

Review

The Invasion Criterion: A Common Currency for Ecological Research

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According to the invasion criterion, stable coexistence requires that all species in a community increase in abundance when rare, which occurs when stabilizing mechanisms cause intraspecific competition to be stronger than interspecific competition. This simple principle has traditionally been applied to tests of local coexistence in a narrow range of ecological systems. However, new theory founded on the invasion criterion is emerging across ecological fields ranging from eco-evolutionary dynamics to global change to macroecology. Concurrently, straightforward methods for testing the invasion criterion have been proposed, but remain underused. Here, we identify the invasion criterion as a common thread linking emerging ecological theory, and we bring this theory together with the methods that can be used to test it.

The Invasion Criterion: Then and Now

The **mutual invasion criterion** (see [Glossary](#)) for stable **coexistence** requires that each species in a community experiences positive population growth rates when invading an established community of competitors from low density [1–3]. This criterion is met when species are more limited by individuals of their own species than by individuals of other species, and negative frequency-dependent growth rates give each species an advantage when rare. This rarity advantage can arise through mechanisms such as host-specific natural enemies, interspecific differences in resource use, or spatial covariance between responses to the environment and competition [1]. The mutual invasion criterion (hereafter invasion criterion) has been championed as a definitive test of coexistence, because when it is met, each species will rebound if population sizes are reduced, long-term population growth rates will be positive, and no species is expected to go extinct ([4,5], but see [Box 1](#)).

Despite a longstanding preoccupation with coexistence in the ecological literature and the recognized value of the invasion criterion for demonstrating stable coexistence, empirical tests of the invasion criterion have, until recently, been exceedingly rare [5]. A review by Siepielski and McPeck [5] found that, of 323 empirical studies focused on coexistence, only seven reported evidence that co-occurring species satisfied the invasion criterion. Unfortunately, the traditionally narrow application of the invasion criterion to tests of local coexistence in two-species communities under equilibrium conditions, along with the practical challenges of empirically testing this principle in many systems, has led to a restricted use of this powerful approach.

Fortunately, there is a growing interest in applying the invasion criterion to a broader range of questions that reach beyond local coexistence in competitive communities. A suite of recent theoretical frameworks advocate for the use of invasibility tests to investigate processes ranging from **character displacement** to range limits to invasive species to trophic interactions ([Table 1](#)). Many use theory developed by Chesson [1], often referred to as **modern coexistence theory**, which describes two quantities that jointly determine whether competing species can mutually invade. First, **stabilizing niche differences** promote mutual invasibility and can arise from any

Highlights

The invasion criterion has historically been applied to tests of local coexistence in a narrow range of ecological systems.

New theory based on the invasion criterion is rapidly emerging, while new methods that allow researchers to test this principle across a broader range of systems have been introduced.

We identify the invasion criterion as a common thread that links emerging theory across a range of ecological fields, and we bring this theory together with the methods that can be used to test it.

We hope to facilitate the empirical application of the invasion criterion to a range of questions that reach beyond tests of local coexistence.

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mechanism that increases the strength of intraspecific competition relative to interspecific competition (e.g., differences in resource use). Second, species' average **fitness differences** allow only one species to invade (**competitive exclusion**) and arise from interspecific differences in growth rates and sensitivity to competition that favor one competitor over the other. Mutual invasibility occurs when competitors' stabilizing niche differences more than offset their fitness differences [1,4]. The range of emerging theories founded on the invasion criterion, and their links to modern coexistence theory, present an exciting opportunity to expand the application of this principle to new questions and systems (Table 1).

Concurrently, several simple but powerful empirical methods that can be used to test the invasion criterion have been introduced (Figure 1) [6–8]. These methods quantify **invasion growth rates** by measuring them experimentally (Figure 1A), by inferring them from parameterized competition models (Figure 1B), or by collecting demographic data in natural populations tracked through space and time (Figure 1C). Some of these methods can incorporate stochastic equilibrium dynamics that occur in fluctuating environments, which increases the relevance of this approach to real-world systems (Figure 1C and Box 1). In addition, many of these methods also allow researchers to calculate fitness and stabilizing niche differences, making them especially powerful (Figure 1A–C) [6,9,10].

Here, we highlight the invasion criterion as a common thread linking a broad range of theoretical concepts emerging across ecological fields (Table 1), and we connect these theories to the methodological advances that are making it possible to test them (Figure 1). We address this interface because many of the theories remain untested, while many of the methods remain underused [6] or poorly understood [8,11]. We also highlight several important shortcomings of the invasion criterion in order to identify research questions that would be better served by alternative approaches and to outline where further research is needed to fill existing gaps (Box 1). We hope that this synthesis will encourage researchers to continue to expand the theoretical and methodological frontiers of the invasion criterion.

Eco-evolutionary Dynamics

The conditions under which organisms evolve shape the traits and demographic responses that drive coexistence [12,13]. Two theoretical frameworks have described how invasibility tests can be used to understand the processes through which evolution shapes species interactions, and vice versa [14,15].

The first framework, proposed by Mayfield and Levine [15], outlines predictions for how competing species' evolutionary relatedness or macroevolutionary history influences their ability to coexist. This framework uses modern coexistence theory to refine the long-held idea that closely related species should be similar, have high niche overlap, and be unlikely to coexist [13,16]. Mayfield and Levine [15] point out that while evolved stabilizing niche differences may indeed be lower between closely related taxa, fitness differences are just as likely to carry a phylogenetic signal. Because closely related species would be expected to have both lower stabilizing niche differences (precluding coexistence) and lower fitness differences (promoting coexistence) if traits regulating these differences are phylogenetically conserved, the relationship between relatedness and coexistence depends on the relative rates at which these two types of species differences evolve [15].

