

ON THE STRUCTURE AND SIGNIFICANCE
OF ECOLOGICAL NICHE BREADTH

by

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On the Structure and Significance of Ecological Niche Breadth

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The niche is a core concept in ecology, evolution, and conservation biology that is used to explain the distributions and abundances of organisms through both space and time. A particularly critical component of the niche is the range of conditions that populations or species tolerate (“niche breadth”). My research deals with the structure and ecological consequences of niche breadth. Namely, in Chapter 1, I review how niche breadth is conceptualized and quantified and how niche breadth underlies fundamental patterns and processes across disciplines. I outline how a focus on the genetic and environmental underpinnings of niche breadth could advance niche breadth research as a whole and provide insights into longstanding questions. Chapter 2 takes a demographic approach to niche breadth, estimating population growth rates of hybridizing taxa to characterize within- and among-species responses to variation in climate. The demographic trajectories quantified in this chapter suggest that distributions of the study species have not kept pace with changing climate, because the most climate-sensitive species is currently the most abundant. In Chapter 3, I analyze a long-term dataset on flowering time and reveal how climate shifts the flowering windows of interbreeding species, increasing the possibility of hybrid formation in wet summers. Together,

these chapters clarify how the interplay between genes and environment shapes the performance of populations across different life stages and ultimately how interacting species respond to changing environments.

PREVIEW

DEDICATION

For my family—my unwavering source of support and the inspiration that sparked
my origin as a scientist:

I'm young, walking beside my mom as we leave the library, my stroller positively teeming with books. With a library card, you could take out 99 books in a single visit. And we did. Constantly. I remember my enchantment as we pored over books of every imaginable topic—the maps of Canada, the illustrations of space, the biographies of dinosaurs from an unfathomable earlier time. I remember my equal parts intrigue and repulsion at a particularly memorable picture book of exotic spiders. My family's encouragement of learning and exploring and asking questions is undoubtedly a big part of why I became a scientist. If we zip forward, more than a few years, my parents and I are hiding out under the large, continuously dripping branches of a tree at a meadow's edge. We've just hiked up a rocky slope speckled with grasses and herbs and moss in search of the telltale flash of tiny yellow petals. My field work had started with a glimmer of a far-fetched idea, poked and prodded until it resembled a project. I had no sooner selected my field sites than my parents had booked their flights to come help make my dream a reality. I owe a huge debt of gratitude to my family. They have ceaselessly encouraged me to chase my passion, to figure out where the limit of our knowledge lies, and to push that limit...ever so slightly...forward.

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

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1.1 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.

1.2 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 (Slatyer, Hirst and Sexton, 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, 1993b, 1993c; Dwire *et al.*, 2006; MacNally, 2011; 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.

1.3 Defining the Niche

1.3.1 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 (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, Laland and Feldman, 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, Laland and Feldman, 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.

1.3.2 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).

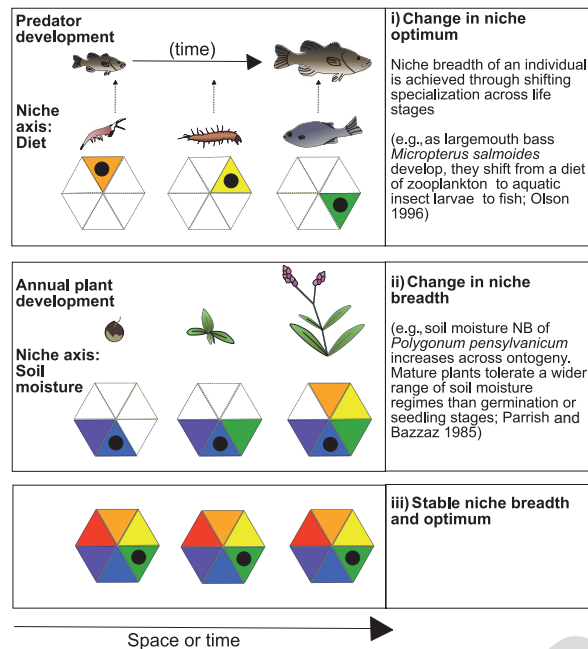
Decomposing population growth rates into performance at specific life stages (measured as vital rates) can clarify whether different response variables are reasonable proxies of population growth rate. Examples of vital rates include rates of germination or birth, survival, growth, and reproduction. 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, Sanford and Grosberg, 2012). However, different life stages can have vastly different niche optima, as in many marine taxa, migratory species, or metamorphosing species such as frogs (Figure 1.1.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 1.1.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 1.1.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, Bell, *et al.*, 2011; Joy, 2013; Sheth, Jiménez and Angert, 2014).

