Re-revisiting the Niche Concept

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Introduction

The niche concept has long been a source of confusion and controversy, likely due to an important but often perplexing historical duality within it. Some critics have even proposed abandoning the concept altogether (e.g., McInerny and Etienne 2012a; Justus 2019; Wakil and Justus 2021; but see Holt 2009, McInerny and Etienne 2012b, 2012c). However, as we argue below, this issue should no longer pose a significant problem. In fact, it is both important and interesting to explore how the niche concept—understood from this updated perspective—can be applied to address novel issues in both pure and applied ecology.

It is also crucial to distinguish between the niche concept itself and the closely (perhaps unfortunately) linked idea of *limiting similarity*—the principle that two species occupying the same niche (however defined) cannot coexist within a closed community. This principle is also known as competitive exclusion, Gause's Axiom, or Hardin's Principle. Using the modern niche concept described below, it is possible to reconcile this idea—primarily concerned with within-community dynamics—with the observed coexistence of similar species across different communities.

The contemporary niche concept is also increasingly being used to address a broad range of issues in both fundamental community ecology and applied fields such as conservation and biodiversity management. These are exciting directions, but they also present new challenges to our understanding of niche dynamics and underscore the continued relevance of the concept.

Describing the Niche Concept

At its most general, the niche of an organism can be thought of as the description of the relationship between that species and its environment—including other species that may be present. Like many relationships, these interactions can be bidirectional and context-dependent, often involving indirect effects. Darwin (1859) captured some of this complexity with his "entangled bank" metaphor, which described the intricate causal links among species and their environments in natural ecosystems. He wondered how any regularities might be found amid such complexity (for him, presumably, in an evolutionary rather than ecological context).

The duality at the heart of the niche concept—responses *versus* effects in the interaction between organisms and their environments—is central to many scientific (and philosophical) debates about the idea (e.g. Griesemer 1992, Holt 2009, Pocheville 2015). This duality has been present since the term's inception. Although Johnson (1910) was apparently the first to use the term, Grinnell (1904,1917) subsequently emphasized how species' geographic distributions are shaped by their responses to environmental factors or gradients. Independently, Elton (1924) used the term to emphasize how organisms affect and influence their environments, including interactions with other species.

Although this distinction is somewhat simplified, it is useful to think of Grinnell's perspective as focusing on the *environment-to-organism* relationship, while Elton's centered on the *organism-to-environment* dynamic. Hutchinson (1957) later formalized the niche as an *n*-dimensional hypervolume representing the set of environmental conditions that support population growth and persistence. While this initially appears similar to Grinnell's idea, Hutchinson also introduced the important distinction between the *fundamental niche*—the potential niche in the absence of other species—and the *realized niche*, which reflects the typically reduced space due to the influence of biotic interactions. It is thus the realized niche that is most obviously derived from the distributions of species, and thus corresponding to Grinnell's usage, rather than the fundamental one.

Subsequent "niche theory" developed by MacArthur and Levins (1967), Colwell and Futuyma (1971), and others explored the dynamics shaping the difference between fundamental and realized niches within communities. However, in doing so, they largely ignored how variation in niches across communities might frame these dynamics (see Giller 1989). Their results we often questioned and countered by empirical ecologists (see Strong et al. 1982) and niche theory, as it was conceived at the time, became neglected (Chase and Leibold 2003, Sales et al. 2021).

Box 1: Defining the niche mathematically:

A Mathematical Framing of the Niche Concept

A mathematical definition of the niche concept is critical for developing clear and logical ways to apply the broader ideas outlined above. Here, we take a somewhat historical perspective to highlight how confusion surrounding the niche concept emerged, how it has been resolved, and how lingering "legacy effects" continue to shape the field.

Vandermeer (1972) attempted an early synthesis by suggesting that Grinnell's interpretation of the niche focused on the spatial-distributional component (i.e., across sites), which he argued corresponds to a species' *fundamental niche*, while Elton's usage centered on the functional component—how a species operates within its environmental setting—representing the *realized niche*. Whittaker et al. (1973) made a similar argument (Figure 1), even suggesting that Grinnell (1924) intuited a distinction between these two meanings—then unnamed—which may explain his comment about the non-coexistence of species with similar niches.

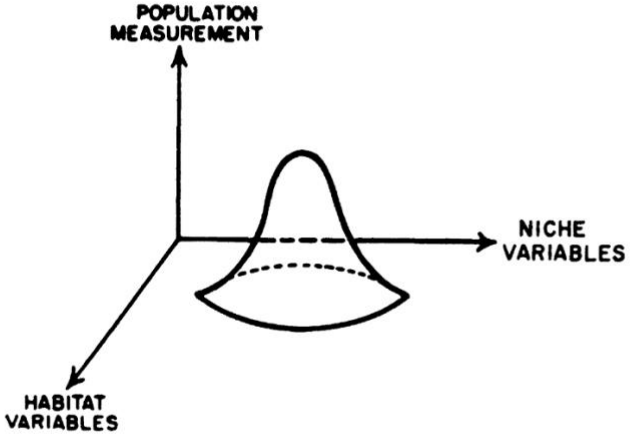

Figure 1: Conceptual dissection of "niche variables" (interactions among species within a locality), "habitat variables" (influence of primarily abiotic factors), and the "ecotope" (joint characterization of both). Their joint action, termed "population measurement," is somewhat vague—possibly because distributional ecologists tend to focus on *density*, while those studying dynamics prefer *per-capita growth*. This distinction supports identifying the *fundamental niche* with habitat variables and the *realized niche* with the ecotope. (Figure from Whittaker et al. 1973.)

This resolution (Grinnell = habitat, Elton = interactions within habitats) is worth examining in greater detail. Figure 2a shows the observed abundances of two species along an environmental gradient—their respective realized niches. According to Vandermeer (1972) and Whittaker et al. (1973), these patterns imply distinct *fundamental* (Grinnellian) niches, suggesting different carrying capacities and potentially no competition (Figure 2b). However, alternative explanations are possible. For instance, the species might have overlapping fundamental niches and weak competition, leading to divergence in abundance at intermediate environmental values (Figure 2c). More strikingly, their fundamental niches might overlap almost entirely, but strong competition could result in one species occupying an area completely different from its fundamental niche (Figure 2d).

