ANNUAL REVIEWS

Annual Review of Ecology, Evolution, and Systematics

Evolution of Ecological Niche Breadth

Jason P. Sexton,[1] Jorge Montiel,[1] Jackie E. Shay,[1] Molly R. Stephens,[1] and Rachel A. Slatyer[2]

[1]School of Natural Sciences, University of California, Merced, California 95343; email: jsexton2@ucmerced.edu

[2]Department of Entomology, University of Wisconsin–Madison, Madison, Wisconsin 53706

Annu. Rev. Ecol. Evol. Syst. 2017. 48:183–206

First published online as a Review in Advance on August 7, 2017

The *Annual Review of Ecology, Evolution, and Systematics* is online at ecolsys.annualreviews.org

https://doi.org/10.1146/annurev-ecolsys-110316-023003

Copyright © 2017 by Annual Reviews. All rights reserved

ANNUAL REVIEWS **Further**

Click here to view this article's online features:

- Download figures as PPT slides
- Navigate linked references
- Download citations
- Explore related articles
- Search keywords

Keywords

adaptation, fundamental niche, realized niche, niche evolution, performance breadth trade-offs, specialization, speciation

Abstract

How ecological niche breadth evolves is central to adaptation and speciation and has been a topic of perennial interest. Niche breadth evolution research has occurred within environmental, ecological, evolutionary, and biogeographical contexts, and although some generalities have emerged, critical knowledge gaps exist. Performance breadth trade-offs, although long invoked, may not be common determinants of niche breadth evolution or limits. Niche breadth can expand or contract from specialist or generalist lineages, and so specialization need not be an evolutionary dead end. Whether niche breadth determines diversification and distribution breadth and how niche breadth is partitioned among individuals and populations within a species are important but particularly understudied topics. Molecular genetic and phylogenetic techniques have greatly expanded understanding of niche breadth evolution, but field studies of how niche breadth evolves are essential for providing mechanistic details and allowing the development of comprehensive theory and improved prediction of biological responses under global change.

1. INTRODUCTION

Niche breadth: the variety of resources, habitats, or environments used by a given species

Niche dimensions: variables (e.g., precipitation) by which the niche is quantified or measured; often interchangeable with the term niche axis

Fundamental niche: the range of environmental conditions and resources in which a species can survive and reproduce, lacking influence of predation or competition

Realized niche: the range of environmental conditions and resources in which a species can survive and reproduce, once biological interactions are taken into account

Ecological niche breadth is essentially the range or variety of conditions defining a species' niche. The set of temperatures a plant can grow in, the variety of foods an animal can eat, or the diversity of habitats a species can inhabit are all captured by this term. Niche breadth is an important concept for understanding biological adaptation and is relevant to many eco-evolutionary topics, including ecological specialization, niche evolution, and speciation. It also has important applications given pressures on species to shift ranges or adapt in response to climate change. The study of niche breadth has underpinnings in classical ecological and evolutionary literature (e.g., Elton 1927, Grinnell 1917, Hutchinson 1957) and has seen a recent resurgence (e.g., Chan et al. 2016, Ikeda et al. 2017, Qiao et al. 2016). Central to this study, it is still largely unknown how ecological niche breadth evolves, particularly how and how quickly niche breadth expands.

The study of niche breadth evolution is complex and applies to many contexts (Futuyma & Moreno 1988), but it is a thread summarized compellingly by Charles Darwin (1859, p. 6) in *On the Origin of Species*:

> Who can explain why one species ranges widely and is very numerous, and why another allied species has a narrow range and is rare? Yet these relations are of the highest importance, for they determine the present welfare, and, as I believe, the future success and modification of every inhabitant of this world.

Niche theory stems from the Darwinian view that two species in coexistence must occupy distinct ecological spaces. Grinnell (1917) first introduced the terms "niche" and "niche-relationships" as a correlation between species performance and resource availability. Elton (1927) defined a species' niche by its role, function, or impact in the environment. The Grinnellian concept was further developed by Hutchinson (1957), who proposed a mechanism for understanding how species develop and evolve their range. Hutchinson introduced niche dimensions as variables affecting ecological niche development and defined the multidimensional spectrum of an ecological niche—a less specialized niche would be distributed among a larger portion of the environment. Further, Hutchinson provided a framework for niche quantification in the context of species interactions through a fundamental niche—the set of environmental conditions a species can live and reproduce in—and a realized niche—the set of conditions a species occupies that includes biological interactions (e.g., competition, predation) (Futuyma & Moreno 1988).

From these early studies, niche breadth research has expanded into a diverse set of applications and contexts and proceeds from many scales and definitions. No one factor explains ecological specialization or niche breadth evolution (Futuyma & Moreno 1988). Dimensionality, or the number of niche dimensions in which niche breadth varies, may influence species divergence, convergence, and coexistence. The question of how and whether niche breadth dimensions interact and are correlated has garnered considerable interest (Brown 1984, Cody 1974). Habitat breadth studies may examine how local abundance and geographic distribution affect resource use and vice versa. Species occurrence data are used to model distributional or functional breadth, especially for assessing potential impacts of climate change (Thuiller et al. 2004). Finally, although a species' niche breadth is composed of individuals and populations, we know little about the proportion of niche breadth these hierarchies contribute to (Bolnick et al. 2003), and this issue may be of considerable importance under conditions of rapid environmental change.

Here, we review research on the evolution of ecological niche breadth and the potential interactions among niche breadth evolution, adaptation, and diversification. We begin by discussing how niche breadth is defined and quantified and then review mechanisms, theory, and contexts

PHENOTYPIC PLASTICITY VERSUS NICHE BREADTH

Phenotypic plasticity describes environmentally induced variation in the phenotype of an individual and can thus be defined as the production of two or more phenotypes from one genotype, as environmental conditions change. Phenotypic plasticity is intrinsically related to niche breadth, with both broadly describing phenotypic breadth. However, whereas niche breadth refers to the shape and width of the fitness curve, plasticity refers to the effects of environment on a particular trait. Further, whereas niche breadth can be defined for individuals as well as for higher taxonomic groupings, plasticity is defined solely at the level of the individual. When plasticity improves fitness in a given environment (i.e., adaptive plasticity), it enhances within-individual niche breadth. Adaptive plasticity might therefore be considered to be a specific subset of niche breadth.

for how niche breadth may evolve. Next, we discuss key topic areas and empirical studies of the evolution of niche breadth. We end by discussing how niche breadth may influence species' responses to global change and suggest research avenues that will improve understanding of the processes of niche breadth evolution.

2. DEFINING NICHE BREADTH

Niche breadth goes by many names and appears in many guises. In the literature, niche breadth evolution is addressed by studies on specialization and generalization, phenotypic plasticity (see sidebar titled Phenotypic Plasticity Versus Niche Breadth), and performance breadth. To a large extent, the prevalent terminology is system specific. For example, the thermal physiology literature primarily discusses thermal tolerance breadth, whereas plant–pollinator interactions predominantly refer to host specializations. All of these terms, however, encompass the same concept: Some individuals, populations, species, or lineages utilize a greater breadth of environments than others (**Figure 1**). Lynch & Gabriel (1987) described niche breadth in terms of a tolerance curve defined by an environmental optimum and a change in fitness over an environmental gradient. At the two ends of the niche breadth continuum are generalists—whose fitness is distributed evenly across multiple environments (in a broad sense)—and specialists—whose fitness is maximized in one environment. This conceptual model of niche breadth is readily applied to aspects of the niche measured as continuous variables (e.g., physiological tolerances) but is less intuitive for categorical niche definitions (e.g., diet). In general, niche breadth has most ecological relevance when considered against a reference. This reference might be other individuals, populations, or species, or it might simply be the available niche space.

2.1. Measuring Niche Breadth

Recent reviews have detailed different niche breadth metrics (Devictor et al. 2010, Poisot et al. 2011). In this review, we focus instead on outlining different forms of niche breadth measure and their utility for addressing questions about niche breadth evolution (**Table 1**). Different methods and metrics represent different conceptual approaches to the measurement of niche breadth. First, one can measure niche breadth directly by examining the resources used along a particular niche axis (resource-based approaches). These types of measures are particularly common for quantifying dietary breadth (e.g., number of different food types used), habitat breadth (e.g., number of different habitat types used), and specialization in plant–pollinator networks (e.g., number of different pollinators visiting a plant).

Niche axis: a scale to quantify or measure niche values for a particular variable (e.g., precipitation); often interchangeable with the term niche dimension

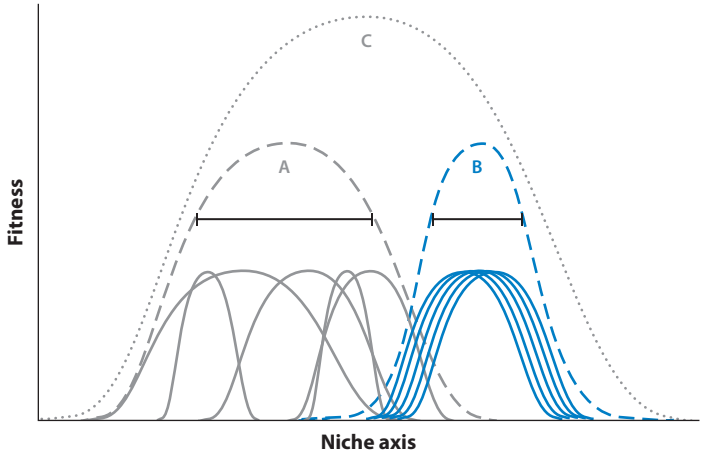


Figure 1

Fitness curves across a niche axis (e.g., temperature, precipitation). The three curve heights represent three levels of biological or phylogenetic hierarchy (primary, secondary, tertiary). The primary level (*solid lines*) could represent individuals or populations. Curves A and B (*dashed lines*) represent equivalent levels (e.g., populations) within the highest level (curve C, *dotted line*) in the phylogenetic hierarchy. Niche breadth is illustrated as horizontal bars in curves A and B. A is a generalist, or broad resource user relative to B, and is made up of a mix of narrow and broad resources users. B is made up of resource users with similar, relatively broad niche breadths, each mostly spanning B's breadth and slightly shifted from the next. Figure adapted from Bolnick et al. (2003) with permission.

Second, niche breadth can be inferred by association (association-based approaches). Commonly, this approach correlates abiotic conditions across a landscape with species occurrences (e.g., Heino 2005). It can thus define either a univariate or multivariate niche breadth measure. Both resource-based and association-based approaches require a priori definition of the niche axes to be investigated.