To test this prediction, researchers have used invasibility tests to partition species' competitive interactions into their component fitness and stabilizing niche differences (Figure 1) and have then looked for relationships between these two types of species differences and evolutionary relatedness derived from phylogenies [17–19]. Of the empirical studies that have taken this approach,

Glossary

Character displacement:

evolutionary outcome of competition between similar species with overlapping ranges in which species' characters (traits) become increasingly dissimilar owing to selection imposed by competitive interactions. This can create a stabilizing niche difference that facilitates coexistence.

Coexistence: in the context of the invasion criterion, coexistence occurs when all competitors have positive invasion growth rates.

Competition coefficient: the *per capita* effect of a competitor on a focal species' population growth rate.

Competitive exclusion: in the context of the invasion criterion, competitive exclusion occurs when one species has a positive invasion growth rate and its competitor has a negative invasion growth rate.

Fitness differences: differences between species in their average ability to compete that facilitate competitive exclusion. Fitness differences result from differences in population growth rates and sensitivity to competition. Note that, in modern coexistence theory, 'fitness' refers to the average fitness of a given species and takes into account all of the conditions that a population of that species experiences. This definition is fundamentally different from the use of this term in evolutionary biology.

Invasion growth rate: the population growth rate of a species when it is rare and a population or community of competitor(s) is at equilibrium. When positive, the invasion criterion for the focal species is satisfied.

Modern coexistence theory: theory by Peter Chesson [1] that decomposes invasion growth rates into fitness differences and stabilizing niche differences. Stable coexistence occurs when stabilizing niche differences are strong enough to overcome fitness differences.

Mutual invasion criterion: the mutual invasion criterion is met when all species in a community have positive invasion growth rates. While we use the term 'invasion criterion' as shorthand for the mutual invasion criterion, the invasion criterion can also refer to the positive growth of a single species when rare in a community.

Priority effects: phenomenon in which the order of arrival of species at a local site determines the outcome of

none has found a significant relationship between evolutionary relatedness and coexistence outcomes and, interestingly, each found different effects of phylogenetic distance on fitness and stabilizing niche differences [17–19]. While an invasion experiment with algae (Figure 1A) reported no effect of phylogenetic relatedness on fitness or stabilizing niche differences [19], competition experiments with annual plants (Figure 1B) have shown that distantly related species have larger fitness differences [18] and that the relationship between species differences and relatedness depends on whether or not competing species had evolved in the same geographic location [17]. These results suggest that more empirical tests of this theory are needed, and that combining evolutionary theory with knowledge of biogeographic history (i.e., whether species evolved in sympatry or allopatry) could generate more nuanced predictions for this framework [17,20].

A second framework, proposed by Germain *et al.* [14], describes how the invasion criterion could be used to test for evidence of character displacement. Traditional tests of character displacement investigate whether traits presumed to be important for competition are more dissimilar between competing species that occur in sympatry than allopatry [21]. Germain *et al.* [14] point out that this approach is biased towards observable trait differences, does not quantify the effect of character displacement on competitive interactions, and is likely to underestimate the prevalence of character displacement. These authors propose that a more rigorous test of character displacement would use invasibility tests to determine whether evolution in sympatry increases or decreases the likelihood of coexistence [14]. Importantly, invasibility tests can identify instances of character displacement that occur via niche divergence (giving both species an advantage when rare) or niche convergence (giving one species an advantage and the other a disadvantage when rare) [14]. Additionally, invasibility tests that allow for the calculation of fitness and stabilizing niche differences (Figure 1A–C) could be combined with trait measurements to determine how displaced characters affect competitive dynamics [14,20]. Germain *et al.* [14] predict that in

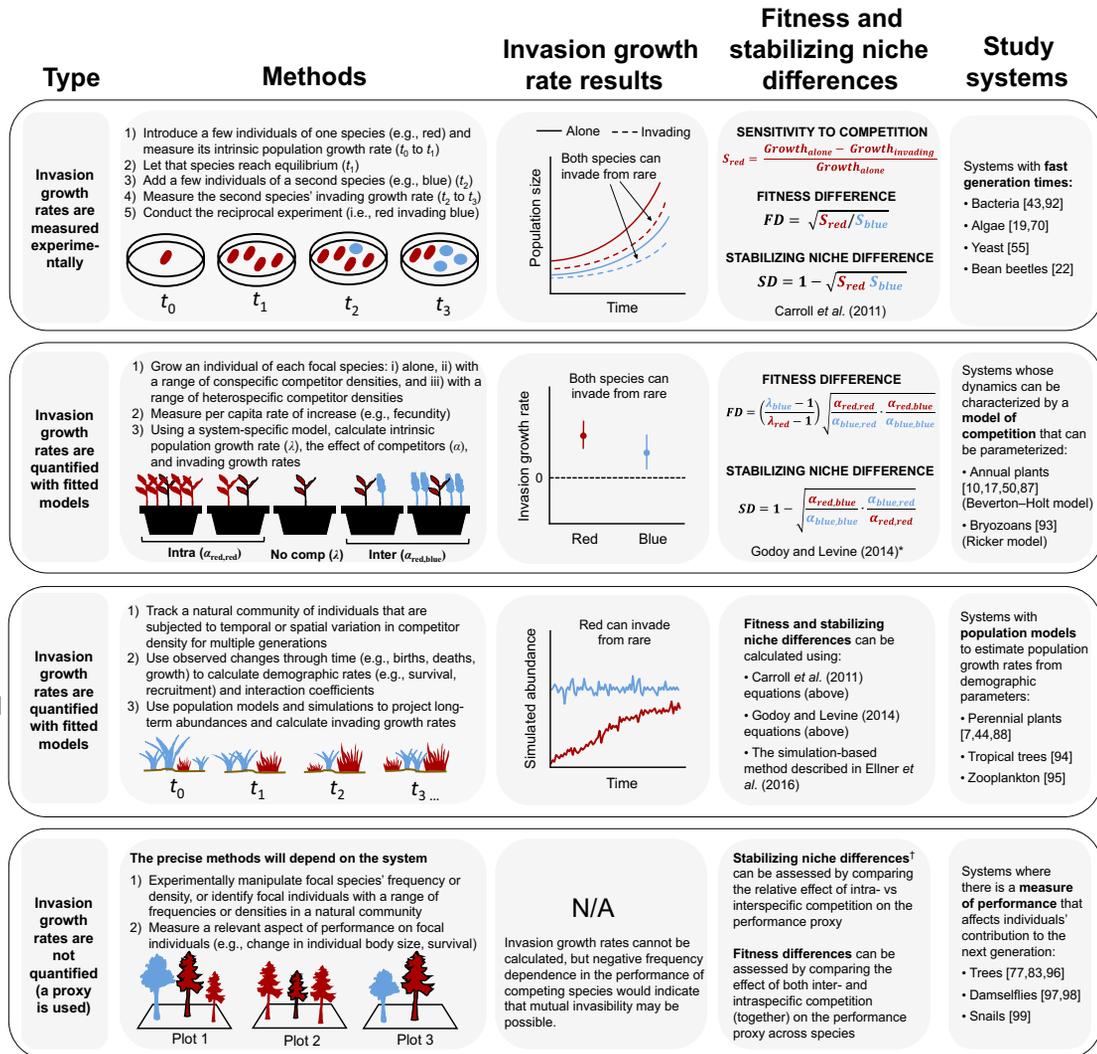
competition. In the context of the invasion criterion, this occurs when species have positive frequency-dependent growth rates that prevent any species from invading (i.e., mutual noninvasibility).

