Opinion

Niche syndromes, species extinction risks, and management under climate change

Dov F. Sax[1], **Regan Early**[2,3], **and Jesse Bellemare**[4]

[1] Department of Ecology and Evolutionary Biology, Brown University, Box G-W, 80 Waterman Street, Providence, RI 02912, USA
[2] Cátedra Rui Nabeiro - Biodiversidade, Universidade de Évora, 7000-890 Évora, Portugal
[3] Museo Nacional de Ciencias Naturales, Calle José Gutiérrez Abascal, 2 28006 Madrid, Spain
[4] Department of Biological Sciences, Smith College, Northampton, MA 01063, USA

The current distributions of species are often assumed to correspond with the total set of environmental conditions under which species can persist. When this assumption is incorrect, extinction risk estimated from species distribution models can be misleading. The degree to which species can tolerate or even thrive under conditions found beyond their current distributions alters extinction risks, time lags in realizing those risks, and the usefulness of alternative management strategies. To inform these issues, we propose a conceptual framework within which empirical data could be used to generate hypotheses regarding the realized, fundamental, and 'tolerance' niche of species. Although these niche components have rarely been characterized over geographic scales, we suggest that this could be done for many plant species by comparing native, naturalized, and horticultural distributions.

Niche concepts and species distribution models

The 'niche' concept has reemerged over the past decade as a major focus of consideration in the ecological, conservation, and global change literature [1–3]. This interest has largely been driven by the widespread application of species distribution models (SDMs) to inform conservation and management challenges associated with global change. Indeed, given the relative ease of obtaining distribution data for large numbers of species, SDMs have been at the core of most estimates of extinction risk associated with climate change (e.g., [4,5]) and frequently used in 'climate-matching' approaches for anticipating invasion risks [6,7]. SDMs have many well-described limitations [8–10], but perhaps the most substantial occurs when the implicit assumption is made that species current distributions are in equilibrium with the environment; that is, that the conditions that occur across the areas where a species is presently found represent the full extent of conditions under which that species can maintain populations. Although few would expect this to be universally true, the possibility that this assumption might often be invalid in substantial ways has been increasingly suggested in macroecological and biogeographical studies [11–16]. A better understanding of when and how this key assumption is likely to be violated can be informed by consideration of the niche and its key components.

There have been varying uses of the niche concept in the ecological literature, but the conceptualization we build from here is that of Hutchinson [17]. He described a species niche as having two primary components: the realized and fundamental niche (see Glossary). The fundamental niche was envisioned to encompass the full set of physical conditions and resources required to enable a species to persist indefinitely, whereas the realized niche encompassed that subset of conditions in which competition with other species did not preclude indefinite persistence. Since

Glossary

Fundamental distribution: the geographical space that could be occupied as defined by the fundamental niche; some portions of this space could be identified by the presence of self-sustaining, naturalized populations.

Fundamental niche: the set of physical conditions and resources that enable a species to maintain self-sustaining populations, but which may not be fully occupied due to the presence of antagonistic species interactions, the absence of required positive species interactions, or dispersal limitation.

Managed relocation (aka assisted colonization or assisted migration): the intentional act of moving species, populations, or genotypes to a location outside their known historical distribution for the purpose of maintaining biological diversity or ecosystem functioning as an adaptation strategy for climate change.

Niche syndrome: a qualitative categorization of specific size and placement relations among the realized, fundamental, and tolerance components of the niche.

Realized distribution: the geographical space occupied by a species within its native range; the conditions occurring within that geographical space are normally equated with the realized niche; however, following changes in environmental conditions (e.g., climate change) it is possible for the realized distribution of a species (i.e., the places where it is located geographically) to have conditions that no longer match the realized niche.

Realized niche: the set of physical conditions, resources, and biotic interactions that correspond with the conditions in which species maintain self-sustaining populations.

Tolerance distribution: the geographical space that could be occupied as defined by the tolerance niche; some portions of this space could be hypothesized to occur based on the presence of individuals, for example, planted through horticulture, that survive ambient conditions but do not establish self-sustaining populations.

