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NICHE BREADTH: CAUSES AND CONSEQUENCES FOR ECOLOGY, EVOLUTION, AND CONSERVATION

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ABSTRACT

Niche breadth is a unifying concept spanning diverse aspects of ecology, evolution, and conservation biology. Niche breadth usually refers to the diversity of resources used or environments tolerated by an individual, population, species, or clade. Here we review key research in ecology, evolution, and conservation biology in light of niche breadth. Namely, we explore the role of niche breadth in shaping geographic distributions and species richness from local to landscape scales, how niche breadth evolves and influences lineage diversification, and its use for understanding species invasions, responses to climate change, vulnerability to extinction, and ecosystem functioning. This diverse literature informs a research agenda that identifies focused needs for further progress: testing the hierarchical nature of niche breadth (e.g., of individuals, populations, and species); quantifying correlations in niche breadth among different niche axes and the role of environmental drivers and organismal constraints in generating these correlations; and evaluating the factors that decouple fundamental and realized niches. We describe how this research agenda could help unify disparate subdisciplines and shed light on key questions in ecology, evolution, and conservation.

INTRODUCTION

THE niche is a core concept in ecology, evolution, and conservation biology. The niche concept is used to help explain the distributions, abundances, and resource use of organisms through both space and time (Chase and Leibold 2003; Peterson et al.

2011). A particularly critical component of the niche is the breadth of conditions that support nonnegative population growth rates—the niche breadth (hereafter NB) of the population or species in question (Hutchinson 1957). NB represents the needs and tolerances of organisms, across both abiotic and biotic axes and is germane to many fundamental

processes in ecology and evolutionary biology, including community assembly and ecosystem functioning (MacArthur and Levins 1967; Duffy et al. 2007), the distribution of species (e.g., Slatyer et al. 2013), and speciation (e.g., Hardy and Otto 2014). Furthermore, NB is relevant to some of today's greatest conservation challenges, including invasive species (e.g., Jeschke et al. 2012), habitat modification (e.g., Sattler et al. 2007), and climate change (e.g., Boulangeat et al. 2012).

The literature on NB is diffuse, in part because of its varied nomenclature. Terms that have been used synonymously with NB include niche width, niche variation, tolerance, ecological specialization, ecological versatility, ecological amplitude and, in certain cases, plasticity (e.g., Roughgarden 1972; Sultan and Bazzaz 1993a,b,c; MacNally 1995; Dwire et al. 2006; Forister et al. 2012). This multiplicity of terminology means that even simply aggregating papers pertaining to NB is challenging. As a result, advances in one area of NB research may go unnoticed in others.

We think that the disconnect in terminology, and the resulting apparent incompatibility between research areas and questions, necessitates a synthesis of this important body of literature. Numerous reviews have been published on various aspects of the niche, including its definition (e.g., Holt 2009), how NB evolves or specialization arises (e.g., Futuyma and Moreno 1988; Poisot et al. 2011; Forister et al. 2012; Sexton et al. 2017), and metrics for quantifying NB (e.g., Colwell and Futuyma 1971; Devictor et al. 2010; Poisot et al. 2012). Yet, this vast literature lacks the unity needed to foster cross-pollination among subdisciplines, enhance our mechanistic understanding of the causes and consequences of NB, and move toward answering long-standing questions in ecology and evolution.

Our synthesis begins by clarifying niche and NB terminology, since defining the niche has long been contentious. Three overarching ideas then form the scaffold for our synthesis: the hierarchical structure of NB (of individuals, populations, species, clades, and communities); the correlation of NB among different niche axes; and the relationships between the realized and fundamental niches. Together, these overarching ideas address

the mechanistic underpinnings of NB—that is, how intrinsic and environmental factors interact to shape NB. We then synthesize research on several key topics within the evolutionary, ecological, and conservation literature with the goal of illustrating insights gained through considering NB. Lastly, we reinforce how targeted studies aligned with the research agenda could promote insights into many research questions across subdisciplines.

DEFINING THE NICHE

THE HUTCHINSONIAN NICHE

In this review, we broadly adopt the Hutchinsonian definition of the niche as the “*n*-dimensional” set of abiotic and biotic conditions under which a species or population can maintain nonnegative growth rates without immigration (Hutchinson 1957, 1978). This definition embraces the suite of biotic and abiotic conditions (e.g., diet, predators, microhabitat, and macroclimatic temperature and precipitation) that influence the persistence of species or populations. We refer to each of these factors as a “niche axis.” Unless we specify otherwise, the topics we discuss in the remainder of the paper pertain to biotic and abiotic axes.

We recognize that alternative niche definitions focus on the roles of organisms in their ecosystems or impacts on their environments, rather than the resources and conditions required for persistence as in the Hutchinsonian definition we adopt here. This “niche as impacts” perspective can be traced back to a definition of the niche that emerged from food web theory (e.g., Elton 1927). Within a network of interacting species, a species' NB can be described in terms of its breadth of functional roles, like the range of prey species it consumes or the number of mutualistic partners it maintains (“interaction NB” or “degree” in the network literature; Devictor et al. 2010; Poisot et al. 2012; Batstone et al. 2018). Furthermore, organisms can construct, destroy, or otherwise modify their own niches by choosing or changing their environment (e.g., Holt 2009; Peterson et al. 2011). For example, animals can construct their niches by choosing habitats, building nests, or digging tunnels (reviewed in Odling-Smee et al. 1996), and destroy their niches by drawing down

resources below the levels needed for survival (Holt 2009). The dynamic relationship between organisms and their resources is central to several classic models of species interactions, such as the resource-ratio theory for competition (Tilman 1982; Chase and Leibold 2003). Because these extensions of Hutchinson's niche concept have been thoroughly reviewed elsewhere (e.g., Odling-Smee et al. 1996; Chase and Leibold 2003), we do not include the impacts that organisms have on their environment as part of our working definition of the niche for this review.

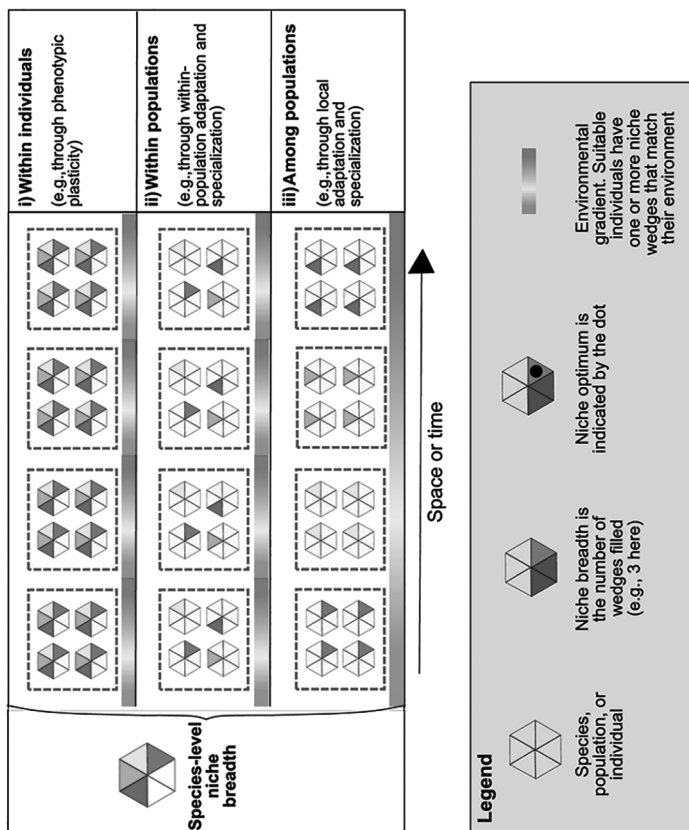
QUANTIFYING THE NICHE

The Hutchinsonian niche (1957) is classically defined in terms of population growth rates. Nevertheless, studies commonly use alternative response variables as surrogate measures (e.g., presence/absence, abundance, performance, and resource consumption). Surrogate measures allow extension of the NB concept beyond species (e.g., to individuals and clades) and can provide estimates of niche parameters when demographic data are too difficult to obtain. We include these proxies for quantifying the niche here; however, niches characterized using surrogate measures (e.g., presence/absence) may not accurately represent population growth rates or fitness responses to environmental variation (e.g., Tittes et al. 2019; Pagel et al. 2020).

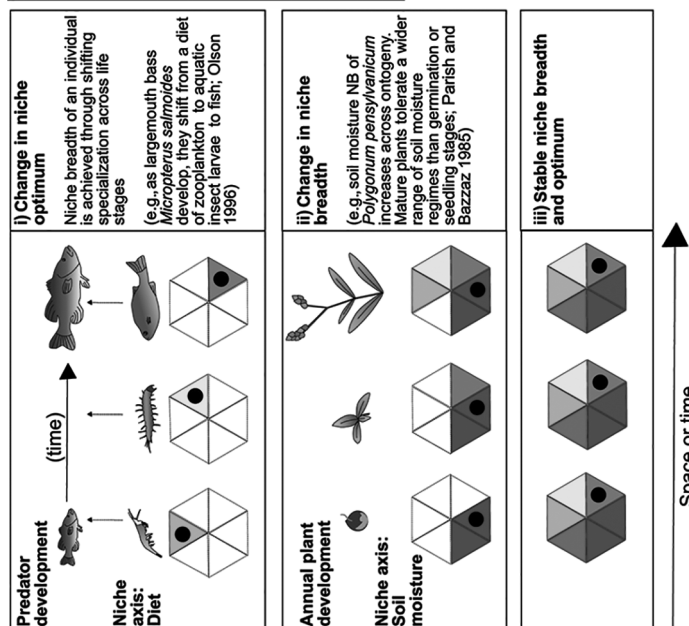
Decomposing population growth rates into performance at specific life stages (measured as vital rates) can clarify whether different response variables are reasonable proxies of population growth rate. Examples of vital rates include rates of germination or birth, survival, growth, and reproduction. Many experimental NB studies assess one of these rates, such as germination across a growing season (temporal breadth of the germination window; e.g., Brändle et al. 2003) or organismal survival under different temperatures (e.g., Kelly et al. 2011). However, different life stages can have vastly different niche optima, as in many marine taxa, migratory species, or metamorphosing species such as frogs (Figure 1.a.i; Olson 1996). Hence, organisms that are specialists in a given life stage could have a broad niche cumulatively across their

lifespan. NB itself can also change across ontogeny, so breadth at one life stage might not consistently predict breadth at other life stages (Figure 1.a.ii; Donohue et al. 2010). Many tree species, for instance, require a narrower suite of conditions for reproduction than for establishment or adult growth (Jackson et al. 2009). NB is often considered to increase with age or size. For example, soil moisture NB of *Polygonum pensylvanicum* plants broadens as they mature (Figure 1.a.ii; Parish and Bazzaz 1985), and in aquatic systems, dietary NB (size range of prey consumed) of gape-limited predators often increases as predators grow larger (Gravel et al. 2013). Additionally, even individuals within the same size class or life stage may exhibit vital rates that are unrelated to each other or show opposing trends across geographic or climatic gradients, when considering the full suite of vital rates (Pironon et al. 2018). Moreover, an organism's size can impact different vital rates in contrasting ways across an environmental gradient, further complicating the relationships among vital rates and with population growth itself (Oldfather and Ackerly 2019). Thus, while collecting data on a single vital rate (e.g., assessing germination NB) can provide insight into the requirements and tolerances of sensitive stage transitions, it might not accurately predict cumulative population growth and, therefore, the Hutchinsonian niche. Despite this challenge, NB proxies have been used extensively and have been shown to have explanatory power in a wide range of studies across ecology, evolution, and conservation biology (e.g., Gravel et al. 2011a; Joy 2013; Sheth et al. 2014).