Stabilizing niche differences:

interspecific differences in resource use, host-specific natural enemies, or other mechanisms that cause intraspecific competition to be stronger than interspecific competition.

Table 1. Summary of Theoretical Frameworks That Use the Invasion Criterion

Topic	Process	Describes how to use invasibility tests to determine:	Framework or theory
Eco-evolutionary dynamics	Phylogenetic community assembly	The relationship between species' evolutionary relatedness and coexistence	Mayfield and Levine [15]
	Character displacement	Whether character displacement has occurred and its effect on coexistence	Germain <i>et al.</i> [14]
Macroecology	Range limits	The role of abiotic and biotic conditions in delineating range limits	Louthan <i>et al.</i> [26] Jones and Gilbert [25] Godsoe <i>et al.</i> [24] Alexander <i>et al.</i> [33]
Global change ecology	Invasive species	The success and impact of biological invasions	MacDougall <i>et al.</i> [38]
	Climate change	The effect of climate change on species interactions and coexistence	Adler <i>et al.</i> [44] Chesson [52]
Complex competitive outcomes	Priority effects	The presence of priority effects in a community and the conditions that promote priority effects	Mordecai [57] Fukami <i>et al.</i> [75] Ke and Letten [56]
	Indirect effects of competition	How intransitive competition and interaction chains impact coexistence	Barabás <i>et al.</i> [64] Saavedra <i>et al.</i> [66] Levine <i>et al.</i> [65] Chesson [67]
Non-competitive species interactions	Facilitation	The presence of facilitation and the conditions that promote it	Venail <i>et al.</i> [70] Ellner <i>et al.</i> [9] Bimler <i>et al.</i> [72]
	Trophic interactions	How predators promote or preclude coexistence	Chesson and Kuang [69] Godoy <i>et al.</i> [76]



Trends in Ecology & Evolution

Figure 1. How to Test the Invasion Criterion. The invasion criterion can be tested by measuring species' invasion growth rates (A) or parameterizing a model to estimate invasion growth rates (B,C), or it can be qualitatively assessed by determining the effect of conspecific and heterospecific density on a proxy for population growth rates such as individual growth or change in body size (D). Detailed descriptions of the methods can be found in [19] (Direct invasion), [8] (Competition experiment), [7] (Observational data), and [77] (Performance proxy). 'Methods' shows a dark red species competing with a light blue species, with the focal individual of the red species in (B,D) outlined in black. 'Invasion growth rate results' gives examples of how the results obtained for each method could be visualized. 'Fitness and stabilizing niche differences' shows the equations that can be used to connect the invasion criterion to modern coexistence theory. The asterisk (*) indicates that although the equations in [10] apply to systems described by the Beverton–Holt or Ricker models of (discrete) competition, this approach can also be used with continuous models of competition (e.g., Lotka–Volterra) [78]. The dagger (†) indicates that estimates of the strength of fitness and stabilizing niche differences obtained using method (D) will be subsets of the true values because they are obtained from a subset of the demographic transitions that contribute to population growth rates. See also [6,9,17,22,43,44,50,55,70,83,87,88,92–99]

sympatry, stabilizing niche differences should be stronger as a result of character displacement that reduces niche overlap, while fitness differences should be weaker as a result of character convergence that reduces competitive asymmetries. While a recent study that used this approach to test mutual invasibility in beetle populations experimentally evolved in sympatry and allopatry found no effect of evolutionary history on invasibility [22], these ideas remain largely untested.

Macroecology

A species' range is defined as the geographical region within which it sustains positive population growth in the presence of competitors and natural enemies, indicating the potential utility of invasibility tests for understanding current and shifting range limits [23–27]. In particular, invasibility tests could be used to more explicitly integrate competitive interactions into range limit experiments in order to help clarify the role of biotic interactions in shaping ranges [24–28].

A common prediction for how biotic interactions contribute to species' ranges is that abiotic conditions limit species' expansion at the stressful (e.g., high latitude or elevation) end of the range, while competitors constrain growth rates at the non-stressful (e.g., low latitude or elevation) end of the range [16,29,30]. Several recent reviews have advocated testing this theory using transplant experiments that compare population growth rates in the presence versus absence of competitors at the range center, range margins, and beyond the range edge [24–26]. While transplant experiments are often used to determine how some component of a species' performance or evolutionary fitness changes across the range (Figure 1D), quantifying invading population growth rates throughout the range would allow for a more explicit test of where species are self-sustaining and where biotic interactions delineate ranges [28,31,32]. Indeed, recent experimental designs (Figure 1A,B) could be used to simultaneously quantify a species' sensitivity to competition and its ability to invade from low density, which would allow for tests of the hypothesis that competition varies across a latitudinal or altitudinal gradient.

