For this reason, examples of these dynamics in insects are currently not known, aside from a theoretical model of cactus tending ants [72]. Overall, much work remains on the contribution of extinction as a process mediating species coexistence. But, understanding how extinctions may affect the ability of species coexist will become an increasingly pressing issue as climate change is expected to accelerate the rate of extinction [14].

Conclusion

Global change is expected to continue altering the makeup of ecological communities. How communities will respond to such changes depends, in part, on whether or not species are currently coexisting. Although insects have long been studied for their diversity, it remains unclear though whether this rich diversity exists because species ecological interactions result in them locally coexisting or simply co-occurring with one another. Evaluating coexistence criteria should be a goal, as this will help determine the prospects for communities to successfully reassemble (i.e., invasibility dynamics) and resume functioning as species move or adapt to altered environmental conditions. Indeed, global change will affect not only the ecological processes structuring communities, but also the evolutionary processes shaping the abilities for species to persist in novel climate conditions and novel biological communities. Consequently, studies integrating ecology and evolutionary perspectives will ultimately be necessary to better understand how and why insect communities will respond to global change.

Conflict of interest statement

Nothing declared.

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as

• of special interest

•• of outstanding interest

- Hutchinson GE: **Homage to Santa Rosalia or why are there so many kinds of animals?** *Am Nat* 1959, **93**:145-159.
 - Erwin TL: Tropical forests: their richness in Coleoptera and other arthropod species. 1982.
 - Stork NE: **Insect diversity: facts, fiction and speculation.** *Biol J Linn Soc* 1988, **35**:321-337.
 - Devries PJ, Walla TR: **Species diversity and community structure in neotropical fruit-feeding butterflies.** *Biol J Linn Soc* 2001, **74**:1-15.
 - Loboda S, Savage J, Buddle CM, Schmidt NM, Høye TT: **Declining diversity and abundance of high Arctic fly assemblages over two decades of rapid climate warming.** *Ecography* 2018, **41**:265-277.
 - Pyne MI, Poff NL: **Vulnerability of stream community composition and function to projected thermal warming and hydrologic change across ecoregions in the western United States.** *Global Change Biol* 2017, **23**:77-93.
 - Parmesan C: **Ecological and evolutionary responses to recent climate change.** *Annu Rev Ecol Syst* 2006:637-669.
 - Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJ, Fromentin J-M, Hoegh-Guldberg O, Bairlein F: **Ecological responses to recent climate change.** *Nature* 2002, **416**:389.
 - Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD: **Rapid range shifts of species associated with high levels of climate warming.** *Science* 2011, **333**:1024-1026.
 - Alexander JM, Diez JM, Hart SP, Levine JM: **When climate reshuffles competitors: a call for experimental macroecology.** *Trends Ecol Evol* 2016, **31**:831-841.
- An insightful piece on thinking about how moderate coexistence theory can be applied in the context of altered community composition.
- Merckx T, Souffreau C, Kaiser A, Baardtsen LF, Backeljau T, Bonte D, Brans KI, Cours M, Dahirel M, Debortoli N: **Body-size shifts in aquatic and terrestrial urban communities.** *Nature* 2018:1.
 - Williams JW, Jackson ST: **Novel climates, no-analog communities, and ecological surprises.** *Front Ecol Environ* 2007, **5**:475-482.
 - Gilman SE, Urban MC, Tewksbury J, Gilchrist GW, Holt RD: **A framework for community interactions under climate change.** *Trends Ecol Evol* 2010, **25**:325-331.
 - Urban MC: **Accelerating extinction risk from climate change.** *Science* 2015, **348**:571-573.
 - Godsoe W, Jankowski J, Holt RD, Gravel D: **Integrating biogeography with contemporary niche theory.** *Trends Ecol Evol* 2017, **32**:488-499.
 - Grainger TN, Rego AI, Gilbert B: **Temperature-dependent species interactions shape priority effects and the persistence of unequal competitors.** *Am Nat* 2018, **191**:197-209.
 - Hoffman AA, Sgrò CM: **Climate change and evolutionary adaptation.** *Nature* 2011, **470**:479-485.
 - Siepielski AM, Morrissey MB, Buoro M, Carlson SM, Caruso CM, Clegg SM, Coulson T, DiBattista J, Gotanda KM, Francis CD: **Precipitation drives global variation in natural selection.** *Science* 2017, **355**:959-962.
 - Schreiber SJ, Patel S, terHorst C: **Evolution as a coexistence mechanism: does genetic architecture matter?** *Am Nat* 2018, **191**.
 - Bassar RD, Simon T, Roberts W, Travis J, Reznick DN: **The evolution of coexistence: reciprocal adaptation promotes the assembly of a simple community.** *Evolution* 2017, **71**:373-385.
 - Germain RM, Williams JL, Schluter D, Angert AL: **Moving character displacement beyond characters using contemporary coexistence theory.** *Trends Ecol Evol* 2017, **33**:74-84.
- An insightful overview articulating how the rich theory of character displacement can be combined with coexistence theory to derive expectations for detecting the demographic signature of character displacement. This paper abounds in presenting testable ideas for combining ecological and evolutionary ideas in species coexistence.
- Hausch SJ, Fox JW, Vamosi SM: **Coevolution of competing Callosobruchus species does not stabilize coexistence.** *Ecol Evol* 2017, **7**:6540-6548.
- The only empirical study with insects demonstrating invasibility and the contribution of ongoing evolution in shaping insect species coexistence.
- Chesson P, Kuang JJ: **The interaction between predation and competition.** *Nature* 2008, **456**:235-238.
 - Hendry AP: **An excellent and substantial overview of contemporary ideas on how ecological processes can be better understood by incorporating evolutionary processes.** *Eco-evolutionary Dynamics*. Princeton University Press; 2016.
 - terHorst CP, Zee PC, Heath KD, Miller TE, Pastore AI, Patel S, Schreiber SJ, Wade MJ, Walsh MR: **Evolution in a community context: trait responses to multiple species interactions.** *Am Nat* 2018, **191**.
- An insightful overview of leading ideas on how evolution can proceed in a community context. Although the complexity of biological communities fascinates community ecologists and evolutionary biologists alike, ideas for how to proceed in thinking about trait evolution in response to multi-