When NB is estimated using static response variables (e.g., presence/absence or abundance without repeat measures over time) rather than dynamic variables (repeated measures, e.g., population growth rate, changes in vital rates over time), shrinking populations are not differentiated from stable or growing ones. Thus, NB estimates from static response variables may be larger than from population growth rate-based niche estimates, which exclude sink habitats (Pulliam 1988; Pironon et al. 2018; but see Merow et al. 2014). For example, Diez et al. (2014) demonstrated that the probability of positive population

b) Within- and among-population phenotypic variation

a) Within-individual phenotypic variation



growth rates for an orchid was not related to its abundance or probability of occurrence within microsites (see also Thuiller et al. 2014, which reported a negative relationship between tree population growth rate and probability of occurrence). Dispersal limitation, source-sink dynamics, and demographic stochasticity can all decouple static and dynamic measures of the niche (Diez et al. 2014). Mismatches between static and dynamic response variables are particularly likely to be exacerbated in long-lived or highly persistent species where current geographical distributions primarily reflect species' responses to past conditions, in less competitive but more broadly tolerant species that have been displaced to suboptimal conditions, and in species with poor dispersal ability (Bohner and Diez 2020; Pagel et al. 2020). Experimental studies of demography involving transplants can illuminate whether populations moved beyond a species' range edge are self-sustaining (Hargreaves et al. 2014; Lee-Yaw et al. 2016) and clarify which response variables (e.g., occurrence, population growth) will paint similar pictures of NB (see the section titled Disentangling Fundamental and Realized Niches: How Ecological Context Shapes Niche Breadth).

Regardless of how the response variable is defined, the niche is often characterized by three properties: niche breadth, niche optimum, and niche position. These can be measured along single niche axes or in multivariate space. NB, the main focus of this paper, is a measure of the span of a niche—the range or diversity of conditions included within the niche. NB estimates can be more information-rich than point estimates of niche position or optimum alone, for example, by including information on the range of conditions a species can tolerate and whether performance is consistent or drops off sharply within that range (e.g., Tittes et al. 2019). Moreover, NB is explicitly a measure of variation, and a focus on NB is in many ways analogous to the resurgence of interest in the importance of intraspecific variation in community ecology (e.g., Bolnick et al. 2011; Cadotte et al. 2011; Violle et al. 2012). In contrast, the niche optimum is the value or category along a niche axis where population growth (or a proxy) is maximized (e.g., Roughgarden 1974; Emery and Ackerly 2014).

The niche position differs from the other two niche parameters in that it is not strictly a property of the species, but rather a function of the relationship between the species' niche and the distribution of resources or conditions in the environment the species occupies. Niche position was originally defined as the mean resource actually used, or condition actually occupied, in the environment (Roughgarden 1974). This definition is still widely used in population biology. The niche position differs from the niche optimum when an organism uses more of the suboptimal resources (or occupies more suboptimal conditions) than expected based on its niche. This can occur when the optimal resources or conditions are relatively rare (or even absent), so that the majority of individuals contributing to population growth exist in conditions that are not at the niche optimum (e.g., Emery and Ackerly 2014). A related but different definition of niche position is used in biogeography, where it is the difference between a species' mean resource use or condition occupied and the mean value available in the environment (Seagle and McCracken 1986; Sheth et al. 2014). This measure provides an estimate of marginality, where a species using widespread or abundant resources has a low niche position and a species using marginal or scarce resources has a high niche position. The biogeographic definition cannot reveal the difference between a species' niche optimum and position, since it is entirely based on occupancy in the existing environment without knowledge of the conditions that are truly optimal for the species. However, the biogeographic definition is commonly used, and because it describes the marginality of a species' niche, this definition can be especially pertinent for understanding species' abundance, geographic range size, and extinction vulnerability (e.g., Dolédec et al. 2000; Gregory and Gaston 2000; Heino 2005; Kotiaho et al. 2005; Thuiller et al. 2005; Sheth et al. 2014).

DEFINING AND MEASURING FUNDAMENTAL AND REALIZED NICHES

Hutchinson (1957) distinguished between fundamental and realized components of the niche. He defined a species' fundamental

niche as those conditions under which it can sustain nonnegative population growth rates in the absence of immigration and competition. This definition has been updated to also assume the absence of predation, pathogens, and facultative mutualists or facilitation (Bruno et al. 2003; Holt 2009). The fundamental niche includes both abiotic conditions and biotic resources (Blüthgen et al. 2006; Peterson et al. 2011).

Fundamental NB can be quantified with experimental approaches such as transplants or environmental manipulations. This allows researchers to isolate the effects of a single environmental variable on key vital rates and/or performance (e.g., Kelly et al. 2011). Transplant experiments might risk overlooking the establishment part of the niche, unless, for example, seeds are transplanted or young reared in different environments from birth. Controlled field experiments in which biotic interactions are reduced (e.g., herbivore exclusion or competitor removal) or dispersal is manipulated can provide valuable complements to laboratory tolerance tests (Kraft et al. 2015). However, implementing field experiments for mobile, large, and long-lived taxa poses numerous challenges. For some species, data on fundamental NB may be prohibitively time-consuming, costly, or invasive to gather experimentally. Species invasions, which essentially serve as uncontrolled transplant experiments, have provided important insights on fundamental NB by revealing the range of resources used or conditions occupied in the introduced range, relative to realized NB in species' native ranges (e.g., Petitpierre et al. 2012; Early and Sax 2014). An alternative approach for characterizing climatic niches is to use mechanistic niche modeling. This approach can estimate species' fundamental niches using diverse data, including physiological tolerances, behavior, and life history (Kearney and Porter 2009; Buckley et al. 2010).

The realized niche represents the conditions a species actually occupies as opposed to those in which it could potentially exist. That is, a species may fail to occupy a portion of environmental (or resource) space because interspecific interactions exclude it from locations where those conditions occur, the species has failed to colonize those areas, or

the conditions do not exist on the landscape at that time (Jackson and Overpeck 2000). Niche limits and geographic range limits frequently coincide (Hargreaves et al. 2014; Lee-Yaw et al. 2016). However, a species' realized niche is not synonymous with its geographic range (e.g., unsuitable conditions can occur inside the geographic range of a species, and suitable conditions can exist outside of the species' range; Sunday et al. 2012).

There are several ways to quantify realized NB, depending on the niche axes of interest. For climatic niches, researchers commonly combine readily available climatic and occurrence data to estimate realized NB (as the range or variance of climatic conditions where the species occur). These same occurrence and climatic data are often used to create ecological niche models, including species distribution models and climatic envelope models (e.g., for projecting suitable habitat on a landscape and estimating species invasive spread or potential range shifts with climate change; Peterson et al. 2011). As another example, realized dietary NB can be determined from interaction networks, as the diversity of prey consumed by a focal taxon in nature (e.g., Poisot et al. 2012).

A COMMON AGENDA: OVERARCHING IDEAS FOR PROGRESS IN NICHE BREADTH RESEARCH

We suggest that three ideas are particularly important for progress in NB research: the hierarchical structure of niches, correlations in breadth among niche axes, and relationships between fundamental and realized niches.

THE HIERARCHICAL STRUCTURE OF ECOLOGICAL NICHEs

NB has a hierarchical nature (Roughgarden 1972) composed of at least three nested scales: within individuals (Figures 1.a and 1.b.i), among individuals within populations (Figure 1.b.ii), and among populations within species (Figure 1.b.iii). For example, a species that spans a wide range of environmental conditions could be a collection of individuals and populations that each tolerate a similarly

wide range of conditions, or many individuals or populations that are highly adapted to local conditions (Figure 1.b; e.g., Via 1991; Ettersson and Shaw 2001; Kelly et al. 2011). Similarly, population-level NB could be composed of individuals with similar NB to that of the collective population, individuals with narrow NB and divergent optima, or some combination of these two extremes (e.g., Sultan and Bazzaz 1993a,b,c; Araújo et al. 2011; Bolnick et al. 2011). Although we focus on the hierarchical nature of species-level NB, NB can also be extended to higher scales (e.g., clade; Gómez-Rodríguez et al. 2015). Indeed, the potential for the NB concept to inform processes at multiple biological scales is a primary reason why it is relevant to a broad range of subdisciplines in the biological sciences.

NB is most commonly reported at the species level (Figure 1), and it is unclear the extent to which inferences at one biological scale are transferrable to other scales. Angert et al. (2011) found that fundamental thermal NB was consistent among 12 populations of scarlet monkeyflower (*Erythranthe cardinalis*). Experimental studies of *Polygonum persicaria* grown along light, moisture, and nutrient gradients revealed very similar fundamental NBs among genotypes across two populations (Sultan and Bazzaz 1993a, b,c). These examples illustrate cases where NB at one biological level would be a reasonable approximation of NB at another level. However, studies that find local adaptation, genetic differentiation, or different patterns of plasticity in performance among populations provide evidence that species-level NB may overestimate the range of conditions that single individuals or populations tolerate (e.g., Clausen et al. 1948; Linhart and Grant 1996; Seigel and Ford 2001; Howells et al. 2012). Several early and influential studies acknowledged NB's hierarchical structure in the contexts of plant transplants and island biogeography (Clausen et al. 1948; Van Valen 1965; Roughgarden 1972, 1974). In a classic test of niche hierarchy, common garden studies of the pine tree (*Pinus contorta*) revealed important among-population differences in cold hardiness. The genetic variation within a single population implies that an average population could persist

across two-thirds of the species' estimated realized niche (Rehfeldt et al. 1999). These foundational works helped motivate more recent studies on the hierarchical nature of NB (Araújo et al. 2011; Quintero and Wiens 2013), its consequences for communities and ecosystems (Quevedo et al. 2009), and its implications for species responses to climate change (e.g., Angert et al. 2011). For example, Kelly et al. (2011) found that broad species-level thermal NB of a tidepool copepod species was almost entirely partitioned among distinct, locally adapted populations, so that each population had a much narrower NB than the species as a whole. Consequently, a climatic niche model based on species-level occurrence data in this system would likely underestimate the vulnerability to climate change of individuals, populations, and the species, especially if dispersal is limited. Conversely, studying the thermal responses of a few individuals, or a single population, could underestimate the NB of a species and, therefore, its capacity to respond to climate change.

CORRELATIONS IN BREADTH AMONG NICHE AXES

Species are often deemed "specialists" if they exhibit narrow breadth along a niche axis, as this can reflect a strict dependency on a particular type or level of resource (e.g., insects that feed on a single host; Poisot et al. 2011) or an obligate association with a specific abiotic environment (e.g., anaerobic bacteria). The extent to which breadth along one niche axis is correlated with breadth along other axes is rarely investigated (Figure 2.a; Futuyma and Moreno 1988; Sultan et al. 1998). We propose that the potential for NB to be correlated across niche axes depends upon: environmental drivers, such as the extent to which the spatial or temporal variation in resources or conditions along different niche axes is correlated with one another in the environment (Figure 2.b); and functional constraints, the extent to which an organism's response to different axes is determined by common physiological or genetic mechanisms (Figure 2.c).