PREVIEW

a) Within-individual phenotypic variation



b) Within- and among-population phenotypic variation

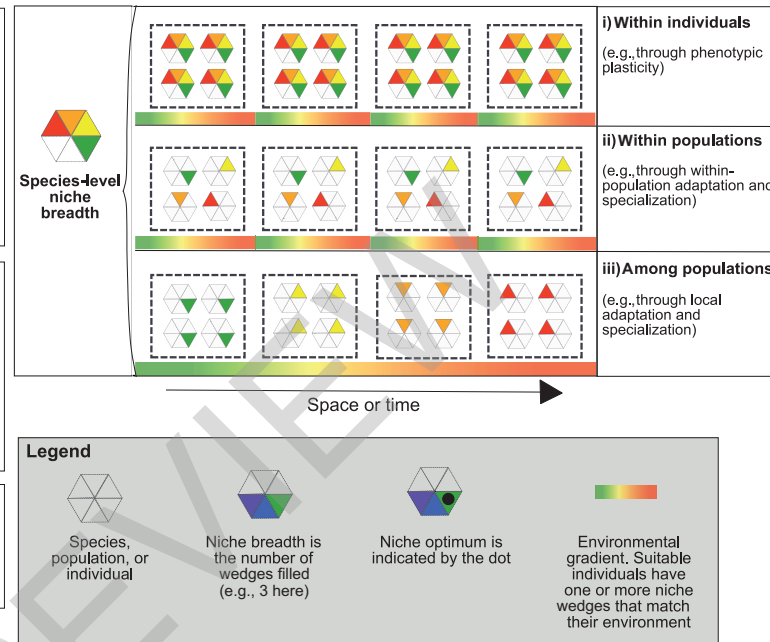


Figure 1.1 The Hierarchical Structure of Niche Breadth (NB)

Using response variables other than population growth rate, species-level NB comprises several biological scales: within individuals (a; b.i), within populations (b.ii), and among populations (b.iii). Within-individual NB may be shaped by changes in niche optimum (a.i) or breadth (a.ii) across ontogeny or environmental gradients in space or time. For example, as bass *Micropterus salmoides* develop, they shift from a diet of zooplankton to aquatic insect larvae to fish (a.i; Olson, 1996). Soil moisture NB of *Polygonum pensylvanicum* increases across ontogeny; mature plants tolerate a wider range of soil moistures than germination or seedling stages (Parish and Bazzaz, 1985). Alternatively, within-individual NB may be consistent (a.iii). Within-population NB results from individuals with different ecologies (Roughgarden, 1972; Araújo, Bolnick and Layman, 2011). Populations specialized on different environmental conditions or resources, or differing in mutualistic associations, can contribute to species-level NB (b.iii).

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; Merow, Latimer, *et al.*, 2014; Pironon *et al.*, 2018). For example, Diez *et al.* (2014) demonstrated that the probability of positive population 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, Samis and Eckert, 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, Carscadden and Mirotchnick, 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, Jiménez and Angert, 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, Chessel and Gimaret-Carpentier, 2000; Gregory and Gaston, 2000; Heino, 2005; Kotiaho *et al.*, 2005; Thuiller, Lavorel and Araújo, 2005; Sheth, Jiménez and Angert, 2014).