species interactions are limited. This paper provide an overview of current thinking and future research directions.

26. McPeck MA: **An invaluable, masterful monograph elaborating how ecological and evolutionary perspectives can be combined in a unified theoretical framework to address outstanding problems in community ecology. Considerable effort is put forth to demonstrate how ecologists and evolutionary biologists are often working on the same basic problems, but tend to use different language..** *Evolutionary Community Ecology*, vol 58. Princeton University Press; 2017.
 27. Siepielski AM, Nemirov A, Cattivera M, Nickerson A: **Experimental evidence for an eco-evolutionary coupling between local adaptation and intraspecific competition.** *Am Nat* 2016, **187**:447-456.
 28. Hart SP, Usinowicz J, Levine JM: **The spatial scales of species coexistence.** *Nat Ecol Evol* 2017, **1**:1066.
 29. Lankau RA: **Rapid evolutionary change and the coexistence of species.** *Annu Rev Ecol Evol Syst* 2011, **42**:335-354.
 30. Siepielski AM, McPeck MA: **On the evidence for species coexistence: a critique of the coexistence program.** *Ecology* 2010, **91**:3153-3164.
 31. Chesson P: **Mechanisms of maintenance of species diversity.** *Annu Rev Ecol Syst* 2000:343-366.
 32. Turelli M: **A reexamination of stability in randomly varying versus deterministic environments with comments on the stochastic theory of limiting similarity.** *Theoretical Popul Biol* 1978, **13**:244-267.
 33. Hubbell SP: *The Unified Neutral Theory of Biodiversity and Biogeography (MPB-32)*, vol 32. Princeton University Press; 2001.
 34. Adler PB, Hillerislambers J, Levine JM: **A niche for neutrality.** *Ecol Lett* 2007, **10**:95-104.
 35. Svensson E, Gomez-Llano M, Torres A, Bensch H: **Frequency-dependence and ecological drift shape coexistence of species with similar niches.** *Am Nat* 2018, **191**:691-703.
 36. Chase JM: **Differential competitive interactions and the included niche: an experimental analysis with grasshoppers.** *Oikos* 1996, **76**:103-112.
 37. Leibold MA, McPeck MA: **Coexistence of the niche and neutral perspectives in community ecology.** *Ecology* 2006, **87**:1399-1410.
 38. Siepielski AM, Hung KL, Bein EEB, McPeck MA: **Experimental evidence for neutral community dynamics governing an insect assemblage.** *Ecology* 2010, **91**:847-857.
 39. Siepielski AM, Mertens AN, Wilkinson BL, McPeck MA: **Signature of ecological partitioning in the maintenance of damselfly diversity.** *J Anim Ecol* 2011, **80**:1163-1173.
 40. Vellend M: **Conceptual synthesis in community ecology.** *Quart Rev Biol* 2010, **85**:183-206.
 41. Vellend M: *The Theory of Ecological Communities (mpb-57)*. Princeton University Press; 2016.
 42. Weber MG, Strauss SY: **Coexistence in close relatives: beyond competition and reproductive isolation in sister taxa.** *Annu Rev Ecol Evol Syst* 2016, **47**:359-381.
 43. Vasseur DA, Amarasekare P, Rudolf VH, Levine JM: **Eco-evolutionary dynamics enable coexistence via neighborhood-dependent selection.** *Am Nat* 2011, **178**:E96-E109.
 44. Reznick DN, Ricklefs RE: **Darwin's bridge between microevolution and macroevolution.** *Nature* 2009, **457**:837.
 45. Pfennig DW, Pfennig KS: *Evolution's Wedge: Competition and the Origins Of Diversity*. Univ of California Press; 2012.
 46. Schluter D: *The Ecology of Adaptive Radiation*. Oxford University Press; 2000.
 47. Taper ML, Case T: **Coevolution among competitors.** *Oxford Surveys Evol Biol* 1992, **8**:63.
 48. Stroud JT, Losos JB: **Ecological opportunity and adaptive radiation.** *Annu Rev Ecol Evol Syst* 2016:47.
 49. Pritchard JR, Schluter D: **Declining interspecific competition during character displacement: summoning the ghost of competition past.** *Evol Ecol Res* 2001, **3**:209-220.
 50. Fox JW, Vasseur DA: **Character convergence under competition for nutritionally essential resources.** *Am Nat* 2008, **172**:667-680.