Third, interaction-based approaches use species co-occurrence data to define ecological niche breadth (e.g., Fridley et al. 2007) (**Table 1**). Unlike the previous two methods, this approach does not have a defined a priori niche axis and is useful for providing an overarching view of relative specialization and generalization within an ecological community. Interaction-based approaches are, however, limited by a lack of comparability among data sets and difficulties incorporating rare species.

Fourth, niche breadth can be defined by directly measuring performance in a range of environments (e.g., transplant experiments) (response-based approaches). Here, species whose fitness varies less across environments (i.e., have a flatter and/or broader response curve) have a broader niche. Although local adaptation studies have compared fitness trade-offs across environments (e.g., Etterson 2004), surprisingly few examples of such studies in the context of niche breadth have been found (but see Griffith & Sultan 2012). This approach does not necessarily rely on defining niche axes a priori, but in practice it often does. Transplant experiments, for example, often incorporate specific axes of interest into the experimental design (e.g., transplants across a temperature gradient). Performance (or fitness) curves, constructed with respect to a single environmental gradient, can represent both resource-based and performance-based measures. End points (i.e., maximum and minimum tolerances) are usually identified and represent a resource-based approach (e.g., Angert et al. 2011), but the shape of the curve—regardless of whether end points are measured—also provides a response-based measure of niche breadth.

Local adaptation: a process of natural selection whereby resident populations evolve higher relative fitness in their local habitat than populations originating elsewhere

Table 1 Summary of approaches for measuring ecological niche breadth (NB)

Type of NB measure	Measurement outcome	Example statistics	Attributes[a]						Example references
			Fundamental NB[b]	Multispecies[c]	Comparable[d]	Flexible[e]	Rarity[f]	Niche position[g]	
Resource-based	Species with a broader niche use a greater number of resources	Raw counts and ranges, Levin's index, Simpson/Shannon coefficient	Sometimes	Yes	Yes	No	Yes	Yes	Hurlbert 1978, Levins 1968
Association-based	Species with a broader niche are associated with a greater variety of conditions	Occurrence with climate- or environment-related variables, assessed through multivariate statistics (e.g., canonical correspondence analysis, redundancy analysis, outlying mean index, kernal density estimation)	No	Yes	Sometimes	Yes	Yes	Yes	Blonder et al. 2014; Dolédec et al. 2000; Ter Braak 1986, 1987
Interaction-based	Species with a broader niche co-occur or interact with a greater number of different species	Czekanowski's Index, Θ, d', $H2'$	No	Yes	No	Yes	No	No	Botta-Dukát 2012, Blüthgen et al. 2006, Ducatez et al. 2014, Feinsinger et al. 1981, Fridley et al. 2007
Response-based	Species with a broader niche have a flatter fitness or performance response curve	Experimental transplants and physiological assays that measure fitness or a proxy across a range of environments	Yes	No	Sometimes	Sometimes	Yes	Yes	Brett 1971, Etterson 2004, Huey & Stevenson 1979, Luna & Moreno 2010, Sheth & Angert 2014

Many statistical methods are available to quantify NB within each approach; we have given just a few examples.

[a]For each type of NB measure, specific attributes may apply (Yes), may not apply (No), or may sometimes apply or apply to a subset of methods (Sometimes).

[b]Method is able to measure the fundamental NB.

[c]NB can be easily measured for many species.

[d]NB measures are comparable across data sets.

[e]NB measurement can be made without a priori definition of the relevant niche axis.

[f]NB can be measured accurately for rare species.

[g]Niche position can be estimated simultaneously.

2.2. Dimensions of Niche Breadth

Budding speciation: a form of speciation, whereby a new species forms from a small colonizing population

For any particular study, defining and estimating niche breadth requires consideration of both dimension and scale (Colwell & Futuyma 1971). Just as the niche can be described for dimensions such as habitat, diet, and physiology, niche breadth is usually defined with respect to the habitats occupied, the resources used, and the environmental conditions tolerated. It is important to distinguish among niche dimensions. For example, dimensions that describe resource use are fundamentally different from those that describe tolerances (e.g., to temperature) because competition for the one is more likely than for the other. Within these broad niche dimensions, niche breadth can be defined along any number of additional axes (Colwell & Futuyma 1971, Hutchinson 1957). A challenge is thus to define niche breadth along the relevant axes, which may or may not be correlated with each other (Bonetti & Wiens 2014, Cody 1974, Emery et al. 2012, Lin & Wiens 2016). Indeed, trade-offs in niche breadth between axes might exist (e.g., Litsios et al. 2014) and could influence whether generalists or specialists evolve (discussed in Section 3.2).

Brown (1984) envisaged species arising in localized regions that differ in several ecological respects from those occupied by parent species, thus promoting multidimensional specialization through speciation, but to date, few direct tests of this idea have been made (but see Bonetti & Wiens 2014 for one example). Budding speciation (Mayr 1954) patterns are consistent with this hypothesis. This mode of speciation appears to be a potentially common mechanism in plants (Anacker & Strauss 2014, Grossenbacher et al. 2014) but requires further study.

2.3. Components of Niche Breadth

Another conceptual issue for measuring and studying niche breadth evolution is the underlying architecture of a species' niche. Roughgarden (1972) outlined a framework for partitioning a population's niche breadth into between- and within-individual components. Individuals are not identical, and the variation among individuals is one component of a species' niche breadth (Van Valen 1965). Recent work has focused on the incidence, degree, and evolutionary importance of individual niche breadth. Bolnick et al. (2003) distinguished individual specialization (or variation) from differences in resource use attributable to age (ontogenetic niche shifts; reviewed in Nakazawa 2015), sex (intersexual niche partitioning; reviewed in Barrett & Hough 2013), or discrete morphological polymorphism (resource polymorphism; reviewed in Smith & Skúlason 1996) and demonstrated that such variation is widespread in nature. Individual niche breadth can manifest either as a broadly/narrowly tolerant phenotype or as phenotypic plasticity (e.g., see sidebar titled Phenotypic Plasticity Versus Niche Breadth), which might be reversible (e.g., physiological acclimation) or irreversible (e.g., developmental plasticity) (West-Eberhard 2003). Individual niche breadth and between-individual variation are encompassed by population niche breadth (**Figure 1**). Roughgarden's (1972) framework can be extended to encompass between-population variation (e.g., local adaptation) and, thus, species niche breadth (e.g., Olsson et al. 2009) (**Figure 1**). Recent research has explored the conditions under which local adaptation is likely to occur (e.g., Atkins & Travis 2010, Richardson et al. 2014). In this vein, niche breadth could be maintained, or expanded, through an aggregate process of adaptation to multiple environments (e.g., Anderson et al. 2015). Alternatively, niche equivalency among populations may occur such that population- and species-level niche breadths are similar (e.g., Wasof et al. 2015).

The distinction between a homogeneous generalist species and one comprised of locally adapted populations is important both conceptually and practically. From a conceptual standpoint, it determines the scale at which comparisons of niche breadth are relevant. Theoretical models (discussed below) also predict an interaction among different levels of niche breadth within a phylogenetic hierarchy. Practically, the hierarchical architecture of niche breadth is important

because a broadly tolerant species and one comprising locally adapted populations might differ in their potential evolutionary and demographic trajectories (Atkins & Travis 2010).

3. MECHANISMS OF NICHE BREADTH EVOLUTION

3.1. Classes of Models for Niche Breadth Evolution

Many topics in evolutionary ecology have their own set of models, theory, and empirical tests for niche breadth evolution. Here, we briefly outline four broad classes of evolutionary models defined by the context in which niche breadth evolution is considered, with subsequent sections focusing on emerging questions related to each model class. Classical evolutionary theory has approached the problem of niche breadth evolution through population genetic and quantitative genetic models that consider fundamental constraints on generalization and specialization and the costs—both direct and indirect—of maintaining a given niche breadth. We refer to such treatments as genetic models (**Table 2**). For example, Whitlock (1996) described a model for niche breadth evolution that did not rely on direct fitness trade-offs (see Section 3.2), whereby specialization was generally favored because specialists could evolve more quickly than generalists. This is because, as specialists should spend a greater proportion of their time in a given environment, fixation of beneficial alleles is both more likely and more quick to occur (Holt 1996, Whitlock 1996). A key question to emerge from these theories is the importance of direct fitness costs (e.g., antagonistic pleiotropy) in maintaining niche breadth. These evolutionary models are also closely related to models of range limits that incorporate evolution (reviewed in Sexton et al. 2009).

Antagonistic pleiotropy: a negative correlation between trait fitness that results when alleles at a single locus change rank fitness across environments or contexts

A second group of models considers niche breadth evolution within the context of the resource environment, for which "environment" could describe, for example, abiotic variables, food, or habitat (**Table 2**). Beginning with the classic models of Levins (1968), these studies have primarily explored how spatial and environmental heterogeneity drives niche breadth evolution and are supported by experimental evolution studies (Kassen 2002). In general, broader niches are favored in more heterogeneous environments, but the spatial and temporal scales of variation—relative to the movements and life span of individuals—are important for model predictions (see Section 3.3). These models have a focus on environmental tolerances.

Third, niche breadth evolution is also likely to depend on behavior (e.g., habitat preferences, philopatry) and biological interactions, including density and inter- and intraspecific competition (biotic models; see **Table 2**). Ravigné et al. (2009), for example, modeled the effects of habitat choice evolution on niche breadth evolution, showing that habitat choice can promote selection for specialists where otherwise (i.e., no habitat choice) generalists would be favored (see also Rueffler et al. 2007). Biotic conditions such as community diversity can also alter the outcome of niche breadth evolution by modifying the fitness landscape (Kleynhans et al. 2016). These biotic models have a focus primarily on resource use (see Section 3.4 and **Table 2**).

Finally, niche breadth evolution may be dependent upon all of the above mechanisms. These combined effects produce patterns of niche breadth change through evolutionary time—patterns that have been described through conceptual or verbal models in a fourth, macroevolutionary context. These models are particularly relevant in the context of adaptation and speciation (Section 3.5), and recent empirical studies are shedding new light on the classic question of whether specialization is an evolutionary dead end (see Section 4.2).