These scenarios demonstrate how environmental gradients and species interactions can become *entangled*, even in simple two-species systems. Without experimental manipulation, it is often difficult to cleanly distinguish between fundamental and realized niches. This entanglement remains at the heart of many challenges in community ecology, as explored below.

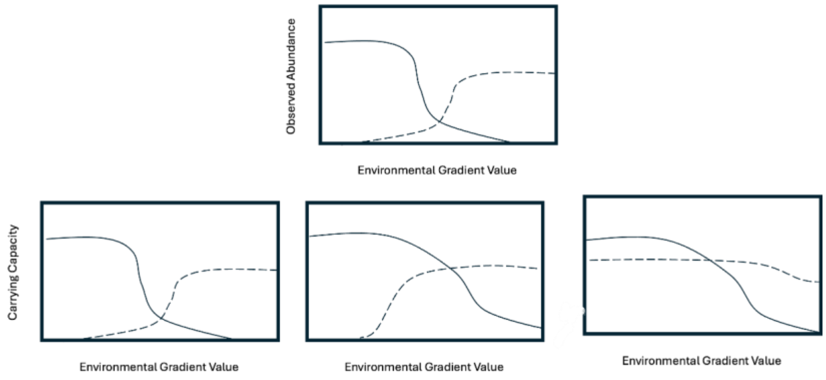

Figure 2: Hypothetical distributions of two along an environmental gradient. a) the observed relationship between abundance and location along the gradient of two species. b) Unobserved relationship between carrying capacity of the same two species along the gradient assuming they don't interact. c) As in b) but adding in interspecific competition so that their fundamental niches (involving carrying capacities) are broader than their realized niches (compare with a). d) As in c) but assuming that both species have qualitatively similar fundamental niches (both do better at lower values of the environmental gradient) but differ in sensitivity to the environment, resulting in lack of correlations between carrying capacity and distribution with respect to environmental value (Rosenzweig and Abramsky (1986) called this form of niche relations 'centrifugal').

More recent work has sought to integrate the environmental and interaction components of niches more subtly (Patton and Auble 1981; Aarssen 1983; Alley 1985; Leibold 1995; Chase and Leibold 2003; McInerny and Etienne 2012a, b, c; Koffel et al. 2021; Meszéna et al. 2023). Figure 3 illustrates how various niche concepts can be related and compared. For instance, in what became known as *Contemporary Niche Theory*, Leibold (1995, 1998) and Chase and Leibold (2003) linked niche components—*effect* and *response*—to elements of mechanistic resource competition models (MacArthur 1974; Tilman 1980). These same models were later extended to include predator-prey interactions, mutualisms, and fluctuating environments (e.g., Leibold 1995, 1998, Chase and Leibold 2003, Koffel et al. 2021).

Graphically, these models involve **Zero Net Growth Isoclines (ZNGIs)**—boundaries along which a species' population growth rate is zero (Figure 3a). These ZNGIs correspond closely to Hutchinson's *n*-dimensional response niche. In the same space, species effects can be represented as **impact vectors** (Figure 3b), paralleling Elton's focus on species' roles in their environment. The dynamics of environmental factors (e.g., resources) can also be shown as vectors (Figure 3c), representing how these factors recover or regenerate. The ecological equilibrium is achieved when species impacts are balanced by environmental regeneration—i.e., when vectors sum to zero and factor densities are on the ZNGI (Figure 3d).

This modeling framework can be extended to other types of interactions and generalized to high-dimensional cases where species traits are defined by their ZNGIs and impact vectors. Importantly, these traits are typically parameterized by the same biological processes—e.g., per-capita resource uptake affects both growth (ZNGI) and impact. Because such traits are difficult to measure empirically, ecologists often rely on more accessible proxies like body size or elemental content (discussed further below).

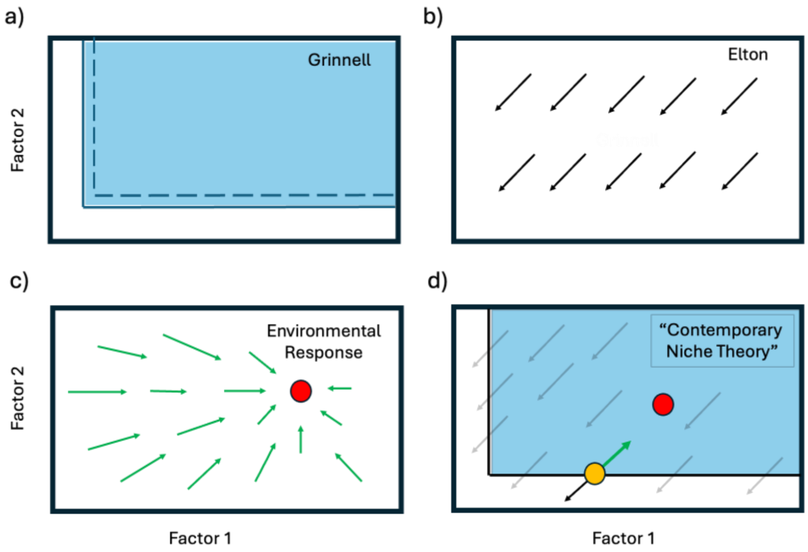

Figure 3: Graphical representations of different niche concepts. a) *Grinnellian niche*: The area in blue summarized the realized niche of the species in relation to two limiting factors (here modeled as resources for clarity). The demarcation solid line separates conditions where the species can grow (in blue) from where it would decline (white). The dashed line corresponds to another species with very similar Grinnellian niche that is marginally inferior to the solid species to contextualize Grinnell's (1904) argument about coexistence (see text). b) *Eltonian niche*: The vectors describe the impacts of species on the two factors (again corresponding to resource uptake). c) *Environmental context*: The vectors describe how the environment responds being altered away from its steady state shown with the red dot in the absence of the consumer. d) *Contemporary Niche Theory*: synthesis of a–c. Both the Grinnellian and Eltonian components are combined with the environmental context. Steady state of the organism with the environment occurs when conditions are on the line denoting the ZNGI (the species is at steady state) and the impact vector is equal to and in the opposite direction as the environmental response vector. this is denoted by the yellow dot.