 51. HilleRisLambers J, Adler PB, Harpole WS, Levine JM, Mayfield MM: **Rethinking community assembly through the lens of coexistence theory.** *Annu Rev Ecol Evol Syst* 2012, **43**:227-248.
 52. Pimentel D, Feinberg EH, Wood PW, Hayes JT: **Selection, spatial distribution, and the coexistence of competing fly species.** *Am Nat* 1965, **99**:97-109.
 53. Nosil P, Villoutreix R, de Carvalho CF, Farkas TE, Soria-Carrasco V, Feder JL, Crespi BJ, Gompert Z: **Natural selection and the predictability of evolution in Timema stick insects.** *Science* 2018, **359**:765-770.
 54. Soria-Carrasco V, Gompert Z, Comeault AA, Farkas TE, Parchman TL, Johnston JS, Buerkle CA, Feder JL, Bast J, Schwander T: **Stick insect genomes reveal natural selection's role in parallel speciation.** *Science* 2014, **344**:738-742.
 55. Ezard TH, Aze T, Pearson PN, Purvis A: **Interplay between changing climate and species' ecology drives macroevolutionary dynamics.** *Science* 2011, **332**:349-351.
 56. Mittelbach GG, Schemske DW: **Ecological and evolutionary perspectives on community assembly.** *Trends Ecol Evol* 2015, **30**:241-247.
 57. Ricklefs RE: **Community diversity: relative roles of local and regional processes.** *Science* 1987, **235**:167-171.
 58. Schluter D: **Ecology and the origin of species.** *Trends Ecol Evol* 2001, **16**:372-380.
 59. Nosil P: *Ecological Speciation*. Oxford University Press; 2012.
 60. Agnarsson I, Gotelli NJ, Agostini D, Kuntner M: **Limited role of character displacement in the coexistence of congeneric Anelosimus spiders in a Madagascan montane forest.** *Ecography* 2016, **39**:743-753.
 61. Rundell RJ, Price TD: **Adaptive radiation, nonadaptive radiation, ecological speciation and nonecological speciation.** *Trends Ecol Evol* 2009, **24**:394-399.
 62. Svensson EI: **Non-ecological speciation, niche conservatism and thermal adaptation: how are they connected?** *Organ Divers Evol* 2012, **12**:229-240.
 63. Wellenreuther M, Sánchez-Guillén RA: **Nonadaptive radiation in damselflies.** *Evol Appl* 2016, **9**:103-118.
- An overview of how non-adaptive mechanism can contribute to species radiations, focusing on damselflies. For those seeking a counter-point to the wealth of evidence for adaptive radiations, this paper presents a balanced perspective.
64. Servedio MR, Boughman JW: **The role of sexual selection in local adaptation and speciation.** *Annu Rev Ecol Evol Syst* 2017, **48**:85-109.
 65. Narwani A, Alexandrou MA, Oakley TH, Carroll IT, Cardinale BJ: **Experimental evidence that evolutionary relatedness does not affect the ecological mechanisms of coexistence in freshwater green algae.** *Ecol Lett* 2013, **16**:1373-1381.
 66. Godoy O, Kraft NJ, Levine JM: **Phylogenetic relatedness and the determinants of competitive outcomes.** *Ecol Lett* 2014, **17**:836-844.
 67. Germain RM, Weir JT, Gilbert B: **Species coexistence: macroevolutionary relationships and the contingency of historical interactions.** *Proc R Soc Lond B Biol Sci* 2016:283.
 68. Gallien L, Zimmermann NE, Levine JM, Adler PB: **The effects of intransitive competition on coexistence.** *Ecol Lett* 2017, **20**:791-800.

69. Levine JM, Bascompte J, Adler PB, Allesina S: **Beyond pairwise mechanisms of species coexistence in complex communities.** *Nature* 2017, **546**:56-64.

A solid overview of multiple ideas in multi-species competitive communities. The ideas of intransitive dynamics are made especially clear in light of modern coexistence theory.

70. Case TJ: **Invasion resistance, species build-up and community collapse in metapopulation models with interspecies**

competition. *Metapopulation Dynamics: Empirical and Theoretical Investigations.* Elsevier; 1991:239-266.

71. Laird RA, Schamp BS: **Calculating competitive intransitivity: computational challenges.** *Am Nat* 2018, **191**.
72. Morris WF, Wilson WG, Bronstein JL, Ness JH: **Environmental forcing and the competitive dynamics of a guild of cactus-tending ant mutualists.** *Ecology* 2005, **86**:3190-3199.