3.2. Trade-Offs and Constraints on Niche Breadth Evolution

The overarching paradigm when considering the evolution of niche breadth is that there must be costs or constraints to being a generalist; otherwise why would all species not use all resources

Table 2 Examples of niche breadth (NB) evolution models, grouped by the context in which they were developed

Description and predictions	Example reference(s)
Genetic context[a]	
Specialization is favored because specialists evolve more quickly than generalists and when genotypes have different fitness rankings in different environments. Niche expansion is prevented because selection is stronger in environments to which a population is already adapted.	Fry 1996, Holt 1996, Holt & Gaines 1992, Whitlock 1996
Generalists are more prone to accumulate mutations that are deleterious in part of their range, which results in inferior performance of generalists in a given habitat, compared with specialists.	Kawecki 1994, 2000; Kawecki et al. 1997
Environmental context[b]	
Specialization is favored in temporally stable, spatially variable environments; temporally variable environments can favor either a monomorphic population of generalists or a population of individual specialists.	Levins 1962, 1965, 1968
Specialization is favored when individuals experience only a subset of the environments experienced by a population and when populations experience only a subset of environments encountered by a species.	Levins 1968
Temporal variation favors generalization; spatial variation selects for higher NB only when within-generation temporal variation is also high.	Lynch & Gabriel 1987
In a shifting environment, intermediate NB is favored because it balances phenotypic lag and performance sensitivity.	Huey & Kingsolver 1993
Without temporal variation, habitat choice and negative density dependence favor extreme specialization; within-generation temporal variation reduces the frequency of extreme specialization.	Wilson & Yoshimura 1994
Specialization is favored in constant environments and environments with high within-generation variation; generalization is favored when among-generation variation is high but within-generation variation is small.	Gilchrist 1995
Biotic context[b]	
Joint evolution of habitat preference and local adaptation promotes specialization.	Ravigné et al. 2009
Competition modulates the match between individual niche width and the diversity of resources; as the number of species in a community increases, individual niche width decreases regardless of resource diversity.	Case 1981
NB contracts through frequency-dependent selection for finding mates at low population densities.	Colwell 1986
NB expands in populations with a locally adapted male mating advantage under certain conditions of ancestral fitness.	Proulx 1999
In the presence of interspecific competition, specialization is favored when species are locally rare, and generalization is favored when species are locally abundant.	Sargent & Otto 2006
Competition via interspecific pollen transfer selects for specialization on different pollinators when visit rates are high and selects for generalization on multiple pollinators when visit rates are low.	Muchhala et al. 2010
Macroevolutionary context[c]	
Specialist clades transition between hosts but remain specialized.	Schluter 2000
Niche expansion without adaptive diversification occurs if there are no costs to niche expansion; otherwise, niche width remains narrow and adaptive diversification occurs.	Ackermann & Doebeli 2004
Lineages undergo alternating phases of niche expansion and contraction, with speciation driven by the evolution of specialists from a generalist, followed by niche expansion.	Janz & Nylin 2008

[a]Genetic context models examine fundamental limits to niche expansion, primarily at the population level.
[b]Environmental and biotic context models primarily describe abiotic and biotic conditions, respectively, in which specialization or generalization are favored or which affect the action of selection on NB by altering the fitness landscape. These include models of individual, population, and species NB.
[c]Macroevolutionary context models describe patterns of NB evolution across lineages, with NB considered at the species or lineage level.

(Levins 1968)? MacArthur (1972) used the term "jack-of-all-trades, master-of-none" to describe the costs of generalization, implying a trade-off between peak performance and performance breadth. Hereafter, we refer to this as a performance breadth trade-off. Performance breadth trade-offs can be conceptualized as performance or tolerance curves, in which the area under the curve remains constant and is either flattened (generalist) or laterally compressed (specialist) (Lynch & Gabriel 1987).

Conditional neutrality: a state in which alleles are favored in one environment but neutral in others

Many models for niche breadth evolution have such trade-offs as an underlying assumption (**Table 2**). However, little evidence shows that direct trade-offs are ubiquitous or even very common (Bennett & Lenski 2007, Forister et al. 2012, Whitlock 1996). Detecting trade-offs between performance breadth and peak performance involves experiments that test whether organisms (e.g., genotypes) that perform well across a wider range of environments do not perform best in any one environment (i.e., a negative correlation between local performance and broad performance). Many studies have now demonstrated positive correlations between performance breadth and peak performance (e.g., Ketola et al. 2013), no correlation (e.g., Latta et al. 2012), or the predicted negative correlations (e.g., Willett 2010).

Several interpretations have been made for a general lack of evidence for niche breadth–performance trade-offs (see Huey & Hertz 1984). First, trade-offs may be difficult to detect. Second, trade-offs may involve different performance dimensions (e.g., speed versus endurance), rather than occurring within a single dimension. Third, trade-offs might be masked by adaptations at higher levels of physiological organization, so they are not important constraints. For example, trade-offs in enzymatic performance may be masked or compensated for by adaptations in muscle tissue or limb enhancements (Huey & Hertz 1984). Finally, trade-offs may not exist or may not be common enough to detect.

One question that remains relatively unexplored is where we expect fitness trade-offs to occur. The thermal biology literature has focused (at least theoretically) on within-locus constraints on enzyme function. For example, thermodynamic constraints might mean that enzymes that function well at one temperature perform poorly at a different temperature (reviewed in Angilletta et al. 2002; see also Huey & Hertz 1984). Other genetic trade-offs are described by antagonistic pleiotropy or mutation accumulation (Cooper & Lenski 2000). Alternatively, adaptation is possible without trade-offs (i.e., conditional neutrality) (Anderson et al. 2013). Bono et al. (2017) reviewed experimental evolution studies and concluded that antagonistic pleiotropy, and hence trade-offs, was more likely to occur in homogeneous environments in which selection is blind to costs that would (hypothetically) occur in another environment. Interlocus trade-offs might also occur if there are negative genetic correlations among genes.

Importantly, although trade-offs are often considered in only one dimension, this need not be the case. In *Daphnia* for example, greater salt tolerance does not incur a fitness cost in low-salinity environments but could incur a cost in terms of predator response (Latta et al. 2012). Similarly, although Ketola et al. (2013) found a positive correlation between niche breadth and performance in bacterial pathogens, generalists had reduced virulence (measured as the death rate in infected flies, the bacterial hosts in this case), suggesting a fitness cost that might become apparent in different ecological contexts.

As noted above, the existence of trade-offs is not a prerequisite for the evolution of specialization, and several models have been developed that describe the evolution of specialists in the absence of fitness costs of generalization (see Remold 2012). For example, Whitlock (1996) and Fry (1996) described models in which specialization evolves because, as a more specialized subpopulation arises, it increases in fitness more rapidly than a generalist subpopulation. Kawecki (1994) described a similar model under which specialization evolves because of the accumulation of mutations that are deleterious in environments to which a population has not yet been (or is

not frequently) exposed. These conditionally deleterious mutations become fixed by drift, thus precluding niche expansion or facilitating niche contraction.

3.3. Environmental Effects on Niche Breadth Evolution: Spatial Variation, Temporal Variation, and Environmental Extremes

Environmental heterogeneity—in space, time, or both—is ubiquitous yet uneven in nature, and unsurprisingly a large theoretical literature has examined its effects on the evolution of niche breadth. Levins (1968) distinguished between fine- and coarse-grained scales of environmental heterogeneity, which generally refer to variation experienced within and between individual lifetimes, respectively. Two key questions emerge from theoretical models: how the scale of heterogeneity influences niche breadth evolution and how spatial and temporal heterogeneity interact.

Recently, studies have shown that temporal variation is a stronger predictor of niche breadth than spatial variation (e.g., Lin & Wiens 2016). This finding is in general agreement with the predictions of Lynch & Gabriel's (1987) model, which suggested that spatial variation should select for higher niche breadth only when within-generation temporal variation is also high. This is because, in the absence of temporal variation, each individual experiences just a subset of the available environments. Because this model considered niche breadth of a given genotype, it focused explicitly on individual niche breadth and did not, therefore, consider the effects on population niche breadth. In contrast to Lynch & Gabriel's (1987) model, which emphasized the importance of within-generation temporal variation for promoting higher niche breadth, Gilchrist (1995) predicted that selection would favor a wider performance breadth only in environments with high among-generation variation and low within-generation variation (although this model did not consider spatial environmental heterogeneity). This scenario is supported by recent empirical tests (Chan et al. 2016). Gilchrist distinguished performance breadth from tolerance breadth, with the former describing the response of growth and reproduction to environmental conditions (e.g., temperature) and the latter describing the probability of survival. It is thus possible for an organism to be a performance specialist (performing well over a narrow range of conditions) while maintaining a broad tolerance (surviving over a large range of conditions) (Gilchrist 1995).

Despite their differences, models incorporating temporal heterogeneity generally agree that the scale of this heterogeneity, in relation to the life span of the organism, has a strong effect on how abiotic conditions affect niche breadth evolution. An analogous situation for models incorporating spatial heterogeneity is the effect of movement and dispersal ability on niche breadth, with greater movement generally favoring a broader niche. Sultan & Spencer (2002), for example, modeled a metapopulation in a heterogeneous environment and showed that a generalist genotype was favored over local specialists as long as there was a moderate rate of movement between sites, even under conditions in which local specialists had higher fitness within their home site.

Environmental extremes can also play an important role in the evolution of niche breadth. This topic has been examined particularly with respect to thermal niche breadth (e.g., Denny & Dowd 2012, Hoffmann 2010, Sunday et al. 2011). Wiens et al. (2013) presented a conceptual model for different ways in which niche breadth might vary among species distributed along an environmental gradient, which included selection for specialization in extreme environments, niche expansion with adaptation to extreme environments (e.g., Hoffmann & Parsons 1993), or niche shift without concurrent change in niche breadth (e.g., Hoffmann et al. 2002). Although few specific tests of these alternatives are available (but see Bonetti & Wiens 2014, Wiens et al. 2013), the thermal tolerance literature provides strong support for unidirectional niche breadth change along an environmental gradient. A large body of work (particularly for ectotherms) shows that heat tolerance is conserved across lineages, whereas cold tolerance varies (e.g., Araújo et al.

2013, Hoffmann et al. 2013). These studies demonstrate that species in cold climates typically have broader thermal niches than those from warm climates. A recent theoretical model by Buckley & Huey (2016) also supported an asymmetrical effect of environmental extremes on niche breadth. Although thermal extremes are expected to promote niche expansion in temperate environments, niche shifts—rather than expansions—are expected in tropical environments in which temperature ranges are narrower. This, in part, is due to reduced genetic variation from heat-related mortality (selection) as well as the physical challenge heat stress imposes on biological structures (e.g., proteins).