While it is worthwhile and informative to determine whether one competitor is able to invade without focusing on the other competitor(s), as described above, conducting full mutual invasibility tests would provide a more complete picture of species interactions across the range. In particular, quantifying fitness and stabilizing niche differences across the range, as suggested in several recent papers [24,25,33,34], would reveal whether declining growth rates towards range margins are due to decreased competitive fitness of the focal species, increased fitness of competitor(s), or increased overlap in resource use (i.e., reduced niche difference) [33]. One challenge with this approach is that modern coexistence theory generally assumes that species have positive growth in the absence of competitors, so the quantification of fitness and stabilizing niche differences would be restricted to within the potential range [1]. Likewise, the integration of broader-scale coexistence mechanisms not captured by local invasibility tests will require the tools of spatial coexistence theory, which can account for the stabilizing effects of species' differential growth rates across heterogeneous environments [24,27,35].

Global Change Ecology

The invasion criterion has primarily been used to understand the mechanisms that promote the coexistence of species in present-day communities [5]. However, this principle can also clarify how novel biotic and abiotic conditions created by anthropogenic change will shape future communities.

Successful biological invasions occur when an exotic species achieves positive growth rates when introduced into a native community, indicating a clear link between the invasion criterion and invasive species research [36]. Experimentally testing the ability of native and exotic species to mutually invade allows researchers to determine whether invasion success results from the inherent competitive dominance of the invader or from other mechanisms such as propagule pressure, disturbance, or enemy release. Experimental work investigating the drivers of species invasions using mutual invasibility tests has revealed that native species can be surprisingly strong competitors and that disturbance, recruitment limitation, and resource availability play important roles in facilitating invasion success [36,37].

Building on these ideas, MacDougall *et al.* [38] point out that while the idea that invasive species are somehow different or better than native species is common in invasive species research [39,40], modern coexistence theory could be used to determine more precisely how niche differentiation and competitive superiority contribute to invasion success [38]. This would allow researchers to predict when exotic species should be expected to invade and displace native populations or to naturalize with little impact on native communities. MacDougall *et al.* [38] hypothesize that strong stabilizing niche differences between native and exotic species should favor whichever species is at low abundance, which would allow natives to coexist with successful invaders (i.e., naturalization) [38]. By contrast, fitness differences that favor exotic species should lead to deterministic invasions that exclude native species [38]. Empirical tests of this principle with plants have demonstrated that fitness differences that favor exotic species contribute strongly to invader success [10,41,42]. However, one recent study that used direct invasion tests with bacteria (Figure 1A) found that invaders' ability to establish and become abundant was positively correlated with the strength of stabilizing niche differences between natives and exotics [43].

Invasibility tests can also be used to understand the effects of climate change on species interactions. It is well recognized that changes in the abiotic conditions under which species compete can alter competitive dynamics [23,44,45] and that these indirect competitive effects can be as important as the direct effects of abiotic conditions in determining species' performance and persistence [46–48]. Research on this topic is often focused on how changing abiotic conditions alter competitive hierarchies (i.e., fitness differences) by differentially affecting competing species' physiological and demographical responses [46,49]. However, as Adler *et al.* [44] point out, a full understanding of how species interactions mediate responses to climate change also necessitates a consideration of stabilizing niche differences, as these determine how strongly species compete and thus dictate how sensitive a species is to changes in the relative fitness of a competitor [4]. Adler *et al.* [44] predict, and demonstrate using a perennial plant system (Figure 1C), that competing species with weak stabilizing niche differences are more likely to experience indirect, competition-mediated effects of climate change than competing species with strong stabilizing niche differences. Additionally, stabilizing niche differences can themselves be altered by anthropogenic change. For example, drought could reduce stabilizing niche differences if water becomes restricted to deep soil layers and niche differentiation resulting from differences in root length are dampened [50]. Likewise, temperature can affect niche overlap by altering the timing of species' life history events [51]. Finally, recent theory describes how to assess invasibility in continually changing, nonstationary environments by summing or integrating population growth rates over time [52,53]. This theory provides empiricists with the tools to understand how coexistence is affected by global changes characterized by gradual directional environmental change, rather than changes in average conditions (e.g., cool to warm, wet to dry). Although these approaches have yet to be widely applied, they could provide a framework for determining how coexistence outcomes will be altered by anthropogenic change [44].

Complex Competitive Outcomes

The invasion criterion has primarily been used to study two outcomes of pairwise competition: coexistence (mutual invasibility) and competitive exclusion (only one species can invade) [1,2,4]. However, this principle can also be extended to investigate **priority effects** (mutual noninvasibility) and the complex competitive outcomes that can emerge in multispecies communities.

Priority effects occur when the order of species' arrival at a local site determines the outcome of competition and the trajectory of community assembly [54]. In the context of the invasion criterion, priority effects can be defined as the inability of either species to invade an established population of its competitor due to positive frequency-dependent population growth rates that favor

whichever species is initially more abundant [55–57]. Positive frequency-dependent growth can result from mechanisms such as plant–soil feedbacks, mutualistic interactions, or reproductive interference [58–60]. Modern coexistence theory can also be extended to include priority effects by recognizing that mutual noninvasibility occurs when species have strong enough negative stabilizing differences (i.e., destabilizing differences) to overcome fitness differences that promote competitive exclusion [1,55,56,61]. This mutual noninvasibility criterion lays a clear path for using invasion tests to understand priority effects [56]. Moreover, empirical evidence from studies that have used a modern coexistence approach report that an average of 17% of species pairs exhibit destabilizing differences [55], suggesting that it would be worthwhile to include this third outcome in coexistence research. Indeed, a recent experiment that used direct invasion tests (Figure 1A) to investigate priority effects in yeast showed that some environmental conditions can promote priority effects by reducing fitness differences [55]. Future work would benefit from including priority effects as a potential competitive outcome and exploring the mechanisms that generate positive frequency dependence.