Grinnell and Elton were motivated by different goals. Grinnell aimed to predict species distributions using environmental variables, while Elton focused on dynamics within communities. Contemporary Niche Theory synthesizes these views and adds environmental feedback, allowing it to describe both species distributions and interactions.

The concepts described thus far apply to single species, but they can also be extended to *pairwise interactions* (Figure 4). Hutchinson (1957) proposed that species' distributions could be predicted from their fundamental niches, but that competition would constrain these to smaller *realized niches*. He did not, however, specify how to determine the shape of these realized niches. Figure 4a reconstructs his intuition in a way that aligns with Contemporary Niche Theory. In contrast, Contemporary Niche Theory (Figure 4b) offers explicit mechanisms—based on differences in ZNGIs and impact vectors—for determining realized niches under competition.

Hubbell's (2001) *neutral theory* proposed that species have effectively identical niches. In this case, ZNGIs overlap, and impact vectors are parallel, leading to realized niches that are indistinguishable from fundamental ones (Figure 4c)—a direct contrast to Hutchinson's view.

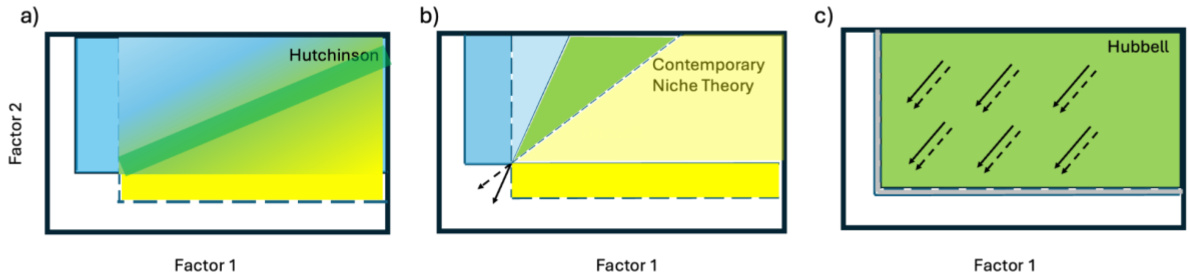

Figure 4: Approaches to modeling pairwise interactions. a) *Hutchinson*: the fundamental niches of the two species overlap. If there is competition, the realized niches will be constrained but there is no quantitative description of the result. Here the gradient in the overlap is shown by gradual shift from blue to yellow. The strong green area indicates that there could be sharp boundary somewhere in this zone where one species or other is eliminated. b) *Contemporary Niche Theory*: Similar to a) but there is an explicit set of boundaries that delimit where each species is extinct and where the two species coexist (green). c) *Hubbell*: Neutral coexistence—species are ecologically equivalent; fundamental and realized niches overlap entirely and impact vectors are parallel.

Limiting Similarity and the Niche

From its earliest applications, the niche concept has been closely tied to the idea of *limiting similarity*—the hypothesis that species with identical (or arbitrarily similar) niches cannot stably coexist in a closed, local community. Grinnell (1917) was the first to make this link, stating: "It is, of course, axiomatic that no two species regularly established in a single fauna have precisely the same niche relationship." His justification was straightforward: if two species respond identically to environmental conditions, one is likely to have an advantage over the other, be it ever so slight, ultimately leading to *competitive exclusion* (Grinnell 1904). In contrast, Elton (1927) did not explicitly address limiting similarity, though he, following Darwin, did suggest that competition is stronger among closely related species.

After Hutchinson (1957) introduced the concept of the *n*-dimensional niche—and with it the distinction between the fundamental and realized niche—an influential literature on "niche theory" developed. MacArthur and Levins (1967) and Colwell and Futuyma (1971) explored how dynamics within communities affect this distinction. However, their focus on within-community dynamics ignored how niches among communities might set the context for these interactions. Empirical tests of these ideas (e.g., Diamond 1975 vs. Connor and Simberloff 1979) produced equivocal results, perhaps due to this oversight—a contradiction noted earlier by Whittaker et al. (1973). Much of this history is summarized by Giller (1989), and its shortcomings have been extensively critiqued (e.g. McInerny and Etienne 2012a; Justus 2019; Wakil and Justus 2021)

Importantly, the niche and limiting similarity are distinct concepts. Limiting similarity is a hypothesis *about* the niche; it uses the niche as a framework but does not define it. Conversely, many applications of the niche concept—such as in food web structure or biodiversity–

ecosystem function relations—do not necessarily involve limiting similarity, even if they can be framed in terms of niche relationships. Nonetheless, the idea of limiting similarity continues to exert a strong influence on community ecology. This is somewhat paradoxical, as the modern niche concept, which separates response and effect components, implies that coexisting species may share certain ecological traits while differing in others. Thus, limiting similarity is a more complex and nuanced idea than it first appears (Abrams 1983; Aarssen 1983; Leibold 1998; Leibold and McPeek 2006).

Box 2: Defining Limiting Similarity (or Not!) Mathematically

There are multiple ways to understand how the relationship between the niche and limiting similarity defies a simple "yes" or "no" dichotomy. Perhaps the clearest is offered by Vandermeer (1975), who analyzed the classic Lotka–Volterra competition model. This model can represent niche-based interactions when species compete directly but is often used as a heuristic even when competition involves shared resources or other indirect effects.

Vandermeer reformulated the standard graphical analysis (in *state space*, where the axes represent species densities) by shifting to *parameter space*, where the axes represent species' carrying capacities (Figure 5). His approach shows how coexistence is determined by three main factors: the relative strengths of intra- and interspecific competition (i.e., the α_{ij} coefficients), and the species' carrying capacities (K_1 and K_2).

Coexistence is possible when interspecific competition is weaker than intraspecific competition (i.e., $\alpha_{12} \cdot \alpha_{21} < 1$), as in Figure 5e. This condition creates a zone in parameter space where coexistence is stable. When the opposite holds ($\alpha_{12} \cdot \alpha_{21} > 1$), coexistence becomes unstable, and the system exhibits *priority effects*—whichever species establishes first excludes the other (Figure 5f). Additionally, coexistence requires *symmetry* in carrying capacities; if one species has a significantly higher K, it will likely outcompete the other regardless of the α_{ij} values.