Allopatric speciation: a form of speciation, whereby a new species forms outside of the geographic distribution of an ancestral species

3.4. Competition and the Niche Breadth of Individuals and Populations

The niche breadth of a population (or species) can evolve via changes to individual niche breadth or through variation among individuals (i.e., variation among genotypes) (Bolnick et al. 2003, Roughgarden 1972, Van Valen 1965). Taper & Chase (1985) examined niche breadth evolution under intraspecific competition and showed that it reaches a stable value: If either individual niche breadth or among-individual variation is constrained, the other expands to compensate (though this is likely to apply only to the use of resources for which individuals compete). Thus, clues as to where constraints on niche breadth evolution exist might come by examining the distribution of niche breadth across the biological/phylogenetic hierarchy. Taper & Chase's (1985) model points to decoupled changes in the two components of population niche breadth, which has also been shown experimentally (Bolnick et al. 2010).

One area in which decoupled changes in niche breadth evolution have frequently been tested is in the context of density dependence. Intraspecific competition is considered to be one of the primary drivers of among-individual variation (individual specialization; see Bolnick et al. 2003), with theory predicting an increase in phenotypic variation—and thus population niche expansion—as competition increases (niche variation hypothesis; see Van Valen 1965) (see also Bolnick 2001, Svanbäck & Bolnick 2005). Experimental studies have supported theoretical predictions, with increases in competition associated with diversification in resource use among individuals (e.g., Martin & Pfennig 2009, Svanbäck & Bolnick 2007, Svanbäck & Persson 2004). Similarly, Bolnick et al. (2007), examining several animal taxa, and Costa et al. (2008), examining lizards, showed that expansion of the population niche breadth is frequently accompanied by greater among-individual variation. Notably, this diversification can arise without a change in individual niche breadth (Svanbäck & Bolnick 2007, Svanbäck & Persson 2004).

3.5. Adaptation or Speciation? Niche Breadth and the Tension Between Micro- and Macroevolution

Niche breadth might play a significant role in shaping patterns of adaptation and diversification. For example, specialization has long been argued to promote population subdivision and, thus, increase rates of allopatric speciation (Futuyma & Moreno 1988). However, specialization permits the coexistence of more species via finer partitioning of the available niche space (Dyer et al. 2007). Niche expansion could also promote speciation if niche breadth is maintained by the development of stable polymorphisms in sympatry, a debated topic (Coyne & Orr 2004).

Adaptive diversification and niche expansion represent contrasting outcomes of frequency-dependent competition for resources (Ackermann & Doebeli 2004). When variation in the available resources is large relative to niche breadth, adaptive diversification is favored, which might, in turn, lead to speciation (Dieckmann & Doebeli 1999). However, an alternative scenario is that niche breadth expands, which hinders, rather than promotes, phenotypic divergence. Notably,

these are alternative scenarios from only an individual perspective. The effect on the population niche breadth is the same (i.e., niche expansion), regardless of the mechanism, until divergence proceeds far enough for sympatric speciation.

Sympatric speciation: a form of speciation, whereby a new species forms within the geographic distribution of an ancestral species

Niche filling: expansion of the realized niche to fill a greater proportion of the fundamental niche

Niche unfilling: contraction of the realized niche to fill a smaller proportion of the fundamental niche

In a model of niche breadth change and diversification under different scenarios of costs and benefits to niche expansion, Ackermann & Doebeli (2004) found that, when niche expansion was costly in terms of resource uptake, adaptive diversification leading to speciation was favored. Without costs to niche expansion, however, a generalist phenotype evolved that precluded the development of divergent specialist lineages. Although these models focused on individual niche breadth, the same ideas can be scaled up to the population level. When, for example, is local adaptation favored? If speciation is driven by divergent natural selection in different environments, it is implied that niche breadth first expands—at least at the species level—and is followed by lineage splitting (Dieckmann & Doebeli 1999, Schluter 2000). Janz & Nylin (2008) proposed a mechanism to explain the high diversity of phytophagous insects; in this mechanism, a specialist adapts to new hosts (i.e., increases its niche breadth), followed by a process of parapatric/sympatric speciation and/or geographic range expansion and local adaptation and finally speciation driven by divergent natural selection in different environments across the newly expanded range (Schluter 2009). This process is envisaged to repeat, so that a lineage oscillates between having a broad niche breadth and being comprised of several taxa with narrower niche breadths. An alternative model of niche evolution is that niche breadth is relatively fixed at the species level, and species shift, rather than expand, their niche (musical chairs hypothesis) (Hardy & Otto 2014). There are few explicit tests for either hypothesis, though Hardy & Otto (2014) found support for the latter among papilionid butterflies. Reflecting on these major mechanisms of niche breadth evolution allows us to identify key tensions and recent insights gained in the practice of niche breadth research.

4. KEY TOPICS AND EMPIRICAL RESEARCH ON THE STUDY OF NICHE BREADTH EVOLUTION

4.1. Detecting Niche Breadth Evolution Versus Fundamental Niche Filling

The study of niche breadth evolution is essentially concerned with changes in the fundamental niche. Nevertheless, although niche and range limits often coincide (Hargreaves et al. 2014), for many and perhaps most species, the realized niche is considerably smaller than the potential niche. As a species niche expands or contracts, we must therefore be able to distinguish between changes to the realized niche breadth by niche filling or niche unfilling—niche space occupied in a native range yet unoccupied in an invaded range (see Guisan et al. 2014)—and those brought about by evolution.

4.1.1. Insights from transplant experiments. One of the only direct ways to test the extent to which a species currently occupies its entire fundamental niche is via transplant experiments, whereby individuals are moved beyond their natural range and population persistence is recorded. In such studies, range limits are considered to represent the borders of the realized niche, and so the question is whether the realized niche is equivalent to the fundamental niche. Reviewing evidence from transplant experiments in plants, Hargreaves et al. (2014) found, in roughly half of the studies examined, that range limits coincided with fundamental niche limits, with individuals performing poorly when transplanted beyond their range boundaries. In a quarter of the studies, however, they found that range limits failed to represent fundamental niche limits. This is strong evidence that, for a considerable proportion of species, the realized and fundamental niches are

quite different. Other studies also suggest that current range limits frequently lag behind potential range limits (e.g., Svenning & Skov 2004).

The concordance between range and niche limits is particularly important for the study of niche breadth evolution when niche breadth is estimated using association-based approaches (**Table 1**). If species differ only in realized niche breadth, then estimates of rates and directions of niche breadth evolution will necessarily be compromised. Comparing the results of transplant experiments and ecological niche models, which use association-based approaches to predict suitable habitats across a landscape, Lee-Yaw et al. (2016) found that, in many cases, niche models appeared to provide a reasonable estimate of the fundamental niche. As detected by Hargreaves et al. (2014), however, nearly a quarter of studies suggested a failure of range limits, and the bounds of habitat suitability predicted by niche models, to meet niche limits (Lee-Yaw et al. 2016). Thus, although measuring the fundamental niche can be both conceptually and logistically challenging, estimates of niche breadth that are as close to the fundamental niche breadth as possible, using transplant, response-based, or ecologically informed niche modeling approaches (Guisan & Thuiller 2005), remain critical for studying and understanding how niche breadth evolves.

Introgression: incorporation of alleles from a species (or a population) into the gene pool of a second species (usually refers to gene flow via hybridization)

4.1.2. Insights from species introductions. Species introductions present an excellent opportunity to study niche evolution (e.g., Petitpierre et al. 2012). In particular, they can help us distinguish between (*a*) niche shifts without niche expansion, which might indicate evolutionary constraints on niche breadth itself, and (*b*) niche expansion, which could indicate ecological constraints on niche breadth or evolutionary release.

Although rapid niche evolution has been demonstrated in invasive species (e.g., Urbanski et al. 2012), remarkably few studies have tested changes in niche breadth. Guisan et al. (2014) recently presented a detailed review of studies examining niche change in the context of biological invasions. Their review focused on changes in the realized niche, and they provided a practical framework for assessing niche change, which can be easily applied to changes in fundamental niche breadth. A niche shift is considered to have occurred if there is a change in the centroid or limits of the niche. Niche shift can occur without changing the niche breadth if expansion at one end of the niche spectrum is accompanied by contraction at the other end. Under this framework, niche expansion can occur by (*a*) a niche shift in the invading population, outside the niche of its source population (species-level niche expansion only) with or without (*b*) an expansion of the niche in the invading population (population- and species-level niche expansion). As an example of the first scenario, Hill et al. (2013) found that invasive populations of the red-legged earth mite (*Halotydeus destructor*) had greater heat tolerance (measured experimentally) than populations in the native South African range. This increased the overall species niche breadth (in this case defined by thermal tolerance limits) by 2.5°C, compared with the native populations alone, but population-level niche breadth was similar between native and invasive populations.

Niche shifts without expansion might indicate evolutionary constraints on niche breadth itself, whereas niche expansion in the introduced range might indicate other ecological limits on niche breadth evolution. Interspecific competition might actively constrain niche breadth in the native range, for example. Alternatively, evolutionary release might occur when novel genetic combinations become available, for example, through genetic introgression with a native species, producing new phenotypes upon which selection can act (Pfennig et al. 2016). Novel allelic combinations could increase adaptive potential through increasing genetic variation, the formation of beneficial gene combinations, and/or increased phenotypic plasticity (see Pfennig et al. 2016). For example, evidence from sunflowers shows that hybridization might facilitate colonization of novel habitats (Rieseberg et al. 2003). Lastly, lack of opportunity for evolutionary change in the native range may be a limiting factor for niche breadth evolution, with colonization providing the

opportunity for selection to increase niche breadth. For example, niche breadth might expand through adaptation to a host that was not present in the native range (see examples in Moran & Alexander 2014). This is different from niche filling (see Guisan et al. 2014), which involves an expansion of the realized niche, without adaptive evolution. It is also possible, at least theoretically, for an invading population to specialize within a subset of the native population's fundamental niche (the equivalent of Guisan's niche unfilling). In this instance, the species-level niche breadth would be unchanged but the population niche breadth of the invading population would decrease. The conceptual framework used for these realized niche shifts is useful in promoting testable hypotheses for niche breadth evolution. More studies of niche breadth change that use such frameworks and experimental evidence are needed to understand how niche breadth evolves in introduced species (e.g., to determine whether expansion involves changes to the realized or fundamental niche), and answers to these questions may have important implications for species management.