Correlations in variability among resources or conditions in the environment can drive

correlations in realized NB across axes. If variability in environmental conditions is positively correlated among niche axes, narrow breadth along one axis causes a species to be exposed to less variation along other niche axes. This may favor the narrowing of the fundamental niche across multiple axes over time, particularly if there are costs to maintaining NB that exceeds the range of conditions experienced in the realized niche (Figure 2.b.i). Alternatively, if environmental variability is negatively correlated among niche axes, specialization along one axis could lead to broader tolerance across another (Figure 2.b.ii; NB tradeoff hypothesis *sensu* Bonetti and Wiens 2014). For example, areas with constant temperature but highly variable precipitation regimes would lead to negative correlations in realized NB among axes. It is the correlations in environmental *variability*, rather than environmental conditions themselves, that should structure NB correlations in the absence of functional constraints.

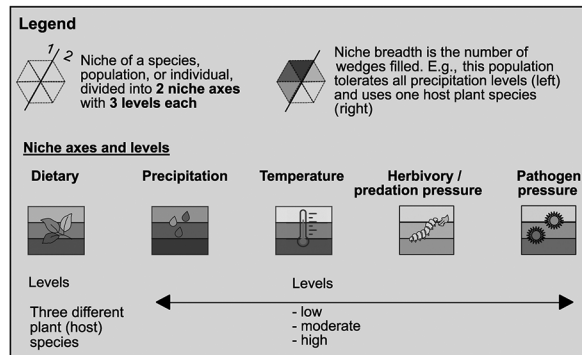
Functional constraints, and their interactions with environmental variation, can also influence the degree to which NB (fundamental or realized) is correlated among niche axes. Positive correlations in breadth among axes can occur if the same traits or genes (or tightly linked loci) convey tolerance to extreme conditions on multiple environmental axes (e.g., pleiotropy; Figure 2.c.i; Latta et al. 2007). Alternatively, negative correlations could arise if traits that enhance tolerance along one niche axis reduce tolerances along others (e.g., antagonistic pleiotropy; Figure 2.c.ii; Etterson and Shaw 2001). Theory predicts that selection will favor narrow NB in stable, homogeneous environments and broader NB in variable environments (e.g., Levins 1962; Sultan and Spencer 2002). This prediction has received some empirical support. For example, an experiment with *Escherichia coli* found that populations evolved reduced tolerance of freeze-thaw cycles after several generations in a constant, benign environment (Sleight et al. 2006). Several factors may restrict the extent to which optimal NB evolves in a given environment. These include inherent physiological or genetic constraints of the organism (e.g., Table 2 in Hoffmann

and Sgrò 2011), the predictability of environmental variation (Reed et al. 2010), and the magnitude of the cost of maintaining tolerance to conditions that are seldom experienced (e.g., Angilletta et al. 2003).

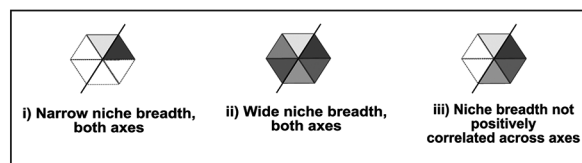
The handful of empirical studies that have tested for correlations in breadth among niche axes have yielded mixed results for the hypothesis that NB on one axis predicts NB on others. Liu et al. (2020) found that realized NBs for temperature and precipitation axes were positively but weakly correlated across hundreds of plant and animal species. However, Litsios et al. (2014) found negative relationships between the realized breadth of host species used and environmental temperature, pH, and salinity axes in clownfishes. Negative relationships were also found between fundamental habitat breadth and environmental stress tolerances in antlions (Rotkopf et al. 2012). No significant correlation in NB was detected among realized moisture and nutrient axes across *Polygonum* species (Sultan et al. 1998). Emery et al. (2012) detected no correlation in realized breadth between climate and microhabitat axes, and limited evidence for correlations among three orthogonal climate axes of NB in a clade of annual plants. Hence, current evidence suggests substantial variation in the extent to which NB is correlated among axes. Several studies examined markedly different sets of variables, and it is not clear if studies examining different facets of large-scale climate are comparable with those examining microhabitat variation in moisture and pH, for example. An increased understanding of correlations and tradeoffs across niche axes may help us clarify the role of NB in ecological and evolutionary processes. For example, understanding if specialists are likely to have narrow NB along multiple axes could help assess species' vulnerability in response to habitat loss and environmental change.

DISENTANGLING FUNDAMENTAL AND REALIZED NICHES: HOW ECOLOGICAL CONTEXT SHAPES NICHE BREADTH

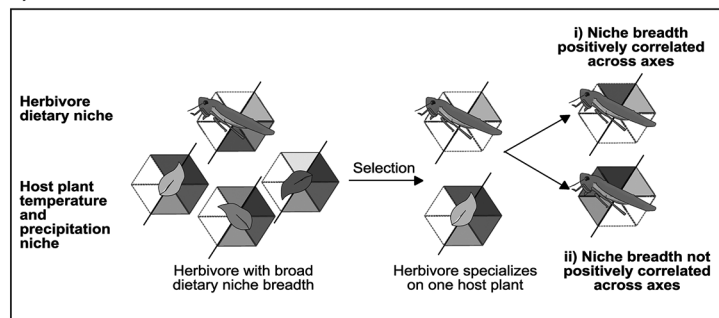
How similar are fundamental and realized niches? In conifers, for example, realized and fundamental NB exhibit a strong positive



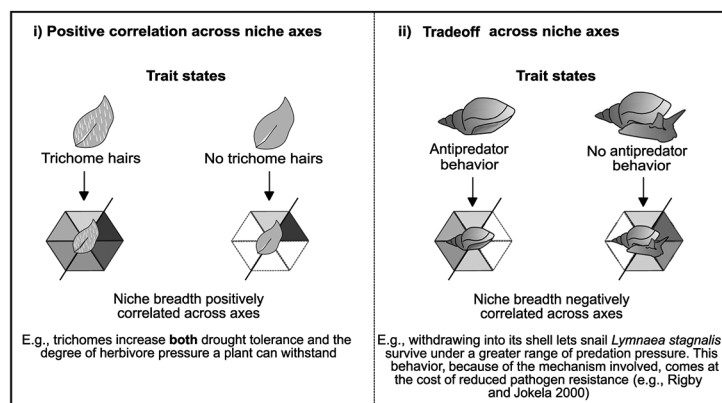
a) Patterns of niche breadth correlation across two niche axes



b) Environmental drivers of niche breadth correlations across niche axes



c) Organismal (trait-based) constraints on niche breadth correlations across niche axes



correlation, but the gap between fundamental and realized NB increases as realized NB narrows (“niche disequilibrium”; Rosenblad et al. 2019). The fundamental niche reflects a species’ innate needs and tolerances in the absence of interspecific competition, predation, parasitism, mutualism, and facilitation. Because the realized niche includes the effects of biotic interactions and dispersal, estimates of fundamental and realized NB may represent different features of a focal species. For example, they might generate contrasting predictions about the species’ invasion potential or responses to environmental change (Buckley et al. 2010; Kearney et al. 2010). However, data on the fundamental and realized niche are sometimes used interchangeably. If we understand the factors that differentiate fundamental and realized NB, we can estimate in which ecological contexts these two facets of the niche will be most similar.

Biotic Interactions

A substantial amount of ecological theory and empirical work has focused on how antagonistic interactions (such as competition and predation) exclude species from habitats or resources that they could otherwise occupy, resulting in realized NB being smaller than fundamental NB (e.g., Leibold 1995). For example, the classic study by Connell (1961) showed that the barnacle *Chthamalus* is restricted to the high zone of rocky intertidal shorelines because it is outcompeted by the barnacle *Balanus* in the otherwise more favorable lower intertidal zone. The interaction between competition and NB is thought to be broadly important for structuring communities, particularly when multiple species draw upon the same abiotic or biotic re-

sources (“shared preferences”; McGill et al. 2006). Coexistence among species with shared preferences can arise from contrasting mechanisms. Competitive species with broad fundamental niches can shift to use alternative forms of a shared resource (e.g., ammonium versus nitrate forms of nitrogen), increasing niche partitioning and coexistence (Ashton et al. 2010). Alternatively, a tradeoff between competitive ability and NB can allow poor competitors to persist because they tolerate the lowest levels of shared resources or endure the least preferred conditions (e.g., Tittes et al. 2019; Böhner and Diez 2020).

In contrast to the extensive work examining how competition drives discrepancies between the fundamental and realized niche, far fewer studies have considered the influence of mutualism and facilitation on NB. Mutualisms can have contrasting effects on host NB. Like competition, mutualisms could reduce host NB. In an obligate aphid-bacterium mutualism, association with a certain bacterial genotype lowered aphid thermotolerance (Dunbar et al. 2007). Moreover, many mutualistic associations involve costs, like provisioning partners with resources (Bronstein 2001) that could limit their investment in strategies that increase their range of environmental tolerances. Positive interactions can also expand the realized niche of a species (Bruno et al. 2003). For example, associations with some fungal endophytes increase drought tolerance and allow range expansion of host plants (Afkhani et al. 2014). Hence, mutualisms can create mismatches between fundamental and realized niches by expanding or constraining host NB, depending on the nature of the tradeoffs and the explicit benefits provided by mutualistic partners. Further, although mutualisms may expand

FIGURE 2. CORRELATIONS AND CONSTRAINTS: NICHE BREADTH (NB) ACROSS AXES

Species could have positively correlated NB across niche axes (a.i; a.ii). Alternatively, NB may be negatively correlated or uncorrelated across niche axes (a.iii). Covariance among environmental axes may shape NB correlations (b). Here, leafhopper dietary specialization could lead to thermal specialization (b.i). If the host plant and thermal regime are distributed across a broad range of precipitation levels, leafhopper precipitation NB may not be positively correlated with NB along these other axes (b.ii). Organismal constraints can also shape NB correlations (c). Here, a single trait influences NB along two axes. For example, trichome hairs can help plants tolerate drought and resist herbivores (b.i), leading to positive NB correlation across axes. In contrast, snail antipredator behavior might constrain NB along other axes: resistance to predators trades off with resistance to pathogens (Rigby and Jokela 2000). See the online edition for a color version of this figure.

realized NB along some axes, they might contract it along others (e.g., Afkhami et al. 2014), again highlighting the need for research that simultaneously considers multiple niche axes and their interactions.

Species' Abundance and Dispersal Limitation

A species' abundance and dispersal ability can shape its likelihood of encountering different species, resources, and conditions. Limited opportunities generate a narrower interaction network (e.g., fewer plant species visited by a focal bee) and thus a narrower realized NB. Indeed, null models based on species' relative abundances have predicted the NBs of freshwater fish and mammalian host-parasite systems reasonably well (Vázquez et al. 2005; Canard et al. 2014). Similarly, low-abundance or dispersal-limited species may be restricted to a few habitat types simply because they have fewer opportunities to sample the full environmental spectrum ("habitat selection"), although this idea has not been supported by many studies (Gaston et al. 1997). Nevertheless, it highlights an important conundrum: is narrow NB in a species a cause or consequence of its abundance? Only the former causal pathway implies narrow NB species have an "intrinsic degree of specialization" (Vázquez et al. 2005: 952), rather than their NB arising solely due to their opportunity to interact with different habitats and species (Vázquez et al. 2005). Therefore, studies that empirically quantify fundamental NB are invaluable for differentiating between NB as a cause or consequence of relative abundance. Such studies could include physiological experiments evaluating growth rates across a range of temperatures or feeding trials assessing growth when an herbivore is fed different plant species. Robust quantification of NB using performance or growth rates, rather than resource usage as a proxy, should help here. Studies using logical tests and null models to illuminate the direction of causality also provide a path for understanding process from pattern (e.g., Sheth et al. 2014; Fort et al. 2016).