Vandermeer also showed that this symmetry condition extends to intrinsic growth rates (not shown). His results imply that coexisting species tend to have *similar fitness* (equalizing traits), but *dissimilar* interaction traits (stabilizing traits).

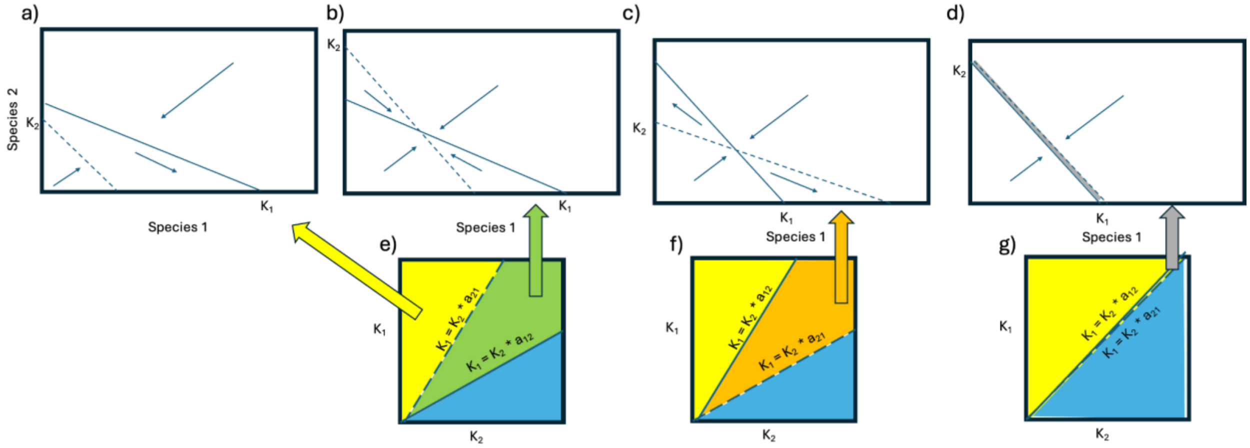

Figure 5: Graphical analysis of the Lotka–Volterra model in both *state space* (top panels) and *parameter space* (bottom). Top panels: Isoclines represent ZNGIs; arrows show direction of system dynamics. panels a-d show conventional graphical analyses of conditions leading to competitive exclusion (a), stable coexistence of both species (b), unstable equilibrium between both species (c, leading to priority effects) and neutral co-occurrence (d). Lower panels: Parameter space descriptions of outcomes as described by Vandermeer (1975). e) delineated parameter combinations that could lead to competitive exclusion with the yellow arrow (here shown for the yellow species, there is a similar symmetric one that corresponds to the blue species that is not shown). There are also parameter combinations that predict co-occurrence (green). f) parameter combinations that can also predict competitive exclusion (yellow and blue) but can also predict unstable steady state that would lead to priority effects (orange). g) Parameter combinations when there are no distinctions in the slopes of the graph. Here there are also parameter combinations that lead to competitive exclusion (yellow and blue) and no stable coexistence or priority effects (there is no green or orange zone). Nevertheless, it is possible for the two species to show neutral co-occurrence for parameters that lay on the line delineating the yellow and blue zones.

Chesson (2000; see also Mayfield and Levine 2010) extended this framework with *Modern Coexistence Theory*. Unlike the linear Lotka–Volterra models, this approach generalizes coexistence in terms of two components: **fitness differences** (which favor exclusion) and **stabilizing niche differences** (which promote coexistence). In essence, Chesson's framework reaches the same conclusion as Vandermeer: coexistence is facilitated when species are similar in fitness but different in interaction traits (Figure 6).

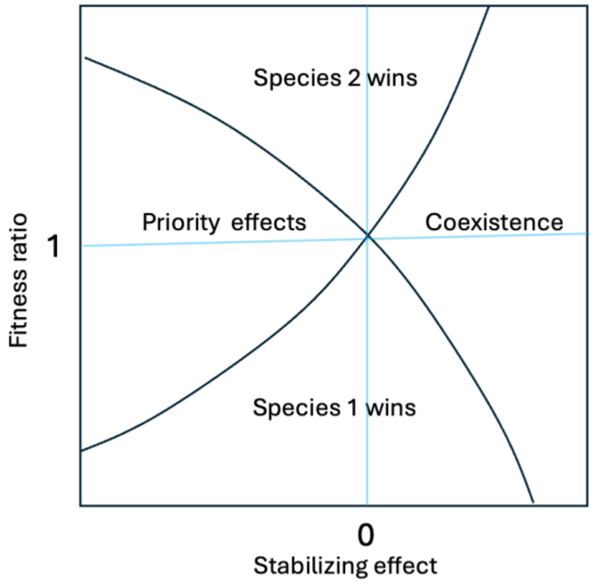

Figure 6: Outcomes of competition between two species as a function of fitness differences and stabilizing potential. There are four regions in parameter space that produce four qualitatively distinct outcomes. These depend on the strength of the stabilizing effect, whether it is positive, (to the right of the vertical blue line) or negative (to the left); and fitness ratios whether greater than 1 (favoring species 2 above the horizontal blue line) or less than 1(favoring species 1). When parameters are exactly in the intersection of the lines, the result is neutral co-occurence. Modified from Ke and Letten (2018).

Although the models developed by Vandermeer and Chesson are not necessarily niche-based (especially when competition occurs via direct interference mechanisms), Leibold (1998) presented a *mechanistic*, niche-explicit model of resource competition based on Tilman (1980) and earlier work (Leibold 1995). This model, illustrated in Figure 7, distinguishes the **response**

component (ZNGIs) from the **effect component** (impact vectors). It can be analyzed both graphically and analytically (Leibold 1998; Koffel et al. 2021; Meszéna et al. 2023).

These models reveal that species with dissimilar *impacts* are more likely to coexist, as their combined effects leave a larger region of resource supply space where both species can persist. However, species with similar *response traits* (i.e., similar ZNGIs) are less likely to be excluded by an intermediate invader, thereby increasing the durability of coexistence.

Letten and Fukami (2017) and Ke and Letten (2018) clarified how these results align with fitness ratio–stabilization tradeoffs: coexistence is promoted by similar ZNGIs (minimizing fitness differences) and dissimilar impact vectors (maximizing stabilization). However, overly large impact differences can *destabilize* coexistence (Figure 7e), highlighting that balance matters. Hawlena et al. (2022) further emphasized the utility of combining mechanistic models with modern coexistence theory for designing and interpreting experiments.