4.2. Directionality of Niche Breadth Evolution

For many years, the prevailing view has been that specialization is an evolutionary dead end (Schluter 2000), with niche breadth proceeding as a directional process of specialization. With the increasing availability of phylogenetic data, testing for directional trends in niche breadth evolution is feasible (Day et al. 2016, Schluter 2000). Perhaps surprisingly, the dead end paradigm of specialization is not well supported, and many studies have shown niche shifts or expansions from specialist lineages. For example, biome shifts (e.g., Donoghue & Edwards 2014) represent lineage-level niche expansion and are a regular feature of plant evolution. Niche breadth can expand and contract in different lineages over evolutionary time. In fact, among taxa for which directional shifts have been tested, most show one or more transitions from specialist to generalist, almost half show a specialist-to-generalist bias, and few studies find support for a model of directional evolution over a nondirectional model (see further discussion in Section 4.3). The phylogenetic depth under consideration is an important factor influencing the interpretation of directional trends. Over macroevolutionary time scales, some features may evolve that are complex, are not easily reversible, and/or commit an organism to a specific way of life (e.g., genome duplication and subsequent pseudogenization). Nevertheless, such changes do not appear to be biased toward specialists (see Gardiner et al. 2008), and irreversible specialization should not be assumed.

4.3. Niche Breadth and Diversification Rate

An important question is whether niche breadth acts as an evolutionary driver, in terms of both diversification and adaptation (see Section 4.4). Although the question of whether niche breadth influences diversification rates is fairly straightforward and might ensue through several different mechanisms, it has been remarkably neglected. In part, this stems from the need for robust phylogenies, and accordingly, several studies have recently tested this relationship using advances in molecular tools. Nevertheless, the authors are unaware of formal models that test the effects of niche breadth on diversification rates or conceptual models that provide contrasting predictions (Nyman 2010).

Diversification rate encompasses the rates of both speciation and extinction, and specialization is thought to increase both, thus increasing rate of species turnover (Dall & Cuthill 1997). The most accepted scenario is one of higher diversification rates with narrower niche breadth, yielding a negative correlation between niche breadth and diversification rate (e.g., Hardy & Otto 2014). For example, one argument for specialist lineages having greater diversification rates is that

they are more likely to suffer from resource limitations and are therefore more susceptible to environmental changes, range fragmentation, and local extinctions than are generalist lineages, such that allopatric speciation occurs more frequently (Vrba 1987). Using simulation, Qiao et al. (2016) predicted that diversification rates should be highest when rates of climatic change are high, niche breadth is low, and dispersal ability is low. Of these parameters, niche breadth had the strongest independent effect on speciation rates, whereas dispersal ability had the strongest independent effect on extinction rates.

An alternative view is that generalists should have higher rates of diversification because they typically have larger range sizes (Slatyer et al. 2013) and are therefore more likely to have these ranges fragmented by ecological or geographical barriers over evolutionary time, promoting allopatric speciation (see Rolland & Salamin 2016). Thus, specialists and generalists can each be predicted to have higher diversification rates under different conceptual frameworks.

Among the few studies that have tested for a niche breadth–diversification relationship, a clear consensus has not been found. Gómez-Rodríguez et al. (2015), for example, found a positive relationship between family-level niche breadth and diversification rate among amphibians but only a weak relationship between the average species-level niche breadth and diversification. By contrast, other researchers (Hardy & Otto 2014, Rolland & Salamin 2016) have found higher speciation and net diversification rates for specialist lineages. Of course, niche breadth may not be a primary contributor to diversification rates. For example, niche position, which describes the distribution of resources across a landscape, might have a stronger influence on range size (and processes related to range size, as described above) than niche breadth does (Hanski et al. 1993). In some cases, niche breadth and diversification rates might simply covary. For example, among amphibians, diversification rates tend to be higher in the tropics, and niche breadth can be either narrower (precipitation niche breadth) or wider (temperature niche breadth) in the tropics (see Kozak & Wiens 2010). Studies that can further address how niche evolution, and its many facets, interacts with diversification rates are needed.

4.4. Niche Breadth and Rates of Niche Evolution

Niche breadth might also influence the rate of adaptation (i.e., niche evolution) independently of its relation to speciation processes (Section 3.5). If all species in a region have broad niches, the potential for divergence between those niches—and thus the potential for niche evolution—is small (Fisher-Reid et al. 2012). Additionally, Huey & Kingsolver (1993) showed, through modeling, that populations with a broad thermal niche were slower to match their mean phenotype to the environmental conditions, and Whitlock (1996) suggested that species with a narrow niche might be able to evolve more quickly than those with a broad niche. Thus, at both broad (i.e., regional, species-level) and fine (i.e., individual-level) scales, niche evolution might be expected to proceed more slowly in generalists (Kassen 2002). However, the few studies that have tested this hypothesis illustrate inconsistent outcomes (Fisher-Reid et al. 2012, Lavergne et al. 2013, Satterwhite & Cooper 2015).

4.5. Genetic Variation and Constraints on Niche Breadth Evolution

The capacity for niche breadth evolution clearly depends on the ability of organismal genomes to produce the phenotypes upon which natural selection may act. Understanding the genetic basis for phenotypic variation is necessary to accurately assign costs and constraints to niche breadth evolution (Rockman 2012). Because most genes underlying ecologically relevant characters are still unknown in most species, quantitative genetic methods to assess genetic variances and

covariances (evolvability) that affect response to selection (reviewed in Houle 1992) can provide useful insight. A number of studies provide evidence for genetic constraints to trait evolution (reviewed in Futuyma 2010). However, it has been questioned whether quantitative genetic parameters such as genetic correlations cause meaningful constraints (Conner 2012), and others argue that selection may actually deplete genetic variance faster than the rate at which favorable mutation can generate it for complex, multitrait adaptations (Blows & Hoffmann 2005).

Epigenetic: facultative, heritable changes in gene expression that do not involve changes to underlying nucleotide sequence (e.g., DNA methylation, histone modification)

Genomic investigations, particularly genome scans, are beginning to elucidate genes and suites of adaptive genes related to recurrent adaptive evolution. For example, Yassin et al. (2016) examined evolution on toxic resources in *Drosophila sechellia* and identified multiple detoxification genes evolving in multiple lineages. The genetic architecture of genomes that underlie phenotypes includes several potential features, such as gene/genomic duplications, mobile (transposable) elements, regulatory changes, accelerated coding evolution, novel microRNAs, structural changes (inversions), and hybridization/introgression. Investigations of the genomes of adaptively radiating clades (reviewed in Berner & Salzburger 2015) have recently attempted to identify common features that may underlie this genetic capacity for adapting or responding to novel environments. Although some common elements have been identified, general trends have yet to emerge, given the relative infancy of multigenome sequence generation. For example, a recent investigation of cichlid phenotypic diversity and adaptive radiations found support for multiple molecular mechanisms at work (Brawand et al. 2014). Comparative genomics studies could provide clues as to why certain adaptations have not arisen among closely related species (but see limitations discussed in Berner & Salzburger 2015). Wedding comparative genomic methods that identify candidate adaptation genes with empirical tests of candidate loci may provide a way forward: for example, empirical tests of resource utilization (carbon utilization, secondary metabolism, and stress response; see de Vries et al. 2017), physiological tolerances (temperature and drought tolerance; see Ojeda Alayon et al. 2017), and application of reverse mutagenesis technologies (see Curtin et al. 2017).

The search for genetic variants underlying important phenotypic traits is complicated by observations of phenotypic plasticity—the ability of one genotype to produce different phenotypes depending on environmental conditions (Nonaka et al. 2015; see sidebar titled Phenotypic Plasticity Versus Niche Breadth). Epigenetic variation is emerging as a molecular mechanism moderating between environment and genotype and enabling rapid adaptive phenotypic responses to environmental stimuli and stressors (Rey et al. 2016). Environmentally induced epigenetic changes have been found to (*a*) facilitate plasticity and broaden resource use (extreme sugar environments) and niche width in a nectar-living yeast (Herrera et al. 2012), (*b*) correlate with response to salinity gradients in select species (Foust et al. 2016), and (*c*) mediate genetic variation for plasticity in drought stress response of offspring relative to their parents (Herman & Sultan 2016). Epigenetic variation has been hypothesized to be a precursor to, and even a facilitator of, more lasting genetic change (Yona et al. 2015), an idea consistent with plasticity-first hypotheses of the evolution of organisms (Levis & Pfennig 2016). In this vein, epigenetic variation may influence the capacity for niche breadth evolution.

5. NICHE BREADTH AND CONSERVATION UNDER GLOBAL CHANGE

Understanding the determinants of niche breadth, and whether and how niche breadth can be predicted from abundance and distributions, has no better application than anticipating population and species responses to global climate change. With global change, ecological communities may disassemble as individual species shift their ranges (Thuiller et al. 2004), resulting in new interspecific relationships (e.g., competition, symbiosis) and changes to the realized niche.

"How much can a species' niche expand (i.e., through adaptation) or shift to accommodate contemporary climate change?" is a critical question. Climate acts as a major constraint on the niche, yet there are many indirect risk factors with global change aside from climate effects (Alexander et al. 2015). Thermal extremes, and how species respond to them at ecological and evolutionary timescales, are important aspects of species' responses to climate change (Khaliq et al. 2014, Sunday et al. 2011). When the limits of the fundamental niche are surpassed (the lowest or the highest temperature tolerance), a shift or an expansion in the niche breadth may occur (Bakkenes et al. 2002). Nevertheless, the vulnerability of cold-adapted taxa to increased warming may be inflated (Araújo et al. 2013).

How niche breadth is partitioned (Section 2.3) and whether common and rare taxa differ in their niche breadth, and thus their endangerment under global change, are critical questions (Colles et al. 2009). There are concerns and signals of global decline of specialist species (Clavel et al. 2011). However, there is a paucity of experiments comparing rare and common taxa for their environmental and ecological tolerances. To our knowledge, no study has experimentally tested rare and common species for comparative performance in field conditions, although a handful of comparisons have been made in laboratory settings (e.g., Kellermann et al. 2009, Sheth & Angert 2014). Using experimental approaches, especially in the field, as well as genetically informed (Ikeda et al. 2017) and ecologically informed (Preston et al. 2008) niche modeling, we can greatly improve our assessments of species tolerances, responses, risk, and conservation under global change.