The Scale-Dependence of Factors Shaping Realized Niche Breadth

The effects of dispersal limitation and biotic interactions on the realized niche likely vary across spatial scales. At large geographic scales, dispersal limitation can reduce a species' ability to colonize environments or resources, thus excluding those conditions from its realized niche (Holt 2009). In contrast, the Eltonian noise hypothesis suggests that biotic interactions primarily influence species' distributions and niches at local scales, while abiotic factors are mostly responsible for species occurrences at the landscape scale (Soberón and Nakamura 2009). The Eltonian noise hypothesis has been used to suggest that discrepancies between a species' fundamental and realized NB should be greater at local scales (e.g., habitat boundaries) than at landscape scales (e.g., across broad climatic gradients). However, this hypothesis has received mixed support (Araújo et al. 2014; Fraterrigo et al. 2014). Since dispersal limitation should have the opposite effect—by decoupling fundamental and realized NB at landscape scales—the scale-dependence of factors shaping the realized niche likely hinges on the relative magnitudes of biotic interactions and dispersal limitation in a system.

HOW NICHE BREADTH INFORMS ECOLOGY, EVOLUTION, AND CONSERVATION

Here, we synthesize key ecological, evolutionary, and conservation research that draws upon the NB concept. We highlight how considering hierarchical niche structure, correlations in breadth among niche axes, and factors that differentiate realized and fundamental niches may enhance our understanding of ecological and evolutionary questions and improve conservation outcomes.

ECOLOGY

We highlight the role of NB in community diversity, biogeography, and latitudinal richness gradients. Additionally, we discuss how explicitly incorporating the biological

foundations of NB could shed light on diverse, complex ecological relationships.

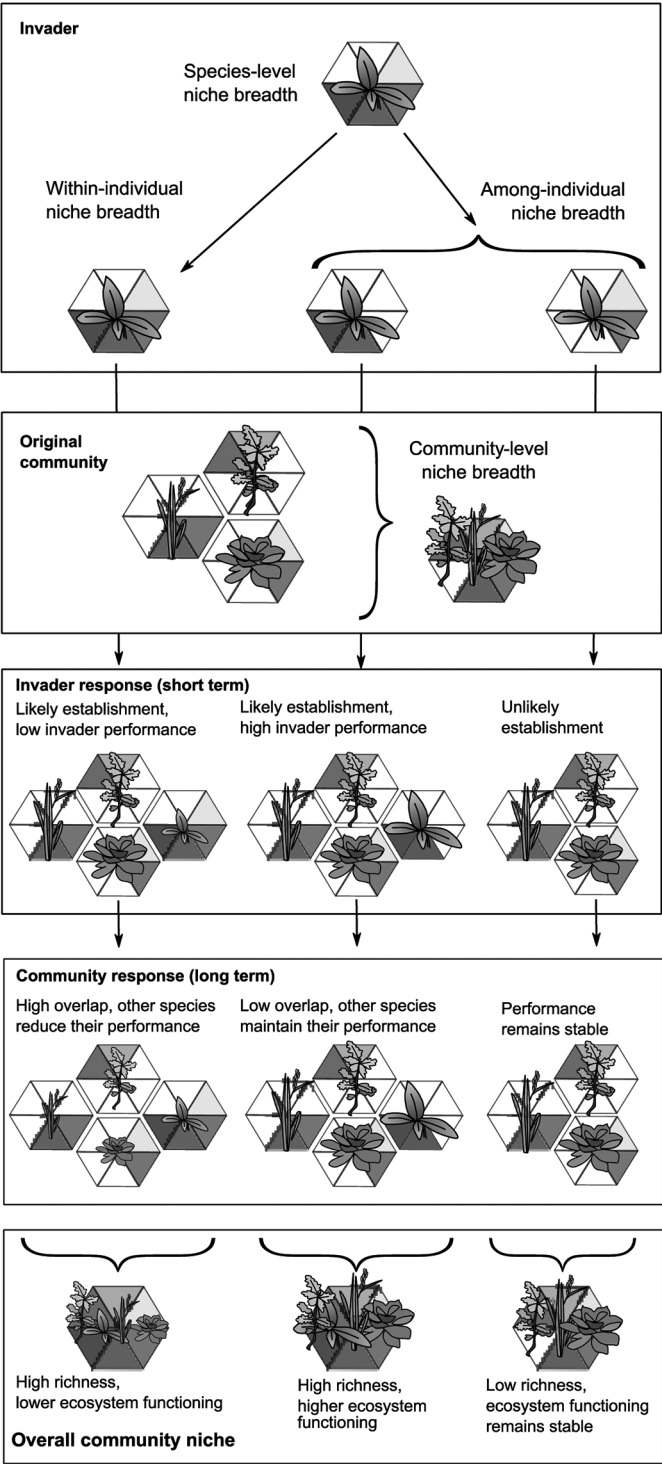
Niche Breadth and Species Richness at the Local Scale

Niche theory provides a mechanistic explanation that helps inform predictions about coexistence when experimental tests are infeasible. There is a long history of interest in how niches influence community diversity (e.g., Pielou 1972; Schoener 1974). However, the impact of NB on local diversity is less studied. If an organism disperses into a community, its niche characteristics determine whether it can tolerate the local environment and biotic interactions (Weiher and Keddy 1995; Violle et al. 2012; Cadotte and Tucker 2017). That is, upon arriving at a site, an individual's niche optimum and niche overlap with resident species impact competitive interactions and the likelihood that the individual successfully establishes there. Often it is implicitly assumed that niche optimum and overlap are captured by phylogenetic or functional trait distances within a community (e.g., Mouquet et al. 2012), and community assembly mechanisms are inferred from phylogenetic or functional trait distributions (i.e., overdispersion or clumping; Webb et al. 2002; Cadotte et al. 2011). NB is a component of niche overlap, but its independent contributions to the assembly and maintenance of diverse communities is underexplored.

We outline three possible (but conflicting) relationships between species' resource-use NB and community species richness: wide NB increases niche overlap among species and *decreases* species richness via competitive exclusion; wide NB increases niche overlap and *increases* species richness (via neutral drift and slowing of competitive exclusion); and NB is mechanistically unrelated to species richness. Under the first scenario, the theory of limiting similarity implies that extensive niche overlap among species precludes coexistence (MacArthur and Levins 1967; Chesson 2008), and thus more narrow NB species can coexist in a community ("niche packing"). This idea is supported by a strong negative relationship between species richness and NB (whether based on

habitat, climate, diet, or other species interactions) reported in a recent meta-analysis (Granot and Belmaker 2020). This is consistent with "stabilizing" niche differences, which reduce resource competition, allowing more species to coexist (Chesson 2000). Niche differences have been linked to coexistence in a number of experimental systems (e.g., Gravel et al. 2011b; Narwani et al. 2013; Kraft et al. 2015), but often underpredict coexistence. The second scenario predicts a positive relationship between average NB and community richness. Le Bagousse-Pinguet et al. (2014) found that within-species (as opposed to among-species) trait variation best explained the distribution of species richness in calcareous grassland communities. They reported that within-species variation in plant height likely increased trait overlap among species and reduced the ability of taller species to exclude other species through shading. Species with high intraspecific trait diversity likely span a broader range of environments (Darwin 1859; Sides et al. 2014) so, in the above study, it is thought that trait diversity and overlap translate to broad, overlapping niches between species. Trait similarity between species also minimized competitive differences, so Le Bagousse-Pinguet et al. (2014) concluded that "equalizing" mechanisms reduced fitness differences between species and would enable species to persist together through neutral processes (Chesson 2000). However, equalizing mechanisms alone, without stabilizing niche differences, are insufficient for stable long-term coexistence (Chesson 2008). This suggests that species richness could decrease in the long term, and in turn reduce the positive correlation between NB and species richness. Under the third scenario, NB is not a primary determinant of community richness. Instead, other factors (e.g., propagule pressure or disturbance) largely shape community composition (Lockwood et al. 2005).

Consistent trends have yet to emerge from tests of a direct relationship between NB and coexistence. Instead, insights into community assembly likely lie at the intersection of NB, niche optimum, and performance under specific conditions. This tripartite approach will be especially productive if there



are tradeoffs between NB and individual performance (jack of all trades, master of none; Futuyma and Moreno 1988). Narrow NB species will be more likely to coexist if they utilize resources that are not used by other narrow NB species, or if they outperform wide NB species where they overlap. Alternatively, species with broader NB might, on average, be more likely to tolerate a given local environment (Kraft et al. 2015) and successfully integrate into an assemblage. In addition, if local temporal heterogeneity in environmental conditions precludes narrow NB species from consistently maintaining a local fitness advantage, broad NB species could be competitively superior and stabilize community composition. However, if narrow NB species can avoid unfavorable years (e.g., in dormant seeds) and capitalize in suitable years, they can coexist by partitioning niches through time in variable environments (“storage effect”; e.g., Angert et al. 2009). Clarifying when these different proposed mechanisms of community assembly are likely to apply may aid restoration efforts (*de novo* community assembly) and help predict how incoming species, such as potential invaders or species displaced due to environmental change, might interact with resident communities (Figure 3).

Niche Breadth in Biogeography

Fundamental NB acts in concert with landscape heterogeneity, dispersal, and interacting species to influence realized NB, species distributions, abundance, geographic range size, and occupancy (the fraction of suitable habitat that is occupied; e.g., Holt et al. 2004; see the section titled Disentangling Fundamental and Realized Niches: How Ecological Context Shapes Niche Breadth). That is, fun-

damental NB determines the suite of conditions under which a species could persist and is therefore useful for predicting range shifts in changing environments and the potential range for invasive species. However, realized NB is more closely related to present-day distributions and is often estimated using occurrence data across species distributions (see the section titled Quantifying the Niche).