Although most coexistence research focuses primarily on pairwise species interactions, ecological communities are rarely composed of isolated pairs of species, and are more accurately characterized as complex, multispecies networks [62]. The invasion criterion can be adapted for use in multispecies communities by determining whether each species has positive growth when invading the remaining community, essentially using the average effect of a community of competitors in place of a pairwise interaction coefficient [10,63]. However, this approach assumes that when one species is absent the other species are able to persist, an assumption that can be violated, for example when interaction chains maintain diversity in communities (e.g., rock–paper–scissors dynamics) (Box 1) [50,64–66]. Chesson [67] has outlined how permanence theory and stochastic persistence theory could be used to circumvent this issue; these approaches consider only the subcommunities that are able to persist stably in the absence of the invading species when assessing the invasibility criterion. Stouffer *et al.* [68] incorporated intransitivity into an annual plant model and ran simulations to determine when positive invader growth rates do and do not lead to coexistence. Although the application of invasion tests to understanding the complex interactions that emerge in diverse communities remains challenging (Box 1), there is a growing interest in improving the realism of coexistence by incorporating these dynamics [66,67].

Non-competitive Interactions

Resource competition has been the central focus of coexistence research, and is often treated by default as the dominant force structuring local diversity. Although the invasion criterion has primarily been applied to understand coexistence of species competing for shared resources, it can also be used to understand the consequences of facilitation and interactions with other trophic levels for coexistence [69,70].

Facilitation occurs when a species benefits from the presence of another species without causing it harm. This phenomenon is widespread in nature [70,71] but is often overlooked in ecological theory. In the context of the invasion criterion, facilitation manifests as a species having higher population growth rates when invading an established population of another species than when grown with no neighbors [70]. Direct invasibility tests that compare a species' growth rate when alone versus invading can thus be used to determine the strength of facilitative interactions (Figure 1A). Venail *et al.* [70] used this method to test whether phylogenetic relatedness predicted the strength or direction of interactions between pairs of algae. Because this method is amenable to the quantification of both negative (competitive) and positive (facilitative) interactions, it could be useful to researchers interested in understanding a broader range of species interactions. While facilitation can be difficult to integrate into modern coexistence theory, which is based on negative species interactions, recent theory has made progress on this front [9,72].

Box 1. Challenges and Limitations of the Invasion Criterion

Theoretical Challenges

A major challenge with relating competitive outcomes from invasibility tests to real-world patterns of diversity is that invasibility tests cannot always accurately predict coexistence [64,65]. For example, in two-species competitive communities, the resident species persists when its competitor is suppressed to low numbers; however, indirect interactions in diverse communities can cause the depression of one species to low density to precipitate the extinction of some residents [64]. Likewise, if a species has a minimum sustainable population size due to Allee effects, long-term coexistence can be possible if both species start at high abundances, even when the invasion criterion is not met [59,79].

The invasion criterion can also be poorly suited to understanding coexistence across trophic levels because specialist consumers go extinct in the absence of their resource species. In these cases, the ability of a species to invade a system that does not include all of the residents is not an adequate test of whether all of the species in the system can coexist. Theory outlining how to assess invasibility in a predator–prey system using permanence theory and stochastic persistence theory [67,80] and how to integrate network and niche theories to understand interactions across trophic levels [76] has made progress on this front; however, most theoretical approaches based on the invasion criterion have yet to capture the unique characteristics of predator–prey interactions.

Finally, demographic stochasticity can have important consequences for low-density invasion growth rates [4,81], but this is frequently overlooked in theory primarily focused on deterministic invasion outcomes. While two recent papers have addressed this issue [67,82], the impact of demographic stochasticity on outcomes predicted by the invasion criterion remains largely an open question.

Methodological Challenges

A key barrier to testing the invasion criterion is that methods for quantifying invading population growth rates rely on fast generation times or models of population and competitive dynamics (Figure 1). In systems that do not meet these requirements (e.g., long-lived trees), proxies for population growth rates can be measured to investigate the potential for stabilization, competitive dominance, and coexistence [77,83] (Figure 1D). However, this method does not determine mutual invasibility and cannot be used to calculate fitness and stabilizing niche differences, limiting its link to the theories described in this review.

An additional barrier faced by empiricists is that the simplest and most accessible conceptualization of the invasion criterion involves a species introduced into a population of a competitor at equilibrium in a constant environment. As such, the most widely used methods for testing the invasion criterion rely on the resident species being at equilibrium when invader growth rates are quantified (Figure 1A,B). One challenge with this is that it can be difficult to experimentally maintain a resident species at equilibrium or to accurately project the equilibrium mathematically. Another challenge is that this static view is likely to be a poor representation of natural communities where disturbance, environmental fluctuations, and long-term environmental change play important roles in structuring coexistence [52,53]. While theory describing how the stochastic dynamics that manifest in fluctuating environments contribute to long-term invasion growth rates lie at the core of the invasion criterion concept [1], the empirical application of these ideas has lagged behind (but see references in Figure 1C). However, recent work highlighting new ways to investigate coexistence in environments that vary across space and time may facilitate future empirical tests [27,84,85].

Finally, because the invasion criterion is inherently a phenomenological approach based on population growth rates, on its own it provides no information about the mechanisms that stabilize coexistence or drive competitive exclusion [86]. To overcome this issue, invasion tests have been paired with data on species traits [87] or climate [88,89] to explore the mechanisms underlying invasibility. Likewise, Chesson [90,91] has described how species' recovery rates when perturbed to low density (i.e., the strength of coexistence) can be partitioned into mechanisms such as the storage effect and relative nonlinearity. While the data-intensive nature of parameterizing these models is an ongoing challenge, this theoretical framework presents the exciting opportunity to quantify how individual coexistence mechanisms contribute to the maintenance of diversity [84,89].