SUMMARY POINTS

1. Niche breadth is a fundamental concept for understanding adaptation, speciation, range shifts, and ecological and evolutionary response to climate change.
2. Niche breadth is multifaceted, and the study of its evolution is likewise diverse, covering many different subfields of evolutionary ecology. Niche breadth encompasses myriad scales, definitions, and applications.
3. Environmental and ecological contexts of niche evolution can affect both breadth and how niche breadth is distributed across scales.
4. Trade-offs in the evolution of niche breadth are not ubiquitous in nature, and thus they should not necessarily be assumed in models of niche breadth evolution. In this vein, conditional neutrality may be a stronger driver of niche breadth evolution than antagonistic pleiotropy.
5. Niche breadth does not appear to evolve in a unidirectional manner, and specialization is not necessarily an evolutionary dead end. This research area has benefitted greatly from the rapid accumulation of large phylogenies over the last decade.
6. Beyond experimental evolution experiments with microorganisms, transplant studies and (intentional or unintentional) species introductions might provide the best opportunities to study the process of niche breadth evolution. Such studies have already demonstrated that niche breadth can expand rapidly via adaptive evolution.
7. Niche breadth evolution could affect how species respond to climate change, habitat disturbance and other environmental stressors.

FUTURE ISSUES

1. How is niche breadth partitioned across the biological hierarchy (populations, species, genera, etc.)? Related to this, the development of models, and accompanying empirical tests, to understand how individual-, population-, and species-level niche breadths respond to environmental extremes is needed. Environmental extremes are likely to increase with climate change and might be more important than changes in means.
2. Is niche breadth actually important to rates of adaptive evolution and, along a similar vein, do rare species actually have narrower niches than common species? These questions are important for understanding extinction risk under global change and whether rare species might face a double jeopardy of rarity and vulnerability. Alternatively, if specialists can adapt more quickly than generalists, we might see alternative evolutionary strategies for coping with environmental change (i.e., specialists adapt, generalists cope).
3. Many earlier models assumed performance breadth trade-offs, which may not be common or could be masked by unmeasured multidimensional trade-offs. If conditional neutrality is a more important driver of niche breadth evolution, new models need to be developed.
4. Are there cross-scale or cross-axis trade-offs in niche breadth evolution, and to what extent is the fundamental niche breadth at different scales linked or decoupled? There are tests of the latter using the realized niche but few examples for axes of the fundamental niche.
5. More studies measuring evolution of the fundamental niche breadth in natural populations (i.e., to complement and corroborate microcosm studies), and at multiple ecological scales simultaneously so that trade-offs or parallel changes across scales can be detected, are needed.
6. Understanding the genetic architecture of niche breadth is of particular importance. What are the genomic differences between closely related taxa having wide and narrow niche breadths? To what extent is specialization or niche expansion driven by a lack of genetic variation?

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank Sally Otto and Dolph Schluter for discussions and Kinsey Brock, Kelly Carscadden, Doug Futuyma, Seema Sheth, and Michael Whitlock for comments that improved the manuscript.

Modeled and highlighted tension between diversification and niche breadth evolution.

LITERATURE CITED

Ackermann M, Doebeli M. 2004. Evolution of niche width and adaptive diversification. *Evolution* 58(12):2599–612

Alexander JM, Diez JM, Levine JM. 2015. Novel competitors shape species' responses to climate change. *Nature* 525(7570):515–18

Anacker BL, Strauss SY. 2014. The geography and ecology of plant speciation: range overlap and niche divergence in sister species. *Proc. R. Soc. B.* 281(1778):20132980

Anderson JT, Lee C-R, Rushworth CA, Colautti RI, Mitchell-Olds T. 2013. Genetic trade-offs and conditional neutrality contribute to local adaptation. *Mol. Ecol.* 22(3):699–708

Anderson JT, Perera N, Chowdhury B, Mitchell-Olds T. 2015. Microgeographic patterns of genetic divergence and adaptation across environmental gradients in *Boechera stricta* (Brassicaceae). *Am. Nat.* 186(Suppl. 1):S60–73

Angert AL, Sheth SN, Paul JR. 2011. Incorporating population variation in thermal niche properties into geographic range shift predictions. *Integr. Comp. Biol.* 51:733–50

Angilletta MJ Jr., Niewiarowski PH, Navas CA. 2002. The evolution of thermal physiology in ectotherms. *J. Therm. Biol.* 27(4):249–68

Araújo MB, Ferri-Yáñez F, Bozinovic F, Marquet PA, Valladares F, Chown SL. 2013. Heat freezes niche evolution. *Ecol. Lett.* 16(9):1206–19

Atkins KE, Travis JMJ. 2010. Local adaptation and the evolution of species' ranges under climate change. *J. Theor. Biol.* 266(3):449–57

Bakkenes M, Alkemade JRM, Ihle F, Leemans R, Latour JB. 2002. Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Glob. Change Biol.* 8(4):390–407

Barrett SCH, Hough J. 2013. Sexual dimorphism in flowering plants. *J. Exp. Bot.* 64(1):67–82

Bennett AF, Lenski RE. 2007. An experimental test of evolutionary trade-offs during temperature adaptation. *PNAS* 104(Suppl. 1):8649–54

Berner D, Salzburger W. 2015. The genomics of organismal diversification illuminated by adaptive radiations. *Trends Genet.* 31(9):491–99

Blonder B, Lamanna C, Violle C, Enquist BJ. 2014. The *n*-dimensional hypervolume. *Glob. Ecol. Biogeogr.* 23(5):595–609

Blows MW, Hoffmann AA. 2005. A reassessment of genetic limits to evolutionary change. *Ecology* 86(6):1371–84

Blüthgen N, Menzel F, Blüthgen N. 2006. Measuring specialization in species interaction networks. *BMC Ecol.* 6:9

Bolnick DI. 2001. Intraspecific competition favours niche width expansion in *Drosophila melanogaster*. *Nature* 410(6827):463–66

Bolnick DI, Ingram T, Stutz WE, Snowberg LK, Lau OL, Paull JS. 2010. Ecological release from interspecifc competition leads to decoupled changes in population and individual niche width. *Proc. R. Soc. B* 277:1789–97

Bolnick DI, Svanback R, Araujo MS, Persson L. 2007. Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. *PNAS* 104(24):10075–79

Bolnick DI, Svanback R, Fordyce JA, Yang LH, Davis JM, et al. 2003. The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.* 161(1):1–28

Bonetti MF, Wiens JJ. 2014. Evolution of climatic niche specialization: a phylogenetic analysis in amphibians. *Proc. R. Soc. B* 281(1795):20133229

Bono LM, Smith LB, Pfennig DW, Burch CL. 2017. The emergence of performance trade-offs during local adaptation: insights from experimental evolution. *Mol. Ecol.* 26:1720–33. https://doi.org/10.1111/mec.13979

Botta-Dukát Z. 2012. Co-occurrence-based measure of species' habitat specialization: robust, unbiased estimation in saturated communities. *J. Veg. Sci.* 23(2):201–7

Brawand D, Wagner CE, Li YI, Malinsky M, Keller I, et al. 2014. The genomic substrate for adaptive radiation in African cichlid fish. *Nature* 513(7518):375–81

Brett JR. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *Am. Zool.* 11(1):99–113

Brown JH. 1984. On the relationship between abundance and distribution of species. *Am. Nat.* 124(2):255–79

Buckley LB, Huey RB. 2016. How extreme temperatures impact organisms and the evolution of their thermal tolerance. *Integr. Comp. Biol.* 56(1):98–109

Reviewed the evidence for individual specialization, suggesting that it is a widespread phenomenon.

Review of experimental evolution studies, addressing questions of antagonistic pleiotropy versus conditional neutrality.

Case TJ. 1981. Niche packing and coevolution in competition communities. *PNAS* 78(8):5021–25
Chan W-P, Chen I-C, Colwell RK, Liu W-C, Huang C, Shen S-F. 2016. Seasonal and daily climate variation have opposite effects on species elevational range size. *Science* 351(6280):1437–39
Clavel J, Julliard R, Devictor V. 2011. Worldwide decline of specialist species: toward a global functional homogenization? *Front. Ecol. Environ.* 9(4):222–28
Cody ML. 1974. *Competition and the Structure of Bird Communities*. Princeton, NJ: Princeton Univ. Press
Colles A, Liow LH, Prinzing A. 2009. Are specialists at risk under environmental change? Neoecological, paleoecological and phylogenetic approaches. *Ecol. Lett.* 12(8):849–63
Colwell RK. 1986. Population structure and sexual selection for host fidelity in the speciation of hummingbird flower mites. In *Evolutionary Processes and Theory*, ed. S Karlin, E Nevo, pp. 475–95. New York: Academic
Colwell RK, Futuyma DJ. 1971. On the measurement of niche breadth and overlap. *Ecology* 52(4):567–76
Conner JK. 2012. Quantitative genetic approaches to evolutionary constraint: how useful? *Evolution* 66(11):3313–20
Cooper VS, Lenski RE. 2000. The population genetics of ecological specialization in evolving *Escherichia coli* populations. *Nature* 407(6805):736–39
Costa GC, Vitt LJ, Pianka ER, Mesquita DO, Colli GR. 2008. Optimal foraging constrains macroecological patterns: body size and dietary niche breadth in lizards. *Glob. Ecol. Biogeogr.* 17(5):670–77
Coyne JA, Orr HA. 2004. *Speciation*. Sunderland, MA: Sinauer
Curtin SJ, Tiffin P, Guhlin J, Trujillo DI, Burghardt LT, et al. 2017. Validating genome-wide association candidates controlling quantitative variation in nodulation. *Plant Physiol.* 173(2):921–31
Dall SRX, Cuthill IC. 1997. The information costs of generalism. *Oikos* 80(1):197–202
Darwin C. 1859. *On the Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life*. London: J. Murray
Day EH, Hua X, Bromham L. 2016. Is specialization an evolutionary dead end? Testing for differences in speciation, extinction and trait transition rates across diverse phylogenies of specialists and generalists. *J. Evol. Biol.* 29(6):1257–67
de Vries RP, Riley R, Wiebenga A, Aguilar-Osorio G, Amillis S, et al. 2017. Comparative genomics reveals high biological diversity and specific adaptations in the industrially and medically important fungal genus *Aspergillus*. *Genome Biol.* 18:28. **https://doi.org/10.1186/s13059-017-1151-0**
Denny MW, Dowd WW. 2012. Biophysics, environmental stochasticity, and the evolution of thermal safety margins in intertidal limpets. *J. Exp. Biol.* 215(6):934–47

Illustrates metrics of ecological specialization.