A positive relationship between abundance and occupancy is one of the most consistent observations in macroecology (Holt et al. 1997; Gaston et al. 2000). Since locally abundant species usually produce more propagules and are less subject to stochastic extinctions than locally rare species, higher abundance should promote a species’ exploitation of its fundamental niche. Abundant species with high fundamental and realized NB should better withstand habitat heterogeneity because population fitness will be less sensitive to spatial environmental variation. In this case, the metapopulation dynamics that drive occupancy will be influenced largely by stochastic colonization and extinction processes rather than deterministic niche-based processes. Similarly, fundamental NB influences occupancy by determining the fraction of physical space in a heterogeneous landscape in which a species might persist (Brown 1984). Hence, NB may help explain variation in the abundance-occupancy relationship among taxa. For example, aquatic invertebrates with broad realized habitat NB were found to occupy more sites, while those with narrow realized habitat NB were more abundant at a given level of occupancy (Verberk et al. 2010). In the same study, the abundance-occupancy relationship fit the data better for species with broad habitat NB. Perhaps there was greater variance in the data for habitat specialists because specialists

FIGURE 3. INVADER SUCCESS AND IMPACT ON COMMUNITY

A potential invading species with broad niche breadth (NB) could have broad or narrow NB individuals. Individuals with broad NB might be more likely to exploit unutilized resources and therefore establish in the community. However, niche overlap with the original community could decrease invader performance initially and come to depress performance of resident species through competition, resulting in lowered ecosystem functioning. Incoming individuals with narrow NB may establish and perform well if their narrow niche matches unutilized resources in the community. If there is low niche overlap of the invader with the resident species, and these species perform complementary roles, we anticipate increased ecosystem functioning. Lastly, incoming individuals with narrow NB may be excluded from a community if they cannot exploit an unutilized resource nor outcompete residents. See the online edition for a color version of this figure.

are more likely to be very abundant within their optimal habitats (Lesica et al. 2006) or have low abundance if the available habitat is outside their ideal conditions. Importantly, aquatic invertebrates with broader NB tended to also be better dispersers (Verberk et al. 2010), revealing part of the difficulty in distinguishing causal relationships among NB, dispersal ability, habitat heterogeneity, abundance, occupancy, and range size. Recent meta-analyses have shown that species' geographic range size increases with NB for a wide range of taxa (Slatyer et al. 2013) at regional and global scales (Kamback et al. 2019). Yet, studies disagree whether low niche position (i.e., use of widely available resources or habitat) or high NB best explain species' geographic distributions (e.g., Gregory and Gaston 2000; Sheth et al. 2014) and occupancy (Heino and Grönroos 2014). Together, these studies suggest that NB (fundamental and realized) interacts with habitat heterogeneity to drive key biogeographical patterns: species' abundance, occupancy, and geographic distributions.

Niche Breadth Across Latitude: Species Richness and Rapoport's Rule

The decline of species richness with latitude is remarkably consistent across taxa and scale of diversity (e.g., alpha, beta) considered (reviewed in Willig et al. 2003). One of many proposed explanations for this latitudinal species richness gradient involves underlying gradients in species' climatic NB. Janzen (1967) hypothesized that reduced seasonal temperature extremes in the tropics would promote the evolution of species with narrow thermal tolerances compared to higher latitude species. This spurred the idea that narrow NB in tropical regions might lead to higher tropical species richness (e.g., Huey 1978; Cadena et al. 2011).

Some explanations for the latitudinal gradient invoke a key role of NB along biotic axes instead (Schemske et al. 2009). Dobzhansky (1950) proposed that stable, moderate tropical climates should render biotic interactions more important than abiotic tolerances in structuring communities and driving specialization and diversification in tropical

regions. Biotic interactions could drive co-evolution, adaptation, and speciation in the tropics (Schemske et al. 2009). Forister et al. (2015) found that the breadth of host plants used by herbivorous insects is narrower in the tropics, with many tropical insect species feeding on a single plant family or even species. Other work on herbivorous insects shows that narrow dietary breadth is associated with increased diversification (Hardy and Otto 2014; see the section titled *Niche Breadth and Macroevolution*). Thus, the narrow NB of tropical species could help explain why tropical regions are so species-rich. However, studies have also documented increased interaction breadths in the tropics (e.g., within mutualistic networks; Schleuning et al. 2012) or no gradient at all (Vázquez and Stevens 2004).

The hypothesis that NB is narrower in the tropics carries several often-untested assumptions. As outlined by Vázquez and Stevens (2004), this hypothesis relies on reduced environmental variability in the tropics, which begets stable populations and thus allows species to become more specialized. However, their cross-taxon analysis revealed that tropical populations are subject to substantial fluctuations in precipitation and population size, even though temperatures are more stable in the tropics (Vázquez and Stevens 2004). Thus, tropical species may have narrower thermal but wider precipitation NB compared to temperate species (Figure 2). This idea is now supported across hundreds of species of plants and animals (Liu et al. 2020). Therefore, the relationship between NB and latitude depends on the niche axis considered. Moreover, whether there is a causal relationship between NB and species richness is unclear (see the section titled *Niche Breadth and Species Richness at the Local Scale*). In the context of interaction breadths, for example, competition could lead to specialization and diversification, or high species richness could increase competition and drive selection for specialization over time (Fischer 1960). Similarly, Vázquez and Stevens (2004) proposed that narrower NB in the tropics is a product, rather than a driver, of the latitudinal species richness gradient.

A competing hypothesis proposes that climate actually fluctuates *more* in low-latitude than high-latitude areas, fragmenting species' ranges and increasing rates of allopatric speciation in the tropics (see Rangel et al. 2018; Saupe et al. 2019). Recent modeling studies have suggested that climate heterogeneity through space and time drives diversification (Rangel et al. 2018); specifically, variation in precipitation at low latitudes increases speciation rates, and extinction rates across latitudes increase with precipitation and temperature fluctuations (Saupe et al. 2019). A relatively bare-bones model of speciation and extinction rates and climatic variability (i.e., species had different but fixed NB and dispersal abilities, biotic interactions not included) generated a latitudinal diversity gradient closely resembling our own, including a preponderance of narrow NB species at low latitudes (Saupe et al. 2019). In another model, intermediate levels of niche evolution maximized diversification and helped the model match realistic species richness gradients across a complex landscape (Rangel et al. 2018). Niche conservatism led to high extinction rates, as species failed to adapt to changing climates, and very rapid niche evolution resulted in a few widespread species and little diversification, since climate variation was tolerable and insufficient to isolate populations (Rangel et al. 2018).

Rapoport's rule posits that species' latitudinal range size increases with latitude (Stevens 1989). This rule may provide a more proximate explanation for the latitudinal richness gradient, since species' distributions across latitudinal climatic gradients can be explained by NB variation. Rapoport's rule has received mixed empirical support. Many taxa, particularly those in the tropics and Southern Hemisphere, do not follow Rapoport's rule (Gaston et al. 1998; Willig et al. 2003). Although Rapoport's rule is typically used to explain the latitudinal richness gradient, Beaupre et al. (2013) instead suggested the reverse: that richness may help explain why certain taxa do not follow Rapoport's rule. They modeled plankton thermal tolerances and geographic distributions and found that species richness of broadly thermotolerant species increased with latitude. But, since

richness of narrow NB species peaked both at the poles and tropics, certain clades showed no discernible NB-latitude gradient.

Latitudinal variation in NB is central to several hypotheses for the latitudinal richness gradient, but single variables are unlikely to adequately predict the distribution of species richness. Synthetic hypotheses (e.g., simultaneously considering NB in temperature and precipitation and other factors that covary with latitude) should provide important insights (Willig et al. 2003).

EVOLUTION

Here, we discuss how NB evolves (see the section titled Niche Breadth and Microevolution) and influences macroevolutionary patterns (see the section titled Niche Breadth and Macroevolution). Previous reviews have clarified how performance tradeoffs, environmental heterogeneity, and/or biotic interactions affect NB evolution (e.g., Sexton et al. 2017). In addition, many studies have investigated how NB influences evolutionary processes, ranging from adaptation to speciation (e.g., Schluter 2000; Coyne and Orr 2004). Much of this literature has emphasized how competition due to niche overlap influences niche and lineage divergence (e.g., M'Closkey 1978; Schluter 1994). We build on these discussions to consider relationships between hierarchical NB structure and niche divergence, and how both positive and competitive interactions can influence lineage divergence by changing NB. We highlight the specific hypothesis that specialists evolve from generalists. Throughout, we illustrate how studying the mechanisms shaping NB has the potential to reveal generalities about the relationships between NB and fundamental evolutionary processes.

Niche Breadth and Microevolution

NB hierarchical structure arises when processes shaping niche overlap among individuals or populations influence NB at higher biological scales. Intraspecific competition can generate disruptive selection, favor divergently specialized individuals, and ultimately increase phenotypic variation at the

population or species level (Bolnick 2001). Similarly, competition among species within a community can lead to character displacement and niche differentiation (e.g., Zuppin-Dingley et al. 2014). For example, niche differentiation in resource (seed size) and habitat use in desert rodent species increased with rodent community diversity, suggesting that competition drives resource partitioning (M'Closkey 1978). Studies with sticklebacks confirmed that competition can drive niche divergence (Schluter 1994). At larger spatial scales, contrasting selection pressures across a heterogeneous landscape can cause populations to diverge, increasing species-level NB (e.g., Linhart and Grant 1996).

Like competition, positive biotic interactions can promote niche differentiation among populations. However, these interactions have received relatively little attention in this context. Positive biotic interactions that increase organismal performance in new or marginal environments (broadening species' realized NB or allowing new niche optima to emerge) could provide the initial ecological opportunity for niche differentiation (e.g., Liancourt et al. 2012; Weber and Agrawal 2014). For example, in the mutualistic interaction between lycaenid butterflies and ant species, ants protect caterpillars from predation in return for nectar rewards secreted by the caterpillars (Forister et al. 2010). Attendant ants were found to increase larval caterpillar survival on a novel host plant. Therefore, they could lead to evolution of increased dietary breadth in lycaenid butterflies (Forister et al. 2010). In another system, fungi provide both food and defense for midge larvae developing in plant galls, and this symbiosis with fungi likely spurred expansion of host-plant resource use for gall-inducing insects (Joy 2013). Symbiotic insect lineages used a breadth of host plant taxa seven times greater than asymbiotic lineages (Joy 2013). In some cases, this increased NB through positive biotic interactions can allow subsequent niche divergence, reproductive isolation, and ecological speciation in diverging lineages, as discussed below (Hawthorne and Via 2001; Nosil 2012).

As competitive inequalities or positive biotic interactions spur populations to explore

new niche space, the balance of coexistence mechanisms (stabilizing niche differences and fitness-equalizing factors; Chesson 2000) should shape successive NB evolution. Fitness-equalizing mechanisms might relax both stabilizing selection and selection against less fit genotypes, thus maintaining NB. In contrast, stabilizing mechanisms could reduce opportunities for further niche expansion for species that are tightly packed along a niche axis. In this case, species at the ends of the niche axis (i.e., that use less contested or more marginal resources) could increase their NB if more extreme environments are available. These ideas would benefit from experimental tests.

Niche Breadth and Macroevolution

Studies of NB and macroevolution have included analyses of how NB impacts diversification (speciation - extinction), and macroevolutionary transitions between specialists and generalists. In vertebrates, studies have found negative relationships between temperature NB and diversification (Rolland and Salamin 2016) and positive relationships (after including precipitation and niche position; Gómez-Rodríguez et al. 2015). In herbivorous insects, two contrasting mechanisms by which NB can influence diversification have been proposed. The oscillation hypothesis (Janz and Nylin 2008) suggests that lineages fluctuate between specialization and generalization over evolutionary time (analogous to Figure 1.a.ii). If breadth comes at the cost of lower performance in any single environment, generalists are expected to give rise to specialists as lineages adapt to that environment and diverge. Over time, specialist lineages evolve into generalists as they disperse across a landscape and broaden their host plant usage. Alternatively, the musical chairs hypothesis (Hardy and Otto 2014) suggests that host switching helps drive insect diversification. Host switching entails changes in niche optimum and/or position that broaden a clade's NB without necessarily changing mean species-level NB (analogous to Figure 1.a.i). Consistent with this idea, diversification of phytophagous butterflies increased with host switching rates,

not changes in species' NB (Hardy and Otto 2014).