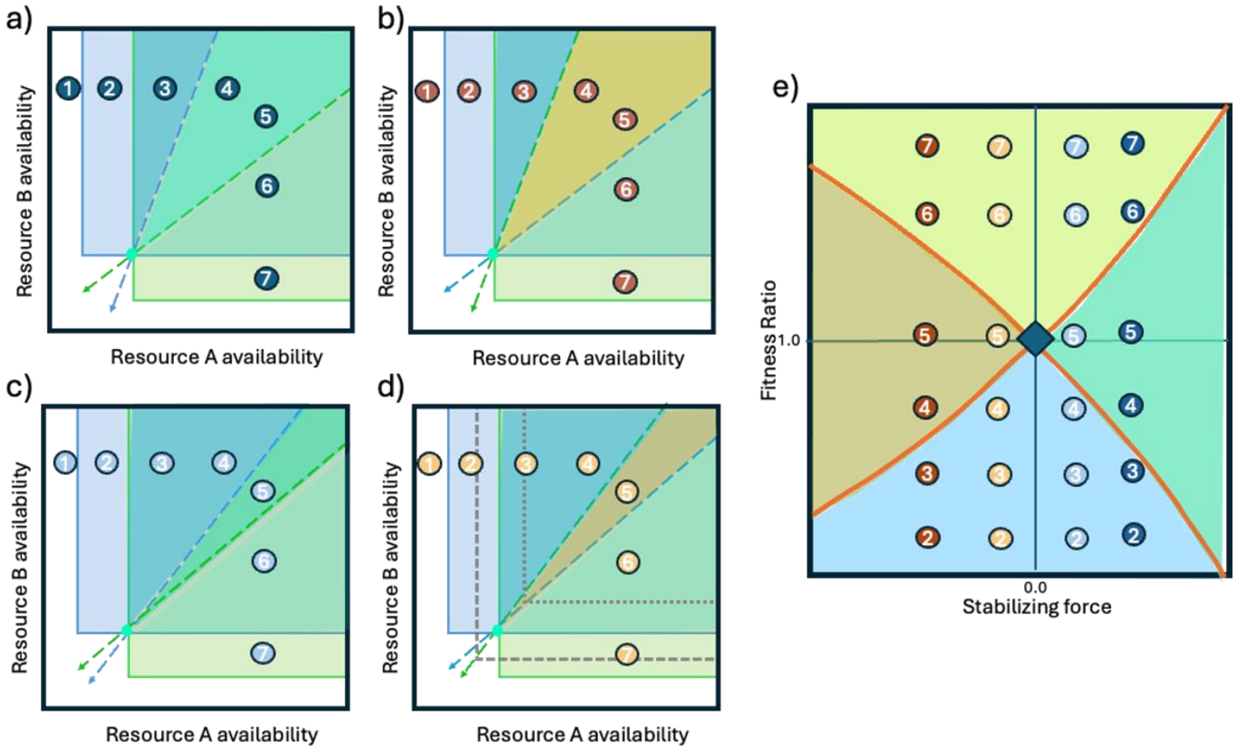

Figure 7: Mechanistic niche model of competition between two species. We consider two consumers that share two resources. In all cases we consider that Species 1 (shown with a blue ZNGI) has a lower requirement for Resource A and that Species 2 has a lower requirement for Resource B. These requirements define the fundamental niches for each of the two species: For Species 1 this will consist of all environments that have supply rates that lay to the upper-right (i.e. "North-East" or NE) sides of the blue rectangle (including zones that are blue, blue-green, green and yellowish green). Similarly, the fundamental niche of Species 2 is to the NE of the green isocline. These two species overlap in their fundamental niches are in the areas that are a rectangular subset of the total colored area. However, this area is larger than their actual realized niches. The panels on the left (panels a) and c)) show predicted distributions when each species has a larger proportional impact on the resource that is more limiting to it: Species 1 consumes proportionately more of Resource B than A (the blue arrow denotes this

effect at the equilibrium point identified by the intersection of the ZNGIs) whereas the reverse is true for Species 2. In this case coexistence is possible for habitats with supply points that lie in the triangular wedge that is bracketed by the impact vectors (green area). In contrast, if each species has a proportionately larger impact on the resource that more strongly limits the growth of the other species (panels b and d), note the reverse slope relations in the impact vectors, this zone (depicted in tan coloration), shows the overlap in their distributions along the environmental axis but indicates that they cannot coexist and will instead show priority effects. Predictions will vary depending not just in the relative position of the impact vectors but also in the magnitude of the difference in slopes. This is illustrated by the difference between panel a) vs b) and c) vs d) where the angle is larger in the left panels (a and c) than in the right-hand panels (b and d). In all 4 cases the resulting occupancy patterns are also depicted by hypothetical supply points (filled dots). These various outcomes can be illustrated in panel e) which outlines each of the possible qualitatively distinct outcomes of each panel in relation to potentially stabilizing effects (x-axis) and differences in 'fitness' (here a function of the ratio of their carrying capacities) denoted by the color of the symbols that correspond to panels a-d. Panel e) also shows the case for 'neutrally' coexisting species (dark blue diamond). Coexistence is facilitated by positive differences in the stability criterion because there will more possible supply points that will produce coexistence the further to the right of the graph. However, coexistence will be enhanced by similarity in relative fitness (closer to 1.0 along the vertical axis). Panel d) also shows possible ZNGIs belonging to two additional species. Species 3 identified by closely spaced grey ZNGI is a species that could have existed in this habitat but cannot adequately compete with either Species 1 or Species 2. In contrast, Species 4 is a species with a ZNGI that represents an intermediate phenotype between Species 1 and 2. As shown, it will invade (increase when rare) because its response niche includes the stability point of the equilibrium of Species 1 and 2. This guarantees that one or the other of Species 1 or 2 would go extinct and the resulting community would have increased similarity between their ZNGIs. The closer together the ZNGIs of species the less likely it will be that another species exists that can similarly constrain the differences among coexisting species. Coexistence will also be less likely with negative differences in the stabilizing effects (to the left of the figure). Overall, this shows that there is no simple prediction between similarity of the Lotka-Volterra parameters and coexistence.