Devictor V, Clavel J, Julliard R, Lavergne S, Mouillot D, et al. 2010. Defining and measuring ecological specialization. *J. Appl. Ecol.* 47(1):15–25
Dieckmann U, Doebeli M. 1999. On the origin of species by sympatric speciation. *Nature* 400:354–57
Dolédec S, Chessel D, Gimaret-Carpentier C. 2000. Niche separation in community analysis: a new method. *Ecology* 81(10):2914–27
Donoghue MJ, Edwards EJ. 2014. Biome shifts and niche evolution in plants. *Annu. Rev. Ecol. Evol. Syst.* 45(1):547–72
Ducatez S, Tingley R, Shine R. 2014. Using species co-occurrence patterns to quantify relative habitat breadth in terrestrial vertebrates. *Ecosphere* 5(12):1–12
Dyer LA, Singer MS, Lill JT, Stireman JO, Gentry GL, et al. 2007. Host specificity of Lepidoptera in tropical and temperate forests. *Nature* 448(7154):696–99
Elton CS. 1927. *Animal Ecology*. London: Sidgwick and Jackson
Emery NC, Forrestel EJ, Jui G, Park MS, Baldwin BG, Ackerly DD. 2012. Niche evolution across spatial scales: climate and habitat specialization in California *Lasthenia* (Asteraceae). *Ecology* 93(8s):S151–66
Etterson JR. 2004. Evolutionary potential of *Chamaecrista fasciculata* in relation to climate change. I. Clinal patterns of selection along an environmental gradient in the Great Plains. *Evolution* 58(7):1446–58
Feinsinger P, Spears EE, Poole RW. 1981. A simple measure of niche breadth. *Ecology* 62(1):27–32
Fisher-Reid MC, Kozak KH, Wiens JJ. 2012. How is the rate of climatic-niche evolution related to climatic-niche breadth? *Evolution* 66(12):3836–51
Forister ML, Dyer LA, Singer MS, Stireman JO, Lill JT. 2012. Revisiting the evolution of ecological specialization, with emphasis on insect-plant interactions. *Ecology* 93(5):981–91

Foust CM, Preite V, Schrey AW, Alvarez M, Robertson MH, et al. 2016. Genetic and epigenetic differences associated with environmental gradients in replicate populations of two salt marsh perennials. *Mol. Ecol.* 25(8):1639–52

Fridley JD, Vandermast DB, Kuppinger DM, Manthey M, Peet RK. 2007. Co-occurrence based assessment of habitat generalists and specialists: a new approach for the measurement of niche width. *J. Ecol.* 95(4):707–22

Fry JD. 1996. The evolution of host specialization: Are trade-offs overrated? *Am. Nat.* 148:S84–107

Futuyma DJ. 2010. Evolutionary constraint and ecological consequences. *Evolution* 64(7):1865–84

Futuyma DJ, Moreno G. 1988. The evolution of ecological specialization. *Annu. Rev. Ecol. Syst.* 19:207–33

Provides a comprehensive summary of historical hypotheses on the evolution of specialization and generalization.

Gardiner A, Barker D, Butlin RK, Jordan WC, Ritchie MG. 2008. *Drosophila* chemoreceptor gene evolution: selection, specialization and genome size. *Mol. Ecol.* 17(7):1648–57

Gilchrist GW. 1995. Specialists and generalists in changing environments. I. Fitness landscapes of thermal sensitivity. *Am. Nat.* 146(2):252–70

Gómez-Rodríguez C, Baselga A, Wiens JJ. 2015. Is diversification rate related to climatic niche width? *Glob. Ecol. Biogeogr.* 24(4):383–95

Griffith T, Sultan SE. 2012. Field-based insights to the evolution of specialization: plasticity and fitness across habitats in a specialist/generalist species pair. *Ecol. Evol.* 2(4):778–91

Grinnell J. 1917. The niche-relationships of the California Thrasher. *Auk* 34(4):427–33

Grossenbacher DL, Veloz SD, Sexton JP. 2014. Niche and range size patterns suggest that speciation begins in small, ecologically diverged populations in North American monkeyflowers (*Mimulus* spp.). *Evolution* 68:1270–80

Guisan A, Petitpierre B, Broennimann O, Daehler C, Kueffer C. 2014. Unifying niche shift studies: insights from biological invasions. *Trends Ecol. Evol.* 29(5):260–69

Proposed a framework for niche change with invasion, incorporating ideas of population- versus species-level niche dynamics.

Guisan A, Thuiller W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* 8(9):993–1009

Hanski I, Kouki J, Halkka A. 1993. Three explanations of the positive relationship between distribution and abundance of species. In *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, ed. RE Ricklefs, D Schluter, pp. 108–16. Chicago: Univ. Chicago Press

Hardy NB, Otto SP. 2014. Specialization and generalization in the diversification of phytophagous insects: tests of the musical chairs and oscillation hypotheses. *Proc. R. Soc. B* 281(1795):20132960

Hargreaves AL, Samis KE, Eckert CG. 2014. Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. *Am. Nat.* 183(2):157–73

Heino J. 2005. Positive relationship between regional distribution and local abundance in stream insects: a consequence of niche breadth or niche position? *Ecography* 28(3):345–54

Herman JJ, Sultan SE. 2016. DNA methylation mediates genetic variation for adaptive transgenerational plasticity. *Proc. R. Soc. B* 283(1838):20160988

Herrera CM, Pozo MI, Bazaga P. 2012. Jack of all nectars, master of most: DNA methylation and the epigenetic basis of niche width in a flower-living yeast. *Mol. Ecol.* 21(11):2602–16

Hill MP, Chown SL, Hoffmann AA. 2013. A predicted niche shift corresponds with increased thermal resistance in an invasive mite, *Halotydeus destructor*. *Glob. Ecol. Biogeogr.* 22(8):942–51

Hoffmann AA. 2010. Physiological climatic limits in *Drosophila*: patterns and implications. *J. Exp. Biol.* 213(6):870–80

Hoffmann AA, Anderson A, Hallas R. 2002. Opposing clines for high and low temperature resistance in *Drosophila melanogaster*. *Ecol. Lett.* 5(5):614–18

Hoffmann AA, Chown SL, Clusella-Trullas S. 2013. Upper thermal limits in terrestrial ectotherms: How constrained are they? *Funct. Ecol.* 27(4):934–49

Hoffmann AA, Parsons PA. 1993. Selection for adult desiccation resistance in *Drosophila melanogaster*: fitness components, larval resistance and stress correlations. *Biol. J. Linn. Soc.* 48(1):43–54

Holt RD. 1996. Adaptive evolution in source-sink environments: direct and indirect effects of density-dependence on niche evolution. *Oikos* 75(2):182–92

Holt RD, Gaines MS. 1992. Analysis of adaptation in heterogeneous landscapes: implications for the evolution of fundamental niches. *Evol. Ecol.* 6(5):433–47

Houle D. 1992. Comparing evolvability and variability of quantitative traits. *Genetics* 130(1):195–204
Huey RB, Hertz PE. 1984. Is a Jack-of-all-temperatures a master of none? *Evolution* 38(2):441–44
Huey RB, Kingsolver JG. 1993. Evolution of resistance to high temperature in ectotherms. *Am. Nat.* 142:S21–46
Huey RB, Stevenson RD. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Am. Zool.* 19(1):357–66
Hurlbert SH. 1978. The measurement of niche overlap and some relatives. *Ecology* 59(1):67–77
Hutchinson GE. 1957. Concluding remarks. *Cold Spring Harb. Symp. Quant. Biol.* 22:415–427
Ikeda DH, Max TL, Allan GJ, Lau MK, Shuster SM, Whitham TG. 2017. Genetically informed ecological niche models improve climate change predictions. *Glob. Change Biol.* 23(1):164–76
Janz N, Nylin S. 2008. The oscillation hypothesis of host-plant range and speciation. In *Specialization, Speciation and Radiation: The Evolutionary Biology of Herbivorous Insects*, ed. KJ Tilmon, pp. 203–15. Berkeley: Univ. California Press

Review of experimental evolution studies addressing the effect of environmental variation on niche breadth.

Kassen R. 2002. The experimental evolution of specialists, generalists, and the maintenance of diversity. *J. Evol. Biol.* 15(2):173–90
Kawecki TJ. 1994. Accumulation of deleterious mutations and the evolutionary cost of being a generalist. *Am. Nat.* 144(5):833–38
Kawecki TJ. 2000. Adaptation to marginal habitats: contrasting influence of the dispersal rate on the fate of alleles with small and large effects. *Proc. R. Soc. B* 267(1450):1315–20
Kawecki TJ, Barton NH, Fry JD. 1997. Mutational collapse of fitness in marginal habitats and the evolution of ecological specialisation. *J. Evol. Biol.* 10(3):407–29
Kellermann V, van Heerwaarden B, Sgro CM, Hoffmann AA. 2009. Fundamental evolutionary limits in ecological traits drive *Drosophila* species distributions. *Science* 325:1244–46
Ketola T, Mikonranta L, Zhang J, Saarinen K, Örmälä A-M, et al. 2013. Fluctuating temperature leads to evolution of thermal generalism and preadaptation to novel environments. *Evolution* 67(10):2936–44
Khaliq I, Hof C, Prinzinger R, Böhning-Gaese K, Pfenninger M. 2014. Global variation in thermal tolerances and vulnerability of endotherms to climate change. *Proc. R. Soc. B* 281(1789):20141097
Kleynhans EJ, Otto SP, Reich PB, Vellend M. 2016. Adaptation to elevated CO_2 in different biodiversity contexts. *Nat. Commun.* 7:12358
Kozak KH, Wiens JJ. 2010. Accelerated rates of climatic-niche evolution underlie rapid species diversification. *Ecol. Lett.* 13(11):1378–89

Shows the power of integrating phenotypic assays with functional genomics to detect potential cross-axis trade-offs.