Much of the literature linking NB and macroevolution has focused on the hypothesis that specialists originate from generalist ancestors, have limited potential for further evolutionary change, and are "evolutionary dead ends" destined for extinction (Cope's Law of the Unspecialized; Cope 1896; Futuyma and Moreno 1988). This idea has received only mixed empirical support (Mayr 1963; Van Valen 1973). There are examples of specialists giving rise to generalists (e.g., Armbruster and Baldwin 1998; Nosil 2002), but other studies suggest that the transition from generalist to specialist is indeed more common (e.g., Kelley and Farrell 1998; Stephens and Wiens 2003). Tip-ratio bias (when two trait states—such as specialization and generalization—are unevenly represented among taxa on a phylogenetic tree), the number of taxa sampled, and how completely a phylogeny is sampled could all impact inferred transitions between generalization and specialization (Day et al. 2016).

There are many potential avenues for future work to explore the contexts in which NB promotes or precludes diversification. As one example, positive interactions can increase species-level NB, which may either maintain gene flow and hinder speciation across an environmental gradient or, alternatively, create opportunities for divergent selection and speciation (e.g., Liancourt et al. 2012). Association with ants increased lycaenid butterfly dietary NB, which is thought to have promoted butterfly diversification (Forister et al. 2010). Similarly, the enhanced species-level NB of symbiotic lineages of gall-inducing insects likely raised diversification rates: symbiotic lineages were 17 times more diverse (Joy 2013).

CONSERVATION

Under the current biodiversity crisis, more than one million species are at risk of extinction from a variety of threats (Scholes et al. 2018). NB is potentially relevant to understanding the spread of invasive species, the response of species to climate change, the vulnerability of species to extinction, and

the impacts of altered communities on ecosystem functioning.

Changing Species Distributions

One current focus in conservation biology is understanding changes in species' geographic ranges—for example, expansion of invasive species and movement of range edges as species track climatic conditions. Climatic NB may be particularly relevant for understanding current and future changes in species' ranges. Species distribution models (e.g., Guisan and Zimmermann 2000; Peterson et al. 2011) built from climatic data are often used to predict the spread of invasive species (e.g., Peterson 2003) and the future distribution and persistence of species under climate scenarios (e.g., Thomas et al. 2004). This approach uses species' current climatic distributions to predict their future spread and occurrence, but there is debate about how effective this approach is for these purposes (e.g., Pearman et al. 2008; Araújo et al. 2011; Petitpierre et al. 2012; Early and Sax 2014; Atwater et al. 2018). Most importantly, this approach assumes that climatic niches will remain broadly similar over time (e.g., Peterson 2003). However, examples of both niche conservatism and rapid niche evolution exist in the literature (e.g., Wiens and Graham 2005; Pearman et al. 2008). In addition, this approach may not accurately predict changes in a species' distribution when its fundamental climatic NB is much greater than its realized climatic NB. If species overcome dispersal limitation or biotic factors change, species can rapidly shift or expand their realized climatic niches (e.g., Wiens et al. 2019). These rapid changes in realized niches can allow species to invade regions with very different climates and potentially persist under rapid climate change (e.g., Petitpierre et al. 2012; Atwater et al. 2018; Wiens et al. 2019). Climate change and species introductions are also expected to expose species to "nonanalog conditions," including unique combinations of climatic variables and biotic factors not currently present in their native ranges (e.g., Jackson and Overpeck 2000; Reu et al. 2014). This possibility underscores the value of understanding which factors

actually set species range limits (and potential correlations among these factors). Below we further discuss how NB can shape species distributions, in the contexts of biological invasions and climate change.

Biological Invasions

The ability to predict which species will likely invade, and where, is a major challenge in conservation and ecosystem management, and is the primary goal of invasion ecology. Three popular hypotheses for invasiveness have employed NB. The first hypothesis is that species with broader fundamental niches are more likely to become invasive (the NB-invasion success hypothesis; Baker 1965). Nonnative species with broader niches can more readily take advantage of unexploited resources in a novel environment, compared to more specialized species. For example, in the eastern U.S., nonnative understory species in deciduous forests tend to maintain their leaves longer than resident native species, which allows them to capture light and fix carbon long after native species have dropped their leaves each autumn (i.e., they have a broader phenological niche; Fridley 2012). The ability of many nonnatives to exploit this open phenological window was likely instrumental in their invasion success (Fridley 2012). Similarly, Olsson et al. (2009) found that a nonnative crayfish species had greater dietary NB than a native crayfish competitor, which allowed the nonnative species to occur where the native crayfish could not. However, in several studies, the NB-invasion success hypothesis has either not been supported (Vázquez 2006; Dyer et al. 2016) or has been contradicted. For example, despite having narrower trophic NB, nonnative rainbow trout are outcompeting redbfin, a native competitor in South Africa (Shelton et al. 2017). The nonnative trout depends on different prey resources than the native redbfin, so the trout's success may be explained by differences in niche optima (see below) rather than NB.

An alternative hypothesis that invokes NB to explain species' invasions proposes that exotic species have a broader realized NB in their nonnative range due to release from

coevolved competitors and predators, thus contributing to their spread in the nonnative range. That is, as a species is introduced into a new area, it leaves behind its natural competitors that compressed its realized niche. This is one of several possible mechanisms related to the enemy release hypothesis (Keane and Crawley 2002; Colautti et al. 2004). In a review by Jeschke et al. (2012), the enemy release hypothesis was supported in about one-half of studies examining it (57 in support, of 106 empirical tests). Consistent with the hypothesis, Godfree et al. (2007) modeled performance of infected and virus-free clover in two habitats and projected that release from pathogens would increase clover population growth and realized NB by enabling persistence in suboptimal habitats. Conversely, other work comparing NBs of species in native and nonnative ranges has found either conservatism of realized NB (Petitpierre et al. 2012; but see Early and Sax 2014) or realized NB reduction in nonnative ranges (Strubbe et al. 2013). Overall, the current evidence to support the NB mechanism of enemy release is decidedly mixed. Large differences between fundamental and realized niches in native ranges could indicate strong potential for enemy release in invaded ranges. However, we rarely have information on both fundamental and realized NB that could be contrasted to predict future invasions. Further, it could be that enemy release does not in fact increase range size but rather manifests as larger average abundance within occupied sites (Colautti et al. 2014).

A final NB-driven hypothesis of species invasions predicts that species-rich communities with high functional diversity are less likely to be invaded, because trait diversity allows the community to exploit a broader range of resources (greater community-level NB), leaving few resources available for a potential invader (Figure 3; the diversity-invasibility or biotic resistance hypotheses; Elton 1958; Levine and D'Antonio 1999). For example, within sessile marine invertebrates, which compete primarily for space, more species-rich communities occupied more area and thus experienced reduced invasion (Stachowicz et al. 1999). Further, a meta-analysis of experimental work found that community

richness and local competitors significantly depressed invader performance and establishment (Levine et al. 2004). However, these effects were apparently not strong enough to prevent invasion. More generally, the biotic resistance hypothesis has garnered only modest empirical support across taxa (37 of 129 tests; Jeschke et al. 2012). Biotic resistance could be weakened, for example, by local resource pulses that reduce competition within communities (Mallon et al. 2015).

Each of the NB-based hypotheses of invasion might explain some, but not all, invasion events. This suggests that multiple mechanisms, potentially involving multiple niche axes, are at play. For instance, invasive cane toads may be able to dramatically increase their geographic spread in Australia through a combination of enemy release, realized niche expansion as populations colonize new environments, and fundamental niche expansion as they evolve to tolerate extreme climates (Urban et al. 2007). In many cases, studies considering multiple niche axes have clarified the mechanisms driving invasion (e.g., Higgins and Richardson 2014; Wolkovich and Cleland 2014). That is, niche differences between invasive species and native communities may only be detected by considering how species sort across multiple niche axes (e.g., length of breeding season, dietary composition, habitat characteristics; Batalha et al. 2013).

NB-invasion relationships vary across biological, spatial, and temporal scales. Exploring scale dependence may therefore help explain why studies differ in the degree of support they find for any NB-invasion relationship and might clarify the path of invasion. In the aforementioned study by Olsson et al. (2009), the invasive crayfish had broader species-level, but not population-level, NB than the native crayfish species. Thus, the wide NB of this invasive species that allowed it to exploit unoccupied streams is accrued across relatively specialized, differentiated populations. This hierarchical NB structure is also related to the spatial and temporal progression of invasion (Figures 1 and 3). If individual populations are highly specialized, successful invasions should require multiple introductions to different geographic

locations, and/or introgression with other populations or closely related taxa (e.g., Kolbe et al. 2004). Spatial scale likely influences the strength of the biodiversity-invasibility relationship. Although at local scales diversity can hinder invasion, the covariance among factors such as propagule pressure and species diversity at broader spatial scales can overwhelm biotic resistance and explain why some diverse communities are highly invaded (Levine 2000). Although regional realized NBs of plant species in the Alps are strongly positively related to their regional range sizes, regional realized NB does not predict global distributions (Kambach et al. 2019). In an invasion context, this general result suggests that realized NB estimates from species' native ranges would be poor predictors of potential invasive spread (Kambach et al. 2019). Lastly, residence time of nonnative species may be an important covariate when interpreting their release from enemies or their niche expansion or breadth. At large temporal or spatial scales, nonnative plant species suffer from increased insect damage as enemies arrive, evolve, or are encountered during range expansion (Schultheis et al. 2015). More generally, since residence time is a good predictor of invasion success in some systems (Dyer et al. 2016), considering temporal variation in NB may clarify any role of NB in invasion potential. There are often significant time lags between the establishment and spread of many nonnative species (Early et al. 2016), and local adaptation and rapid evolution following establishment can drive subsequent niche expansion (Oduor et al. 2016). In other cases, there can be dramatic niche shifts that occur concomitantly with invasion (Wiens et al. 2019).