Thus, the niche-explicit approach reaches conclusions that converge with both Vandermeer (1975) and Chesson (2000): **similarity in traits that match species to the environment promotes coexistence**, while **similarity in traits related to competitive interactions inhibits it**. Notably, these traits often share underlying parameters in the models used to describe them. Conventional traits (e.g., body size, stoichiometry) are even more abstracted from these dynamics and may not reliably distinguish between response and effect components—an issue we explore further below.

Neutral Co-Occurrence and the Niche

In all the models discussed above, there is the possibility that species can *co-occur* in the absence of differences in ecological traits (e.g., ZNGIs and impact vectors), corresponding to *neutral* mechanisms (Bell 2000; Hubbell 2001; see Figure 4c). However, two important caveats should be emphasized.

First, such cases occupy very specific regions of parameter space (see Figures 5d, 5g, 6, and 7e), where deviations from these conditions favor either competitive exclusion (as Grinnell 1904 argued) or stable coexistence. Second, in truly neutral dynamics, species' relative abundances are expected to drift over time due to stochastic variation, eventually resulting in the extinction of one species. To reflect this difference from stabilized coexistence, the term *co-occurrence* is used rather than *coexistence* (McPeek 2005).

Compared to other mechanisms of coexistence in metacommunities, neutral models lack stabilizing effects at the regional scale (Shoemaker and Melbourne, unpublished). Thus, it is unlikely that neutral dynamics dominate entire biotas (Grinnell 1904; Leibold and McPeek 2005), although they may apply to some species pairs embedded within larger communities governed by stabilizing niche differences. Indeed, experimental studies have found occasional evidence for neutral-like interactions among species pairs (e.g., Siepelski et al.; Smith et al.), even in communities where niche differences are generally observed (Siepelski and McPeek 2013). Grinnell's original argument likely reflects concern over fitness equalizing processes, though he was probably unaware of the stabilizing aspects of neutrality since the Lotka–Volterra framework had not yet been developed.

In diverse communities, there seems to be a regime that matches up with the predictions of neutral theory that can be quantified on the basis of the average population size of the species and the disturbance regime (Fisher and Mehta 2014) indicating that the neutral theory would apply to small and stochastic communities but that there is a threshold beyond which neutral theory would not.

Niche Differences and Trait- and Phylogeny-Based Ecology

As discussed above, niche-based coexistence is often analyzed through trait differences affecting either *fitness* (e.g., carrying capacities) or *competition coefficients*. Unfortunately, such traits are logistically difficult to measure directly (Narwani et al. 2013), especially in natural systems (but see Kraft et al. 2015). As a practical alternative, researchers often use "ecological traits" that are presumed to influence dynamics but are easier to quantify.

Historically, limiting similarity was frequently evaluated using body size (Hutchinson 1959; Diamond 1975; Bowers and Brown 1982), but results have been mixed (Simberloff and Boecklen 1981; Dayan and Simberloff 2005). This variability may reflect whether body size differences contribute more to fitness variation or to stabilizing mechanisms.

How other commonly measured traits contribute to fitness differences versus stabilizing effects remains poorly understood. Kraft et al. (2015) addressed this by examining correlations between plant traits and components of coexistence (Figure 7). They found that most significant correlations were associated with *fitness differences*, not stabilizing effects. This implies that trait similarity may correlate positively with coexistence, rather than providing evidence for limiting similarity. Detecting the latter would require identifying traits that directly mediate stabilizing niche differences—ideally, traits uncorrelated with those affecting fitness.

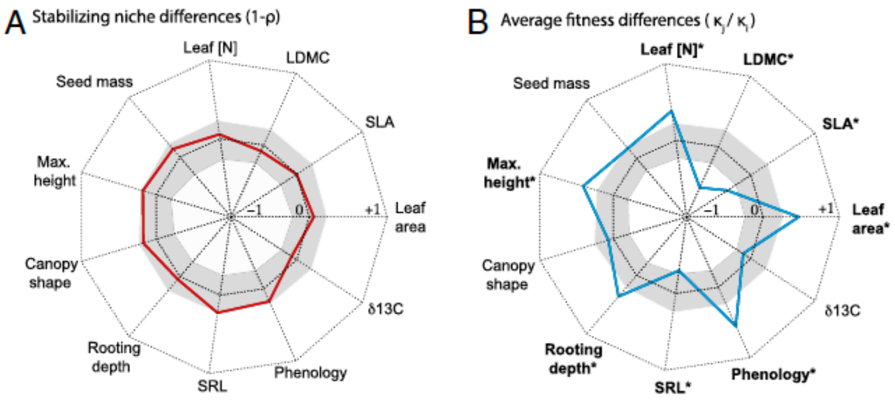

Figure 7: Associations between commonly measured plant traits (outer labels of each pinwheel) and their correlation with either (A) stabilizing effects or (B) fitness equalizing effects. Shaded areas show null expectations; significant positive correlations lie outside the shaded area, and negative ones lie within. None of the stabilizing trait correlations are significant; five positive and one negative correlation are significant for fitness effects. Figure from Kraft et al. (2015)

Trait-based studies also face the persistent challenge of *entanglement*—the difficulty in separating the effects of environmental filtering from species interactions. Levine et al. (2024) propose that resolving this issue requires the use of strongly grounded mechanistic models—*if* there is sufficient confidence in the model's structure and assumptions.

In summary, while trait variation likely underpins patterns of species coexistence, partitioning this variation into components associated with fitness versus stabilization remains a major challenge.

Phylogenetic approaches have also been proposed as a way to infer coexistence mechanisms. These assume *trait conservatism*—that closely related species tend to share ecological traits—thereby sidestepping the need to specify particular traits (McGill 2010). The approach involves comparing the phylogenetic dispersion of locally co-occurring species against null models.

Phylogenetic overdispersion—where coexisting species are more distantly related than expected—suggests that stabilizing niche differences allow coexistence. Conversely, *phylogenetic underdispersion* suggests environmental filtering (i.e., sorting along gradients). Some studies, especially those that incorporate both phylogeny and traits, have demonstrated the potential of this approach (e.g., Cavender-Bares et al.), but others are inconclusive. Overall, inference remains difficult, particularly when trait–niche mappings are unclear (Mouquet et al. 2012). As with trait-based methods, phylogenetic approaches are also challenged by the entanglement of environmental and biotic factors (Kraft et al. 2015b).