Ellner *et al.* provide a mathematical way to decompose the invading and resident growth rates of each species in a community into various mechanisms (including facilitative interactions), and to then compare the contribution of each factor to invasibility and stabilizing and fitness differences [9]. Likewise, Bimler *et al.* [72] incorporated facilitation into an annual plant model that they used to estimate both positive and negative **competition coefficients**, determine fitness and stabilizing niche differences, and demonstrate that species interactions often shift from competition to facilitation across environmental gradients.

Just as differences in the amount and type of resources each species uses determine whether species limit themselves more than a competitor and can thus invade from rare, species' differential responses to predation pressure can drive the frequency-dependent growth rates that result in mutual invasibility [69]. And just as the demographic consequences of resource competition can be partitioned into fitness and stabilizing niche differences, so too can the effects of other trophic levels such as predators [69,73], pathogens [57], and pollinators [74]. For example, Chesson and Kuang [69] demonstrate that because predator attack rates depend on prey density, predation can contribute to frequency-dependent prey population growth when predators specialize on different prey. As such, top-down pressure can be incorporated into the modern coexistence framework by including the effect of predators on species' frequency-dependent growth in the calculation of stabilizing niche differences [69]. Likewise, a recent experiment demonstrated that the presence of floral visitors promoted coexistence by reducing fitness differences [74]. However, empirical studies using the invasion criterion have overwhelmingly focused on resource competition as the primary determinant of coexistence, and there is an exciting opportunity for future work to fill this research gap.

Concluding Remarks

The invasion criterion is a powerful tool that can be used to understand ecological patterns spanning a broad range of processes and scales. Despite observations from many systems of seemingly stable coexistence, empirical evidence that competitors or communities satisfy the invasion criterion remains scarce and narrowly focused. We hope that by highlighting links between recent theory and emerging empirical methods based on this principle, and by outlining how and when the invasion criterion can be used when complex dynamics such as facilitation, environmental change or trophic interactions structure communities, we will encourage a wider use of the invasion criterion. As this approach becomes increasingly common and researchers test the limits of its application, new theory and methods may help to overcome the challenges that currently restrict its use (Box 1). If so, it is possible that the scope of the invasion criterion outlined here represents a starting point that continues to expand in the coming years.

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References

- Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* 31, 343–366
- MacArthur, R. and Levins, R. (1967) The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* 101, 377–385
- Turelli, M. (1978) Does environmental variability limit niche overlap? *Proc. Natl. Acad. Sci. U. S. A.* 75, 5085–5089
- Adler, P.B. *et al.* (2007) A niche for neutrality. *Ecol. Lett.* 10, 95–104
- Siepielski, A.M. and McPeck, M.A. (2010) On the evidence for species coexistence: a critique of the coexistence program. *Ecology* 91, 3153–3164
- Carroll, I.T. *et al.* (2011) Niche and fitness differences relate the maintenance of diversity to ecosystem function. *Ecology* 92, 1157–1165
- Chu, C. and Adler, P.B. (2015) Large niche differences emerge at the recruitment stage to stabilize grassland coexistence. *Ecol. Monogr.* 85, 373–392
- Hart, S.P. *et al.* (2018) How to quantify competitive ability. *J. Ecol.* 106, 1902–1909
- Ellner, S.P. *et al.* (2018) An expanded modern coexistence theory for empirical applications. *Ecol. Lett.* 22, 3–18
- Godoy, O. and Levine, J.M. (2014) Phenology effects on invasion success: insights from coupling field experiments to coexistence theory. *Ecology* 95, 726–736
- Levine, J.M. *et al.* (2008) On testing the role of niche differences in stabilizing coexistence. *Funct. Ecol.* 22, 934–936
- Lankau, R.A. (2011) Rapid evolutionary change and the coexistence of species. *Annu. Rev. Ecol. Syst.* 42, 335–354
- Webb, C.O. *et al.* (2002) Phylogenies and community ecology. *Annu. Rev. Ecol. Syst.* 33, 475–505
- Germain, R.M. *et al.* (2017) Moving character displacement beyond characters using contemporary coexistence theory. *Trends Ecol. Evol.* 33, 74–84
- Mayfield, M.M. and Levine, J.M. (2010) Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecol. Lett.* 13, 1085–1093
- Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection*, John Murray
- Germain, R.M. *et al.* (2016) Species coexistence: macroevolutionary relationships and the contingency of historical interactions. *Proc. Biol. Sci.* 283, 20160047
- Godoy, O. *et al.* (2014) Phylogenetic relatedness and the determinants of competitive outcomes. *Ecol. Lett.* 17, 836–844
- Narwani, A. *et al.* (2013) Experimental evidence that evolutionary relatedness does not affect the ecological mechanisms of coexistence in freshwater green algae. *Ecol. Lett.* 16, 1373–1381
- Hart, S.P. *et al.* (2019) Effects of rapid evolution on species coexistence. *Proc. Natl. Acad. Sci. U. S. A.* 116, 2112–2117

Outstanding Questions

Is the invasion criterion useful for studying ecological systems characterized by high species diversity or complex food webs?

How well do invasion outcomes from experiments match patterns of co-occurrence found in natural communities?

Is it possible to use the invasion criterion in systems that do not have rapid population dynamics or models of competitive interactions (i.e., systems not represented in Figure 1A–C)?

Which competitive mechanisms underlie stabilizing niche differences, destabilizing differences (i.e., positive frequency-dependent growth), and fitness differences?