Latta LC, Weider LJ, Colbourne JK, Pfrender ME. 2012. The evolution of salinity tolerance in *Daphnia*: a functional genomics approach. *Ecol. Lett.* 15(8):794–802
Lavergne S, Evans MEK, Burfield IJ, Jiguet F, Thuiller W. 2013. Are species' responses to global change predicted by past niche evolution? *Philos. Trans. R. Soc. B* 368(1610):20120091
Lee-Yaw JA, Kharouba HM, Bontrager M, Mahony C, Csergő AM, et al. 2016. A synthesis of transplant experiments and ecological niche models suggests that range limits are often niche limits. *Ecol. Lett.* 19(6):710–22
Levins R. 1962. Theory of fitness in a heterogeneous environment. I. The fitness set and adaptive function. *Am. Nat.* 96(891):361–73
Levins R. 1965. Theory of fitness in a heterogeneous environment. V. Optimal genetic systems. *Genetics* 52(5):891–904
Levins R. 1968. *Evolution in Changing Environments*. Princeton, NJ: Princeton Univ. Press
Levis NA, Pfennig DW. 2016. Evaluating 'plasticity-first' evolution in nature: key criteria and empirical approaches. *Trends Ecol. Evol.* 31(7):563–74
Lin L-H, Wiens JJ. 2016. Comparing macroecological patterns across continents: evolution of climatic niche breadth in varanid lizards. *Ecography*. **https://doi.org/10.1111/ecog.02343**
Litsios G, Kostikova A, Salamin N. 2014. Host specialist clownfishes are environmental niche generalists. *Proc. R. Soc. B* 281(1795):20133220
Luna B, Moreno JM. 2010. Range-size, local abundance and germination niche-breadth in Mediterranean plants of two life-forms. *Plant Ecol.* 210(1):85–95
Lynch M, Gabriel W. 1987. Environmental tolerance. *Am. Nat.* 129(2):283–303

MacArthur RH. 1972. *Geographical Ecology: Patterns in the Distribution of Species*. Princeton, NJ: Princeton Univ. Press
Martin RA, Pfennig DW. 2009. Disruptive selection in natural populations: the roles of ecological specialization and resource competition. *Am. Nat.* 174(2):268–81
Mayr E. 1954. Change of genetic environment and evolution. In *Evolution as a Process*, ed. J Huxley, AC Hardy, EB Ford, pp. 157–80. London: Allen and Unwin
Moran EV, Alexander JM. 2014. Evolutionary responses to global change: lessons from invasive species. *Ecol. Lett.* 17(5):637–49
Muchhala N, Brown Z, Armbruster WS, Potts MD. 2010. Competition drives specialization in pollination systems through costs to male fitness. *Am. Nat.* 176(6):732–43
Nakazawa T. 2015. Ontogenetic niche shifts matter in community ecology: a review and future perspectives. *Popul. Ecol.* 57(2):347–54
Nonaka E, Svanbäck R, Thibert-Plante X, Englund G, Brännström Å. 2015. Mechanisms by which phenotypic plasticity affects adaptive divergence and ecological speciation. *Am. Nat.* 186(5):E126–43
Nyman T. 2010. To speciate, or not to speciate? Resource heterogeneity, the subjectivity of similarity, and the macroevolutionary consequences of niche-width shifts in plant-feeding insects. *Biol. Rev.* 85(2):393–411
Ojeda Alayon DI, Tsui CKM, Feau N, Capron A, Dhillon B, et al. 2017. Genetic and genomic evidence of niche partitioning and adaptive radiation in mountain pine beetle fungal symbionts. *Mol. Ecol.* 26(7):2077–91
Olsson K, Stenroth P, Nyström P, Granéli W. 2009. Invasions and niche width: Does niche width of an introduced crayfish differ from a native crayfish? *Freshw. Biol.* 54(8):1731–40
Petitpierre B, Kueffer C, Broennimann O, Randin C, Daehler C, Guisan A. 2012. Climatic niche shifts are rare among terrestrial plant invaders. *Science* 335(6074):1344–48
Pfennig KS, Kelly AL, Pierce AA. 2016. Hybridization as a facilitator of species range expansion. *Proc. R. Soc. B.* 283(1839):20161329
Poisot T, Bever JD, Nemri A, Thrall PH, Hochberg ME. 2011. A conceptual framework for the evolution of ecological specialisation. *Ecol. Lett.* 14(9):841–51
Preston KL, Rotenberry JT, Redak RA, Allen MF. 2008. Habitat shifts of endangered species under altered climate conditions: importance of biotic interactions. *Glob. Change Biol.* 14(11):2501–15
Proulx SR. 1999. Matings systems and the evolution of niche breadth. *Am. Nat.* 154(1):89–98
Qiao H, Saupe EE, Soberón J, Peterson AT, Myers CE. 2016. Impacts of niche breadth and dispersal ability on macroevolutionary patterns. *Am. Nat.* 188(2):149–62
Ravigné V, Dieckmann U, Olivieri I. 2009. Live where you thrive: Joint evolution of habitat choice and local adaptation facilitates specialization and promotes diversity. *Am. Nat.* 174(4):E141–69
Remold S. 2012. Understanding specialism when the jack of all trades can be the master of all. *Proc. R. Soc. B* 279(1749):4861–69
Rey O, Danchin E, Mirouze M, Loot C, Blanchet S. 2016. Adaptation to global change: a transposable element-epigenetics perspective. *Trends Ecol. Evol.* 31(7):514–26
Richardson JL, Urban MC, Bolnick DI, Skelly DK. 2014. Microgeographic adaptation and the spatial scale of evolution. *Trends Ecol. Evol.* 29(3):165–76
Rieseberg L, Raymond O, Rosenthal D, Lai Z, Livingstone K, et al. 2003. Major ecological transitions in wild sunflowers facilitated by hybridization. *Science* 301(5637):1211–16
Rockman MV. 2012. The QTN program and the alleles that matter for evolution: All that's gold does not glitter. *Evolution* 66(1):1–17
Rolland J, Salamin N. 2016. Niche width impacts vertebrate diversification. *Glob. Ecol. Biogeogr.* 25(10):1252–63
Roughgarden J. 1972. Evolution of niche width. *Am. Nat.* 106(952):683–718

Provided a quantitative framework for thinking about the structure of the niche across different scales.

Rueffler C, Van Dooren TJM, Metz JAJ. 2007. The interplay between behavior and morphology in the evolutionary dynamics of resource specialization. *Am. Nat.* 169(2):E34–52
Sargent RD, Otto SP. 2006. The role of local species abundance in the evolution of pollinator attraction in flowering plants. *Am. Nat.* 167(1):67–80
Satterwhite RS, Cooper TF. 2015. Constraints on adaptation of *Escherichia coli* to mixed-resource environments increase over time. *Evolution* 69(8):2067–78

Schluter D. 2000. *The Ecology of Adaptive Radiation*. Oxford, UK: Oxford Univ. Press
Schluter D. 2009. Evidence for ecological speciation and its alternative. *Science* 323(5915):737–41
Sexton JP, McIntyre PJ, Angert AL, Rice KJ. 2009. Evolution and ecology of species range limits. *Annu. Rev. Ecol. Evol. Syst.* 40:415–36
Sheth SN, Angert AL. 2014. The evolution of environmental tolerance and range size: a comparison of geographically restricted and widespread *Mimulus*. *Evolution* 68(10):2917–31
Slatyer RA, Hirst M, Sexton JP. 2013. Niche breadth predicts geographical range size: a general ecological pattern. *Ecol. Lett.* 16(8):1104–14
Smith TB, Skúlason S. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. *Annu. Rev. Ecol. Syst.* 27(1):111–33
Sultan S, Spencer H. 2002. Metapopulation structure favors plasticity over local adaptation. *Am. Nat.* 160(2):271–83
Sunday JM, Bates AE, Dulvy NK. 2011. Global analysis of thermal tolerance and latitude in ectotherms. *Proc. R. Soc. B* 278(1713):1823–30
Svanbäck R, Bolnick DI. 2005. Intraspecific competition affects the strength of individual specialization: an optimal diet theory method. *Evol. Ecol. Res.* 7(7):993–1012
Svanbäck R, Bolnick DI. 2007. Intraspecific competition drives increased resource use diversity within a natural population. *Proc. R. Soc. B* 274(1611):839–44
Svanbäck R, Persson L. 2004. Individual diet specialization, niche width and population dynamics: implications for trophic polymorphisms. *J. Anim. Ecol.* 73(5):973–82
Svenning J-C, Skov F. 2004. Limited filling of the potential range in European tree species. *Ecol. Lett.* 7(7):565–73
Taper ML, Chase TJ. 1985. Quantitative genetic models for the coevolution of character displacement. *Ecology* 66(2):355–71
Ter Braak CJF. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67(5):1167–79
Ter Braak CJF. 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. In *Theory and Models in Vegetation Science: Proceedings of Symposium, Uppsala, July 8–13, 1985*, ed. IC Prentice, E van der Maarel, pp. 69–77. Dordrecht, Neth.: Springer
Thuiller W, Brotons L, Araújo MB, Lavorel S. 2004. Effects of restricting environmental range of data to project current and future species distributions. *Ecography* 27(2):165–72
Urbanski J, Mogi M, O'Donnell D, DeCotiis M, Toma T, Armbruster P. 2012. Rapid adaptive evolution of photoperiodic response during invasion and range expansion across a climatic gradient. *Am. Nat.* 179(4):490–500
Van Valen L. 1965. Morphological variation and width of ecological niche. *Am. Nat.* 99(908):377–90
Vrba ES. 1987. Ecology in relation to speciation rates: some case histories of Miocene-Recent mammal clades. *Evol. Ecol.* 1(4):283–300
Wasof S, Lenoir J, Aarrestad PA, Alsos IG, Armbruster WS, et al. 2015. Disjunct populations of European vascular plant species keep the same climatic niches. *Glob. Ecol. Biogeogr.* 24(12):1401–12
West-Eberhard MJ. 2003. *Developmental Plasticity and Evolution*. Oxford, UK: Oxford Univ. Press

One of the first models to specifically consider how niche breadth might evolve in the absence of trade-offs.

Whitlock MC. 1996. The red queen beats the jack-of-all-trades: the limitations on the evolution of phenotypic plasticity and niche breadth. *Am. Nat.* 148:S65–77
Wiens JJ, Kozak KH, Silva N. 2013. Diversity and niche evolution along aridity gradients in North American lizards (Phrynosomatidae). *Evolution* 67(6):1715–28
Willett CS. 2010. Potential fitness trade-offs for thermal tolerance in the intertidal copepod *Tigriopus californicus*. *Evolution* 64(9):2521–34
Wilson DS, Yoshimura J. 1994. On the coexistence of specialists and generalists. *Am. Nat.* 144(4):692–707
Yassin A, Debat V, Bastide H, Gidaszewski N, David JR, Pool JE. 2016. Recurrent specialization on a toxic fruit in an island *Drosophila* population. *PNAS* 113(17):4771–76
Yona AH, Frumkin I, Pilpel Y. 2015. A relay race on the evolutionary adaptation spectrum. *Cell* 163(3):549–59