Species Distribution Modeling and the Niche

The niche concept has broader applications beyond limiting similarity—for instance, in modeling species distributions. Early approaches in this area were often referred to as "ecological niche models" (ENMs; Peterson 2001). While conceptually distinct from the niche ideas discussed above, contemporary efforts are beginning to reconcile these perspectives.

The current terminology favors *Species Distribution Models* (SDMs, Peterson and Soberon 2012), which attempt to predict species' distributions based on observed occurrences and environmental data. These models are often motivated by practical concerns such as forecasting responses to climate change, land use, eutrophication, or biological invasions.

Early SDMs typically related presence/absence or abundance data to environmental predictors. These models, superficially at least, follow the logic of Grinnell (1917) and Hutchinson, wherein environmental gradients define the species' distributional limits. They were typically developed for individual species and did not incorporate species interactions or address coexistence.

More recent work has expanded SDMs to include spatial constraints, such as barriers to dispersal or land-use change, leading to efforts like assisted dispersal or corridor planning. In response, the field has increasingly adopted the SDM label (e.g., Peterson and Soberón 2012; Melo-Merino et al. 2020).

One major limitation of SDMs is their treatment of species interactions. Even when modeling a single species, predictions can often be improved by including the distributions of interacting species. This has led to the *BAM* framework (Soberón and Peterson 2005), which partitions determinants of species distribution into Biotic (B), Abiotic (A), and Movement (M) components (BAM). However, disentangling B and A remains difficult—echoing the long-standing problem of entanglement discussed throughout this review.

Joint Species Distribution Models and Entanglement

A promising development has been the rise of *Joint Species Distribution Models* (JSDMs), which estimate co-occurrence patterns among species while also accounting for environmental and spatial structure (e.g., Pollock 2014; Ovaskainen et al. 2017). These models attempt to decompose variation in species composition into components attributable to abiotic, spatial, and biotic factors.

Ovaskainen et al. (2017) propose a sequential variance partitioning framework: first attributing variation to environmental predictors, then to spatial autocorrelation, and finally to residual co-distributions among species (Figure 8a). This works best when biotic interactions are relatively weak. However, if environmental and biotic factors are entangled, this approach will misattribute causality.

Figure 8b presents a more complete decomposition, including four additional interaction terms that reflect combinations of environmental, spatial, and co-distribution effects. These "entangled" components reflect the reality that ecological processes are rarely neatly separable. In practice, the explained variation often lies within these entangled components (Figure 8c), limiting the interpretability of SDMs and JSDMs in terms of direct ecological mechanisms.

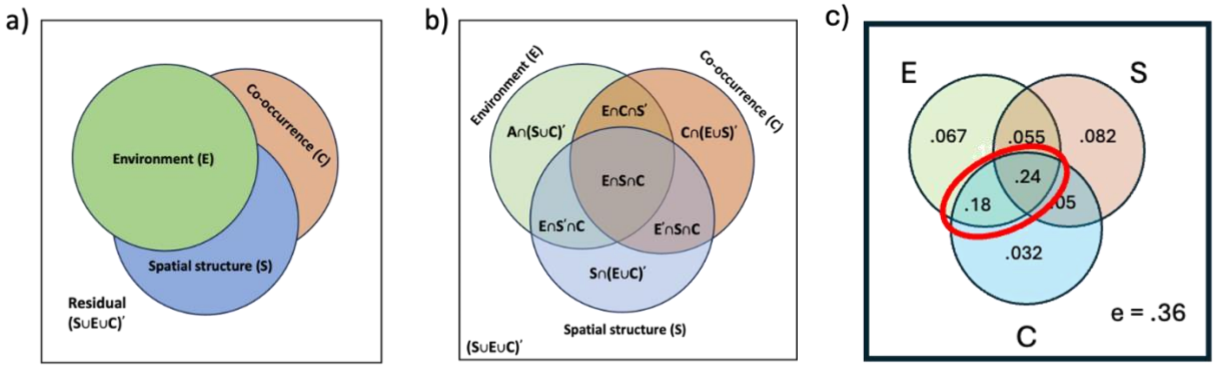

Figure 8: Venn diagrams depicting the decomposition of community variation. a) Sequential decomposition: variation is first attributed to environment (E), then to space (S), and finally to residual species co-distribution (C). b) Full decomposition: includes additional intersection terms representing entangled components of E, S, and C. c) Example from freshwater fish communities in Ontario showing that most explained variation lies in entangled components rather than uniquely attributable factors. Figure and data courtesy of Dr. Pedro Peres-Neto (Concordia University)

The persistent entanglement of biotic and abiotic influences continues to limit the utility of niche concepts in explaining species distributions. That said, rapid progress is being made in linking statistical modeling approaches to mechanistic ecological theory. The point of this review is not to argue that Darwin's "entangled bank" is intractable, but rather to highlight that it has yet to be resolved.

Microbial Niches

The field of microbial ecology—especially through advances in *omics* technologies (genomics, transcriptomics, proteomics, etc.)—has revealed novel aspects of niches that were previously unimaginable to ecologists studying other organisms. This section illustrates how the niche concept can evolve in scope and complexity without losing its original meaning.

A defining feature of microbes is that many enzymatic reactions involved in decomposition occur *extracellularly*, meaning their byproducts can be accessed by other organisms. This has important implications for niche dynamics. San Roman and Wagner (2021), using metabolic modeling, asked how many species could coexist on a single carbon compound (e.g., sucrose, fructose). Surprisingly, they found that an average of 30 species could coexist on a single carbon source. Moreover, the addition of further carbon source types only modestly increased species richness (Figure 9a). This occurs because different carbon compounds often break down into overlapping sets of simpler molecules. Dal Bello et al. (2021) provided experimental support for this prediction (Figure 9b). These findings challenge early interpretations of the competitive exclusion principle—namely, that no more species than there are distinct resources can coexist in a well-mixed system. Instead, they highlight that species can and do specialize on different metabolomic reactions—even when associated with the same compound—demonstrating that niche-based reasoning remains applicable.