21. Stuart, Y.E. and Losos, J.B. (2013) Ecological character displacement: glass half full or half empty? *Trends Ecol. Evol.* 28, 402–408
22. Hausch, S.J. *et al.* (2017) Coevolution of competing *Callosobruchus* species does not stabilize coexistence. *Ecol. Evol.* 7, 6540–6548
23. Alexander, J.M. *et al.* (2016) When climate reshuffles competitors: a call for experimental macro-ecology. *Trends Ecol. Evol.* 31, 831–841
24. Godsoe, W. *et al.* (2017) Integrating biogeography with contemporary niche theory. *Trends Ecol. Evol.* 32, 488–499
25. Jones, N.T. and Gilbert, B. (2016) Biotic forcing: the push–pull of plant ranges. *Plant Ecol.* 217, 1331–1344
26. Louthan, A.M. *et al.* (2015) Where and when do species interactions set range limits? *Trends Ecol. Evol.* 30, 780–792
27. Usinowicz, J. and Levine, J.M. (2018) Species persistence under climate change: a geographical scale coexistence problem. *Ecol. Lett.* 21, 1589–1603
28. Hargreaves, A.L. *et al.* (2013) Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. *Am. Nat.* 183, 157–173
29. Dobzhansky, T. (1950) Evolution in the tropics. *Am. Sci.* 38, 209–221
30. MacArthur, R.H. (1972) *Geographical Ecology: Patterns in the Distribution of Species*, Harper & Row
31. Angert, A.L. (2009) The niche, limits to species' distributions, and spatiotemporal variation in demography across the elevation ranges of two monkeyflowers. *Proc. Natl. Acad. Sci. U. S. A.* 106, 19693–19698
32. Villellas, J. *et al.* (2013) Plant performance in central and northern peripheral populations of the widespread *Plantago coronopus*. *Ecography* 36, 136–145
33. Alexander, J.M. *et al.* (2018) Species' distributions as a coexistence problem: a response to Godsoe *et al.* *Trends Ecol. Evol.* 33, 144–145
34. Godsoe, W. *et al.* (2018) Which coexistence mechanisms should biogeographers quantify? A reply to Alexander *et al.* *Trends Ecol. Evol.* 33, 145–147
35. Hart, S.P. *et al.* (2017) The spatial scales of species coexistence. *Nat. Ecol. Evol.* 1, 1066
36. Seabloom, E.W. *et al.* (2003) Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proc. Natl. Acad. Sci. U. S. A.* 100, 13384–13389
37. Going, B.M. *et al.* (2009) Abiotic and biotic resistance to grass invasion in serpentine annual plant communities. *Oecologia* 159, 839–847
38. MacDougall, A.S. *et al.* (2009) Plant invasions and the niche. *J. Ecol.* 97, 609–615
39. Shea, K. and Chesson, P. (2002) Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.* 17, 170–176
40. Keane, R.M. and Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.* 17, 164–170
41. Gross, N. *et al.* (2015) Functional equivalence, competitive hierarchy and facilitation determine species coexistence in highly invaded grasslands. *New Phytol.* 206, 175–186
42. Ocampo-Ariza, C. *et al.* (2018) Strong fitness differences impede coexistence between an alien water fern (*Azolla pinnata* R. Br.) and its native congener (*Azolla rubra* R. Br.) in New Zealand. *Biol. Invasions* 20, 2889–2897
43. Li, S.-P. *et al.* (2018) Niche and fitness differences determine invasion success and impact in laboratory bacterial communities. *ISME J.* 13, 402–412
44. Adler, P.B. *et al.* (2012) Forecasting plant community impacts of climate variability and change: when do competitive interactions matter? *J. Ecol.* 100, 478–487
45. Levine, J.M. *et al.* (2010) Do competitors modulate rare plant response to precipitation change? *Ecology* 91, 130–140
46. Davis, A.J. *et al.* (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature* 391, 783
47. Grainger, T.N. *et al.* (2018) Temperature-dependent species interactions shape priority effects and the persistence of unequal competitors. *Am. Nat.* 191, 197–209
48. Suttle, K. *et al.* (2007) Species interactions reverse grassland responses to changing climate. *Science* 315, 640–642
49. Ives, A.R. (1995) Predicting the response of populations to environmental change. *Ecology* 76, 926–941
50. Matias, L. *et al.* (2018) An experimental extreme drought reduces the likelihood of species to coexist despite increasing intransitivity in competitive networks. *J. Ecol.* 106, 826–837
51. Alexander, J.M. and Levine, J. (2019) Earlier phenology of a non-native plant increases impact on native competitors. *Proc. Natl. Acad. Sci. U. S. A.* 116, 6199–6204
52. Chesson, P. (2017) AEDT: a new concept for ecological dynamics in the ever-changing world. *PLoS Biol.* 15, e2002634
53. Chesson, P. (2018) Contributions to nonstationary community theory. *J. Biol. Dyn.* Published online September 30, 2018. <https://doi.org/10.1080/17513758.2018.1526977>
54. Fukami, T. (2015) Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annu. Rev. Ecol. Syst.* 46, 1–23
55. Grainger, T.N. *et al.* (2019) Applying modern coexistence theory to priority effects. *Proc. Natl. Acad. Sci. U. S. A.* 116, 6205–6210
56. Ke, P.-J. and Letten, A.D. (2018) Coexistence theory and the frequency dependence of priority effects. *Nat. Ecol. Evol.* 2, 1691–1695
57. Mordecai, E.A. (2011) Pathogen impacts on plant communities: unifying theory, concepts, and empirical work. *Ecol. Monogr.* 81, 429–441
58. Callaway, R.M. *et al.* (2004) Soil biota and exotic plant invasion. *Nature* 427, 731–733
59. Schreiber, S. *et al.* (2019) When rarity has costs: coexistence under positive frequency-dependence and environmental stochasticity. *Ecology* Published online February 17, 2019. <https://doi.org/10.1002/ecy.2664>
60. Liang, M. *et al.* (2015) Arbuscular mycorrhizal fungi counteract the Janzen–Connell effect of soil pathogens. *Ecology* 96, 562–574
61. Cardinaux, A. *et al.* (2018) Do soil biota influence the outcome of novel interactions between plant competitors? *J. Ecol.* 106, 1853–1863
62. Bascompte, J. (2009) Disentangling the web of life. *Science* 325, 416–419
63. Levine, J.M. and HilleRisLambers, J. (2009) The importance of niches for the maintenance of species diversity. *Nature* 461, 254–257
64. Barabás, G. *et al.* (2016) The effect of intra- and interspecific competition on coexistence in multispecies communities. *Am. Nat.* 188, E1–E12
65. Levine, J.M. *et al.* (2017) Beyond pairwise mechanisms of species coexistence in complex communities. *Nature* 546, 56–64
66. Saavedra, S. *et al.* (2017) A structural approach for understanding multispecies coexistence. *Ecol. Monogr.* 87, 470–486
67. Chesson, P. (2018) Updates on mechanisms of maintenance of species diversity. *J. Ecol.* 106, 1773–1794
68. Stoffer, D.B. *et al.* (2018) Cyclic population dynamics and density-dependent intransitivity as pathways to coexistence between co-occurring annual plants. *J. Ecol.* 106, 838–851
69. Chesson, P. and Kuang, J.J. (2008) The interaction between predation and competition. *Nature* 456, 235
70. Venail, P.A. *et al.* (2014) The influence of phylogenetic relatedness on species interactions among freshwater green algae in a mesocosm experiment. *J. Ecol.* 102, 1288–1299
71. Bruno, J.F. *et al.* (2003) Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.* 18, 119–125
72. Bimler, M.D. *et al.* (2018) Accurate predictions of coexistence in natural systems require the inclusion of facilitative interactions and environmental dependency. *J. Ecol.* 106, 1839–1852
73. Stump, S.M. and Chesson, P. (2017) How optimally foraging predators promote prey coexistence in a variable environment. *Theor. Popul. Biol.* 114, 40–58
74. Lanuza, J.B. *et al.* (2018) Opposing effects of floral visitors and soil conditions on the determinants of competitive outcomes maintain species diversity in heterogeneous landscapes. *Ecol. Lett.* 21, 865–874
75. Fukami, T. *et al.* (2016) A framework for priority effects. *J. Veg. Sci.* 27, 655–657
76. Godoy, O. *et al.* (2018) Towards the integration of niche and network theories. *Trends Ecol. Evol.* 33, 287–300
77. Kunstler, G. *et al.* (2016) Plant functional traits have globally consistent effects on competition. *Nature* 529, 204
78. Chesson, P. (2012) Species competition and predation. In *Encyclopedia of Sustainability Science and Technology* (Meyers, R.A., ed.), pp. 10061–10085, Springer