Response to Climate Change

Current work indicates that NB, its underlying hierarchy, and correlations in breadth among niche axes all influence species' responses to climate change. Most studies using NB to infer sensitivity to climate change focus on thermal or other abiotic axes (e.g., precipitation, growing degree days). Empirical evidence suggests that species with narrow climatic NBs might be more sensitive to

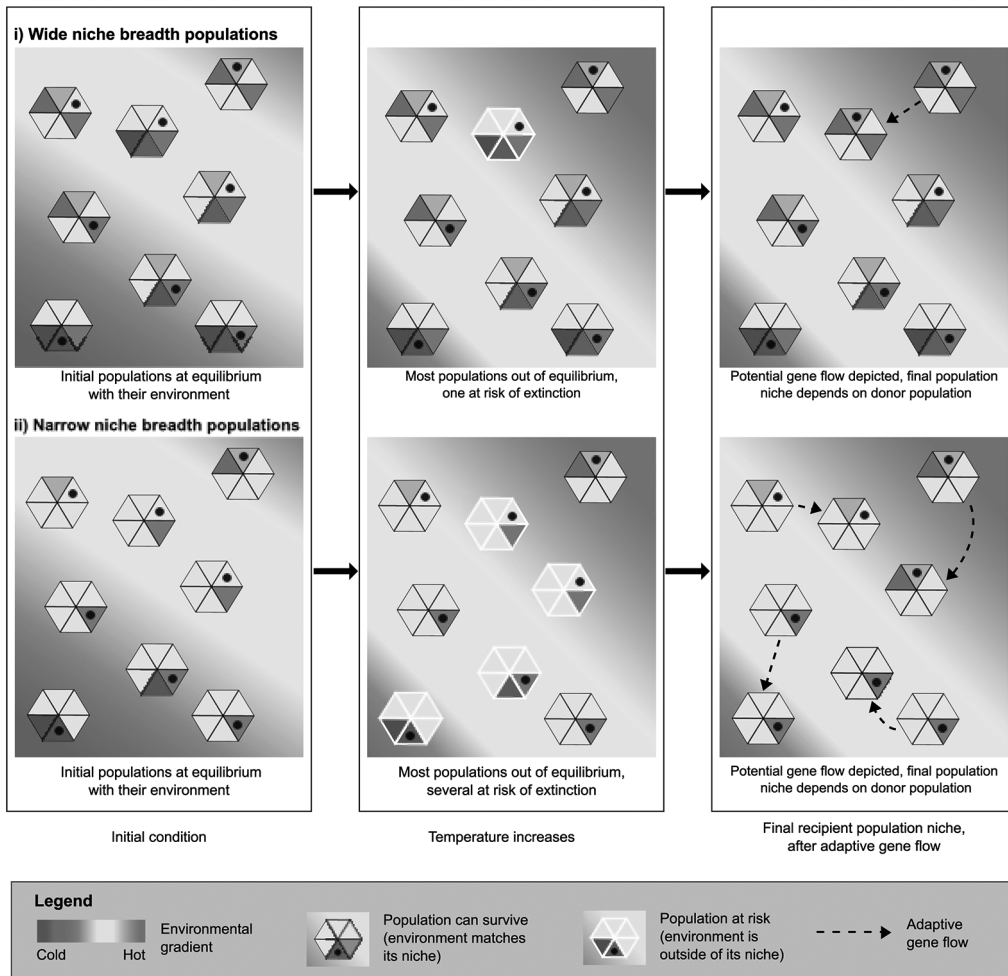


FIGURE 4. HIERARCHICAL NICHE BREADTH (NB) STRUCTURE CAN IMPACT SPECIES' RESPONSES TO CLIMATE CHANGE

A species with two different NB hierarchies is depicted across a landscape temperature gradient. Initially, the species' distribution matches its optimal environment. As temperatures increase, we predict different outcomes based on NB hierarchy. When species-level NB is composed of wide NB populations (i), this breadth allows most populations to persist, whereas several narrow NB populations (ii) are at risk of extinction because they cannot tolerate the new conditions. Adaptive gene flow (dashed lines) could help provide the necessary alleles and genetic variation to allow threatened populations to adapt. See the online edition for a color version of this figure.

climate change (e.g., Thuiller et al. 2005) if climate shifts outside of their small range of tolerances and they cannot track preferred conditions over space (e.g., Loarie et al. 2009). In contrast, species with wide climatic NB are expected to be relatively robust to climate change (e.g., Schwartz et al. 2006).

The idea that species with wide NB will better withstand climate change (versus nar-

row NB species) is implicitly rooted in the idea that individuals and populations of those species are themselves broadly tolerant. However, the mechanisms and consequences of a NB advantage under climate change likely depend on the underlying hierarchy of NB (Figure 4). Given the same climatic NB, a species composed of broad NB individuals and/or genetically diverse populations is

expected to have a higher probability of persisting in situ than one composed of highly specialized, differentiated populations, especially under dispersal limitation (Etterson and Shaw 2001). From an evolutionary perspective, if species-level NB results from high genetic variation among individuals, wide NB species could instead appear relatively insensitive to climate change not because they possess broader tolerances, but rather because they have the propensity to evolve to local conditions (Thomas et al. 2012). However, climatic NB is generally uncorrelated with rates of climatic niche evolution (Liu et al. 2020). Furthermore, niche change might not keep pace with projected rates of climatic change (e.g., Román-Palacios and Wiens 2020), especially given widespread local extinctions already observed (Wiens 2016).

Climate change could have contrasting effects on narrow NB species, depending on their niche position, dispersal ability, and how climate change impacts their communities. If the conditions or resources a species requires become more available with climate change, the species could become more abundant or widespread. For example, migratory songbirds inhabiting mixed deciduous forests are predicted to show range expansion as this habitat spreads in southern Ontario (Naujokaitis-Lewis et al. 2013). Climate change could also offer respite to narrow NB species by altering communities and species' interactions. For instance, changing interaction networks could lead to a novel mutualistic interaction that ameliorates abiotic stress (Hoffmann and Sgrò 2011). Conversely, climate change could adversely affect narrow NB species. For many species, dispersal limitation could prevent them from escaping unfavorable conditions by colonizing new habitat patches or tracking preferred conditions (e.g., Thomas et al. 2004). A recent study of over 500 plant and animal species found that most are unlikely to disperse quickly enough to stay in their past thermal niches, based on their recent dispersal rates (Román-Palacios and Wiens 2020). Additionally, species declines from climate change often stem from changes in species interactions (Cahill et al. 2013; Ockendon et al. 2014). Climate change could precipitate species declines through

novel competitive environments, intensified pathogen infections, and weakened mutualistic associations (Tylianakis et al. 2008; Alexander et al. 2015), which may disproportionately impact narrow NB species.

Even if species have narrow climatic NB, broad tolerances along nonclimate niche axes could buffer the effects of climate change (Figure 2). If climate change triggers range shifts, species that can use a wider range of resources (e.g., broad dietary NB) may be less impacted because they can meet their requirements in new habitats (Gravel et al. 2011c). Simulated diet expansion substantially reduced predicted extinction rates of alpine butterflies under climate change, even when just a few closely related host plant species were added (Descombes et al. 2015). Thus, predictions of species' responses to climate change might differ between studies that consider nonclimatic niche axes versus those that focus on climate alone.

Niche Breadth and Conservation Planning

NB, abundance, and geographic range size interact to generate different forms of rarity (Figure 5), which influence how robust a species is to different types of environmental change (Rabinowitz 1981). Although these ecological characteristics are often positively correlated (see the section titled Niche Breadth in Biogeography), species can have, for example, narrow NB but high abundance (e.g., *Juniperus cedrus*) or broad NB but restricted geographic ranges (e.g., *Acacia sciophanes*; Figure 5; Rabinowitz 1981; Espeland and Emam 2011). Depending on their form of rarity, species could be more vulnerable to certain threats (Figure 5). Species that have low abundance but wide NB, for instance, if they occupy multiple habitat types but are not particularly competitive, should be more susceptible to diffuse perturbations such as nonpoint source pollution or regional climate change. In contrast, species that are both scarce and have a narrow range of habitat affinities will be more vulnerable to acute perturbations such as point-source pollution, a species' invasion, or local land-use change (Sattler et al. 2007). Thus, the first type of

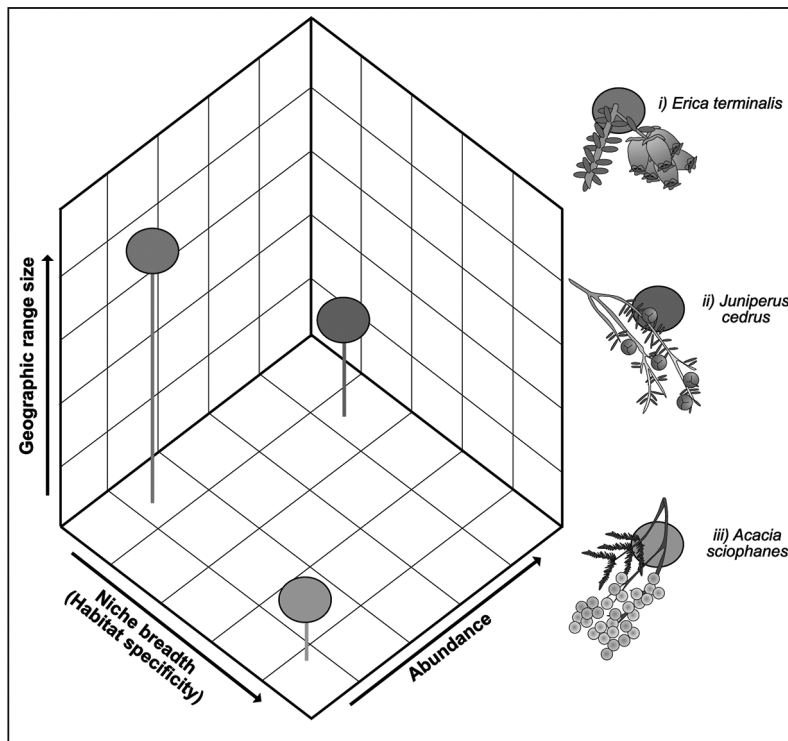


FIGURE 5. NICHE BREADTH (NB) AND FORMS OF RARITY

Circles are species, and lines place species in three-dimensional space. Using these three graph axes, seven forms of rarity can be distinguished (Rabinowitz 1981). We focus on three: species with (i) narrow NB and low local abundance but large geographic range size; (ii) narrow NB and small geographic range but high abundance; and (iii) wide NB but small geographic range and abundance (Espeland and Emam 2011). *Erica terminalis* is restricted to humid grasslands and is vulnerable to wetland desiccation (Blanca et al. 1998). *Juniperus cedrus*, limited to fragmented patches across its small range, is threatened by grazing (Rumeu Ruiz et al. 2011). Despite occurring across woodland and scrub heath communities, *Acacia sciophanes* occupies less than 10 km² and is threatened by inbreeding depression and vegetation clearing (Coates et al. 2006). See the online edition for a color version of this figure.

species will be best protected by regional management plans dealing with land-use change and connectivity among habitats, for example, while the second type of species will be better served by local restoration efforts such as removal of invasive species or remediation of degraded habitat.

A fundamental goal of conservation biology is to determine which characteristics make species vulnerable to extinction. Narrow NB has been linked to extinction risk in more than 80% of studies included in a cross-taxon literature review (Colles et al. 2009). Estimates of fundamental climatic NB of 55 species of island-endemic conifers revealed that 3.6–

23.6% of these species (depending on the climate change model) are expected to be in environments that fall outside of their fundamental niches within the next 50 years, with narrow NB species the most affected (Rosenblad et al. 2019). By teasing apart areas within species' realized, fundamental, and tolerance (i.e., survival but no reproduction) niches, Rosenblad et al. (2019) made targeted conservation recommendations: prioritize conservation of areas within realized niches, protect microrefugia within fundamental niches, and enhance recruitment for species that will only have conditions within their tolerance niche remaining.