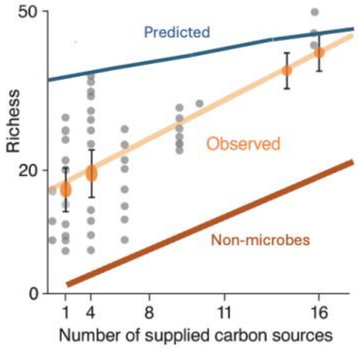

Figure 9: Metabolomic partitioning of carbon sources by microbes. Blue line: Predicted number of potentially coexisting species as a function of the number of carbon sources in a chemostat (San Roman and Wagner 2021). Orange line: Observed number of coexisting species in a daily-dilution/transfer microbial experiment (Dal Bello et al. 2021). Brown line: Predicted maximum number of species in organisms conventionally following Gause's axiom. Modified from San Roman and Wagner (2021) and Dal Bello et al. (2021)

Another complexity in microbial communities is the production of bacteriocins—chemicals that inhibit competitors. These interactions are *non-trophic* and often occur among genetically distinct conspecifics or between species. Kerr et al. (2002) demonstrated a well-known example of *non-transitive competition* among three *E. coli* strains (equivalent to species in this asexual taxon): a bacteriocin producer, a resistant non-producer, and a susceptible lineage. Because production and resistance are metabolically costly, these strains form an evolutionary rock-paper-scissors dynamic. Spatial structure is critical: in well-mixed environments, coexistence breaks down, but in structured settings, all three lineages persist through dynamic cycling. This shows that complex, direct interactions—still fundamentally niche-based—can mediate coexistence even in highly simplified systems. Notably, all three strains in the experiment competed for the *same* resource.

As new biological mechanisms continue to be uncovered in microbial systems, niche theory is increasingly challenged to accommodate them. Yet, these findings remain broadly consistent with the foundational view of the niche as a dual relationship involving *response* and *effect* components between organisms and their environments.

Conclusions

Some have questioned the usefulness and clarity of the niche concept (e.g., McInerny and Etienne 2012a; Justus 2019; Wakil and Justus 2021; but see McInerny and Etienne 2012b, 2012c). As a practicing community ecologist (and admittedly an amateur philosopher), we have found the niche concept—particularly as defined by Leibold (1995), Chase and Leibold (2003), Koffel et al. (2023), and Meszéna et al. (2025)—to be invaluable in studying various aspects of community ecology (as summarized here and in more detail by Chase and Leibold 2003 and Leibold and Chase 2018).

Early treatments of the niche were often informal and lacked mathematical rigor. But as theory developed, especially via models that captured the entangled responses and effects among species and their environments, the niche concept became central to addressing some of ecology's most challenging questions.

For instance, much has been made of the supposed conflict between niche-based and neutral dynamics. However, as discussed throughout this chapter, neutral dynamics can be comfortably accommodated within niche theory. In fact, neutral outcomes represent limiting cases within niche-based models—occupying narrow regions of parameter space (Figures 4–6). Grinnell's (1917) early skepticism about neutral coexistence anticipated this insight: neutral co-occurrence is possible but unlikely, and it is even more improbable that entire biotas are governed by neutral processes (Gravel et al. 2006; Leibold and McPeek 2006; Adler et al. 2007).

Wennekes et al. (2012) framed the debate as one between *realism* (detailed interactions matter) and *instrumentalism* (useful generalizations can sacrifice detail). While this distinction is interesting, neutral models often produce predictions that are empirically false—failing to account for patterns such as species abundance distributions, species–area relationships, and distance decay (Mayfield et al., in review). In contrast, newer *niche-based statistical models*, such as those developed by Barbier et al. (2018), Cui et al. (2024), and Akjouj et al. (2024), offer robust, general insights *without* relying on the problematic assumptions of neutrality. These models draw from statistical mechanics to generalize community assembly patterns while remaining grounded in niche theory.

Similarly, it may seem intuitive that species distribution patterns in metacommunities can be dissected into abiotic and biotic components. Yet even simple models (Figure 2) and sophisticated JSDMs (e.g., Figure 8c) highlight the difficulty of untangling these influences. Progress here will require novel approaches for teasing apart intertwined effects—though the path forward remains uncertain.

Contemporary Niche Theory, as articulated by Leibold (1995), Chase and Leibold (2003), Meszéna et al. (in review), and Koffel et al. (2023), provides a clear and mechanistically grounded definition of the niche. It captures both within- and among-community dynamics and retains fidelity to the historical dual meanings of the term.

Linking this conceptual framework with mechanistic models and modern coexistence theory has yielded major advances in community ecology. Nonetheless, substantial challenges remain—most stemming from the persistent *entanglement* of biotic interactions with environmental variation. While the exact solutions are unknown, there is no reason to believe that they lie outside the scope of niche theory.

A more recent challenge involves the realization that pairwise interactions—even when fully understood—do not necessarily scale predictably to multispecies contexts. For example, Chang et al. (2023) showed that species exhibiting strong pairwise competition could nonetheless coexist in large, diverse communities of up to 24 species. Clark et al. (2020) found that models estimating detailed species interaction parameters underperformed relative to simpler models using average intra- and interspecific effects. Similarly, Barbier et al. (2023) and Xiao et al. (in review) showed that regression-based estimates of individual interaction strengths are unreliable, whereas their *means and variances* can be robustly inferred. These results suggest that coexistence in diverse communities depends on more than just the additive outcomes of pairwise interactions.

Even when environmental effects are controlled, species interactions can remain difficult to resolve. Spaak and Schreiber (2023) argue that this problem can be addressed by integrating Modern Coexistence Theory with *permanence theory* and *invasion graphs*—models that track community assembly over time (Law and Morton 1996; Godoy et al. 2024). They propose that robust coexistence predictions require knowledge of all n–1 subcommunities, where *n* is the full set of species. Though beyond the scope of this chapter, this approach underscores the complexity of inferring coexistence from direct interactions alone.

Final Thoughts

Despite its conceptual challenges, the niche remains a vital and evolving tool in ecology. The contemporary niche concept, grounded in both historical insights and modern mechanistic models, continues to shape our understanding of species distributions, coexistence, and community dynamics. It offers both theoretical clarity and empirical relevance—and, as this review shows, it remains central to meeting the pressing challenges of ecological research.

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