79. Barabás, G. *et al.* (2018) Chesson's coexistence theory. *Ecol. Monogr.* 88, 277–303
80. Kang, Y. and Chesson, P. (2010) Relative nonlinearity and permanence. *Theor. Popul. Biol.* 78, 26–35
81. Lande, R. (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am. Nat.* 142, 911–927
82. Schreiber, S. *et al.* (2018) Does deterministic coexistence theory matter in a finite world? Insights from serpentine annual plants. *bioRxiv* Published online March 28, 2018. <https://doi.org/10.1101/290882>
83. Comita, L.S. *et al.* (2010) Asymmetric density dependence shapes species abundances in a tropical tree community. *Science* 329, 330–332
84. Ellner, S.P. *et al.* (2016) How to quantify the temporal storage effect using simulations instead of math. *Ecol. Lett.* 19, 1333–1342
85. Shoemaker, L.G. and Melbourne, B.A. (2016) Linking metacommunity paradigms to spatial coexistence mechanisms. *Ecology* 97, 2436–2446
86. HilleRisLambers, J. *et al.* (2012) Rethinking community assembly through the lens of coexistence theory. *Annu. Rev. Ecol. Evol. Syst.* 43, 227–248
87. Kraft, N.J. *et al.* (2015) Plant functional traits and the multidimensional nature of species coexistence. *Proc. Natl. Acad. Sci. U. S. A.* 112, 797–802
88. Adler, P.B. *et al.* (2006) Climate variability has a stabilizing effect on the coexistence of prairie grasses. *Proc. Natl. Acad. Sci. U. S. A.* 103, 12793–12798
89. Angert, A.L. *et al.* (2009) Functional tradeoffs determine species coexistence via the storage effect. *Proc. Natl. Acad. Sci. U. S. A.* 106, 11641–11645
90. Chesson, P. (2008) Quantifying and testing species coexistence mechanisms. In *Unity in Diversity: Reflections on Ecology After the Legacy of Ramon Margalef* (Valladares, F., *et al.*, eds), pp. 119–164, Fundación Banco Bilbao Vizcaya Argentaria
91. Sears, A.L. and Chesson, P. (2007) New methods for quantifying the spatial storage effect: an illustration with desert annuals. *Ecology* 88, 2240–2247
92. Tan, J. *et al.* (2017) Species ecological similarity modulates the importance of colonization history for adaptive radiation. *Evolution* 71, 1719–1727
93. Hart, S.P. and Marshall, D.J. (2013) Environmental stress, facilitation, competition, and coexistence. *Ecology* 94, 2719–2731
94. Usinowicz, J. *et al.* (2012) Coexistence in tropical forests through asynchronous variation in annual seed production. *Ecology* 93, 2073–2084
95. Cáceres, C.E. (1997) Temporal variation, dormancy, and coexistence: a field test of the storage effect. *Proc. Natl. Acad. Sci. U. S. A.* 94, 9171–9175
96. LaManna, J.A. *et al.* (2017) Plant diversity increases with the strength of negative density dependence at the global scale. *Science* 356, 1389–1392
97. Szeplowski, A.M. *et al.* (2010) Experimental evidence for neutral community dynamics governing an insect assemblage. *Ecology* 91, 847–857
98. Svensson, E.I. *et al.* (2018) Frequency dependence and ecological drift shape coexistence of species with similar niches. *Am. Nat.* 191, 691–703
99. Wilson, W. *et al.* (1999) Complementary foraging behaviors allow coexistence of two consumers. *Ecology* 80, 2358–2372