NB is seldom considered in most widely used vulnerability criteria, such as the IUCN Red List (<http://www.iucnredlist.org>). Rather, these criteria generally focus on geographic range size, population trends, and population viability (Yu and Dobson 2000). Viability assessments sometimes factor in habitat requirements where these data exist. The IUCN Red List is a globally recognized index of species' vulnerability, grounded in ecological data that is applicable across taxa and informative for conservation planning (Rodrigues et al. 2006). Indeed, variables such as geographic range size may be reasonable surrogates for NB data in many cases, since NB is positively correlated with range size across a broad range of taxa (Slatyer et al. 2013; Kambach et al. 2019). However, in insectivorous bats, for example, narrow dietary NB was associated with extinction risk and was independent of geographic range size (Boyles and Storm 2007). Furthermore, by comparing traits of butterfly species listed as threatened and nonthreatened by the IUCN, Kotiaho et al. (2005) found that threatened taxa often had narrow larval dietary NB, narrow adult habitat NB, poor dispersal ability, and high niche position (i.e., the larvae specialize on geographically restricted plant species). By considering different forms of rarity and identifying the traits underlying vulnerability, beyond the ecological data used to construct the IUCN listing, the authors predicted that several species listed as nonthreatened would likely be at risk of extinction. More generally, if species ranges have been recently reduced by human activities, range size may be an underestimate of NB, so species may be more resilient than they appear based on their current distributions (Faurby and Araújo 2018). Since rarity is multifaceted, and species that exhibit multiple forms of rarity are most vulnerable (Davies et al. 2004), conservation assessments that include NB and other dimensions of rarity when available will provide a more comprehensive view of vulnerability while also pointing to possible solutions.

Conservation practitioners that wish to include explicit NB data in vulnerability assessments would first need to determine which (and how many) niche axes to consider. To this end, it would be valuable to know if

and when breadth is correlated among niche axes and the functional or environmental constraints underlying that correlation (see the section titled Correlations in Breadth among Niche Axes). If NB is largely independent across niche axes, then species that are vulnerable to one threat, like higher temperatures, might nevertheless be robust to others, such as drought. Instead, if positive correlations in NB are common, a species' vulnerability to habitat modification or climate change could be predicted by its NB along a single representative axis. In this case, species that have narrow breadth along one axis will likely have narrow breadth along others, increasing their extinction risk. An important additional step is to assess whether the environmental axes likely to be most affected (e.g., by invasive species or land-use change) are also the axes along which NB is most restricted.

Some ways of estimating NB for conservation assessments rely on data that are already collected for vulnerability assessments or existing information. The variables most often considered in vulnerability assessments, such as geographic range size and population trends, are derived from occurrence data or repeat counts over time. These same occurrence data could be used to estimate realized NB of potentially at-risk species. Existing information from experts could also be included. Floras and online databases often list habitat affinities. If, for example, a species is threatened by disappearing wetland habitat, knowledge of its fundamental NB could explain whether the species is intrinsically specialized on that habitat type or if conservation efforts that included assisted dispersal could allow it to establish in other habitats. However, estimating fundamental NB requires experimentation or parameterization of mechanistic models, which is not likely to suit all conservation contexts.

Niche Breadth and Biodiversity-Ecosystem Functioning Relationships

Ecosystem function is the measurable stocks, flows, and stability of energy and nutrients moving through an assemblage (e.g., primary production, nutrient cycling, support or control of other trophic levels; see, for

example, Duffy et al. 2007). NB is thought to have important implications for how changes in biodiversity influence the magnitude and stability of ecosystem functioning (Figure 3; Duffy et al. 2007). The positive impact of biodiversity on ecosystem functioning occurs via complementarity among functionally diverse forms or via a numerical sampling effect by which diverse communities are more likely to contain single highly productive species (Loreau and Hector 2001). We couch our discussion of NB within these proposed mechanisms for the biodiversity-ecosystem functioning relationship.

Complementarity among species, and therefore ecosystem functioning, should be greatest in an assemblage of species that each specialize on different resources (Figure 3; Poistot et al. 2013; Turnbull et al. 2013). Theoretically, species with narrower NB along a resource axis will overlap less along that axis (on average) than those with broader niches and contribute in more distinct ways to system functioning. Consequently, a large proportion of narrow NB species within communities could lead to strong species richness-ecosystem functioning relationships (e.g., Gravel et al. 2011a). Even if species have broad NB along a resource axis, if they are composed of genotypes specialized on different parts of that axis (Cook-Patton et al. 2011), this could generate a similar level of functional diversity as a community of specialists and thus increase ecosystem functioning.

If biodiversity primarily increases ecosystem functioning through sampling of a high-performing species, rather than complementarity among species, the impact of NB on the biodiversity-ecosystem functioning relationship should depend on the availability and heterogeneity of resources. If resource availability is fairly homogenous, a narrow NB species with low niche position (in the biogeographic sense; see the section titled *Quantifying the Niche*) should perform best, assuming a NB performance tradeoff. However, on average, broad NB species should contribute relatively more to ecosystem functioning because many narrow NB species could have high niche position (i.e., specialize on marginal resources) and be ill-suited to the existing conditions, and the “best-performing”

narrow NB species might not be present in each community (Huston 1997). In species-poor assemblages with high resource heterogeneity, broad NB species should best increase ecosystem functioning (e.g., Gravel et al. 2011a). As community species richness increases, this benefit of broad NB species would dissipate if narrow NB species are added that best exploit the available resources.

NB can have contradictory influences on the stability of ecosystem functioning in temporally heterogeneous systems. Ultimately, the effect of NB on ecosystem stability will depend on how NB influences niche overlap and competition, as well as how well community NB encapsulates temporal environmental variation. Highly overlapping niches among species within a community should reduce the stability of ecosystem functioning because strong competition among species with overlapping niches has been shown to be destabilizing (Loreau and de Mazancourt 2013). Although it is traditionally thought that competition stabilizes system functioning by creating asynchronous population dynamics, Loreau and de Mazancourt (2013) show that compensatory dynamics among asynchronous populations can be offset by increased population variability that can also be produced by competition. Given this, the NB mechanisms that promote coexistence, especially if they allow greater niche partitioning, should also result in greater stability. These ideas apply for biotic or abiotic niche axes: even if species stably coexist via niche partitioning under a set of conditions, changes to prey availability or climate, for example, can impact species' fitness and ability to coexist (Cadotte and Tucker 2017), thus altering the stability of ecosystem functioning. Further, the interaction between species- and community-level NB could dictate how assemblages respond to environmental change. As local conditions fluctuate, performance of narrow NB species may be more variable as conditions deviate from their optima. Therefore, scaling up, ecosystem functioning should fluctuate more for assemblages with more narrow NB species, if species that can quickly compensate are not available in the system (Thébault and Loreau 2005). Community-level NB should predict the ability of compensatory

dynamics to maintain stability of ecosystem functioning in changing environments.

Mapping traits to NB can help generate testable predictions about the mechanistic relationship between NB and ecosystem functioning. For example, on a given focal niche axis, the idea that variable performance of narrow NB species would translate into variable ecosystem functioning in changing environments (discussed above) seems most applicable when the traits that respond to the environment and that shape NB (“response” traits) also drive ecosystem functioning (“effect” traits; Lavorel and Garnier 2002). However, the overlap between these response and effect traits remains an area of active research (Funk et al. 2017; Refsland and Fraterrigo 2017). Ecosystem functioning depends on the relative abundances of effect traits, so we envision two general pathways by which traits, NB, and ecosystem functioning interact. First, response traits directly influence fundamental NB. NB in turn shapes the species’ survival and abundance in an area and, therefore, relative abundances of the effect traits that drive ecosystem functioning. Second, response traits could influence ecosystem functioning based solely on their impact on species’ abundances. In this scenario, realized NB arises from abundance and is not a driver of ecosystem functioning; rather, the correlation between realized NB and ecosystem functioning is due to their common cause (see the section titled Species’ Abundance and Dispersal Limitation). Linking traits to NB could also identify which niche axes are likely to be correlated with one another due to reliance on shared traits (e.g., Figure 2c where trichome hairs influence tolerance to both drought and herbivore pressure). Moreover, if we determine how traits influence NB in a given system (e.g., Lennon et al. 2012), we can gain ecological insight into other systems with similar traits (McGill et al. 2006). For example, we could predict that trichomes may generally make plants more drought tolerant and increase NB (Figure 2c), if trichomes do not also reduce plants’ ability to withstand nondrought conditions. Hence, identifying traits that underpin NB across specific environmental gradients may suggest pathways by which environmental

changes are likely to modify ecosystem functions, including those functions that affect human well-being (i.e., ecosystem services).

Despite the conceptual outline above, the role of NB in modulating biodiversity-ecosystem functioning relationships has seldom been directly empirically tested (but see Gravel et al. 2011a). Thus, additional experimental tests are needed. Such empirical studies could productively be extended to consider multiple ecosystem functions and evaluate how negative correlations in NB across axes affect the stability of these functions.

ALIGNING NICHE BREADTH RESEARCH ACROSS FIELDS

Many research fields are linked by the NB concept. As a result, greater integration among fields may provide important gains toward addressing classic and contemporary questions and problems. For example, understanding the mechanistic underpinnings of NB can improve predictions of how species and populations will respond to climate change (e.g., Angert et al. 2011) while increasing our ability to predict which species might be lost. Moreover, understanding how ecosystem functioning is modulated by NB can help us develop more comprehensive predictions about the effects of changing environmental conditions on community and ecosystem dynamics. In addition, interspecific interactions, such as competition, can drive the niche differentiation among species that impacts ecosystem functioning (Zupping-Dingley et al. 2014). Hence, further meshing studies that explore the origins of niche divergence with assessments of its consequences may help reveal the factors structuring ecosystem functioning and services.

Understanding how NB is partitioned hierarchically from individuals to species (Figure 1), and the consistency among niche axes of this partitioning, will generate insights into the processes that structure biodiversity. Determining when NB is most likely to be similar among individuals of a species versus variable within or among populations is also relevant to many subdisciplines. For example, in ecosystem science, we might predict stronger

relationships between biodiversity and ecosystem function if species' NBs are composed of among-individual variation (i.e., diverse, narrow NB genotypes).

A deeper mechanistic knowledge of the correlations in NB across niche axes may provide insights into ecological and evolutionary dynamics (Figure 2). For instance, quantifying NB of invasive species across multiple niche axes could help resolve when and where invasions occur. More broadly, instead of asking how "specialization" or "generalization" affects a particular phenomenon, hypotheses can address how environmental correlations and functional constraints shape axis-specific NB differences that influence ecological and evolutionary dynamics.

Resolving how biotic interactions influence the distribution of species across environments, and the diversity of resources they use, can clarify the ecological scenarios under which estimates of fundamental and realized NB will converge and diverge. Most studies that have investigated how biotic interactions influence NB focus on individuals, the scale at which interactions occur. However, it is not always clear how results from these studies translate to NB patterns at other biological scales (e.g., populations, species). For example, facultative mutualisms could increase species-level NB if partner-associated individuals occupy different environments compared to partner-free individuals (Afkhami et al. 2014). Therefore, research on how interaction-mediated changes to NB at one biological level transfer to other levels would be particularly valuable. Additional studies that consider a wide range of conditions along each niche axis and/or incorporate multiple

niche axes are needed to resolve the effects of biotic interactions on NB.

We propose that exploring the ecological and evolutionary underpinnings of NB will help researchers generate more robust predictions about the conditions that influence species' interactions, range dynamics, evolutionary trajectories, and the maintenance of biodiversity and ecosystem functioning. Answers to fundamental questions about NB hierarchy, correlations in breadth among niche axes, and how biotic interactions and dispersal impact NB would also provide useful information to managers and policymakers. The natural world is in flux, and how species and ecosystems respond will be determined, in part, by the breadth of resources they use and environments they tolerate.

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