Tolerance niche: the set of physical conditions and resources that enable individuals to live and grow, but preclude a species from establishing self-sustaining populations; just as the fundamental niche is unlikely to be entirely occupied by self-sustaining populations due to dispersal limitations, the presence of antagonistic species interactions, or the absence of required positive species interactions, these same factors will exclude individuals from living and growing in all parts of the tolerance niche.

Corresponding author: Sax, D.F. (dov.sax@gmail.com)

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Hutchinson [17], the distinction between the realized and fundamental niche has been expanded to include limitations imposed by not only competitive interactions, but also by any antagonistic interactions among species, by the absence of needed beneficial interactions among species, and by dispersal limitation [2]. Ultimately, both the realized and fundamental niche are simplified abstractions that cannot fully represent the complex dynamics associated with species distributions [18,19], but these abstractions are useful because they provide a simple conceptual framework that is highly relevant to considering species responses to global change. One particular advantage of these niche concepts is that they can be extended to consider the manifestation of niche space in geographical space; that is, to consider the realized and fundamental distributions of species.

The nature and magnitude of differences between realized and fundamental distributions have substantial implications for how we should interpret findings from SDM approaches. When differences between realized and fundamental niche components are small, the conditions that occur within the realized distribution (on which SDMs are based) will closely approximate the full range of conditions in which a species is able to persist over the long term. However, when such differences are large, SDMs based on realized distributions will substantially underestimate species tolerances and potentially overestimate risks of extirpation and extinction under global change [20]. Available evidence suggests that mismatches between the realized and fundamental distribution commonly occur [13,14,20]. For instance, many naturalized species occupy climatic conditions that exceed the conditions realized in their native distributions [21–23], but see [24]. Likewise, despite significant changes in climate since the late Pleistocene, some species have survived *in situ*, without shifting their geographical distributions [25–27]. Although some invasions and survival *in situ* beyond conditions in the former realized niche might be the result of evolutionary change (e.g., [28]), it is likely that some of these cases have occurred because formerly realized conditions represented only a subset of the fundamental niche. The latter case seems particularly likely for naturalizations by long-lived species, such as trees, where there has typically been limited time for evolutionary change in recently established populations.

The tolerance niche

The focus of both the realized and fundamental niche is on those conditions in which species can persist indefinitely [17]. Indeed, modern formulations of the niche are often defined strictly as those places where population birth rates equal or exceed death rates [18]. However, there is a marginal zone beyond the fundamental niche: areas in which individuals of a species can survive, even if they do not currently establish self-sustaining populations. Against the backdrop of rapid climate change, such areas might be of major importance in predicting range shifts and extinction risks, as well as planning conservation actions. Consequently, here we define the 'tolerance niche' as the set of physical conditions and resources that allow individuals to live and grow, but preclude a species from establishing self-sustaining populations. Just as the fundamental niche is unlikely to be entirely occupied by self-sustaining populations due to dispersal limitations, the presence of antagonistic species interactions, or the absence of required positive species interactions, these same factors will exclude individuals from living and growing in all parts of the tolerance niche. The tolerance niche of a species could include places where no reproduction occurs, or where reproduction and recruitment occur at insufficient rates to support population growth over the long term. This conceptualization of the tolerance niche shares similarities with some other niche concepts, but is distinctive in that it explicitly considers only those conditions that occur beyond the bounds of the fundamental niche (Box 1). Conditions that exist beyond the fundamental niche have previously been investigated relative to source–sink dynamics [29,30], adaptation [31], and range edges [32]. However, we believe that a formal extension of the niche concept is needed that considers the tolerance niche in concert with the realized and fundamental niche.

Characterizing the fundamental and tolerance niche of species could improve understanding of their responses to climate change. For example, Early and Sax [33] showed that the likelihood that amphibian species in the western USA will be able to shift their geographic distributions in response to climate change is strongly influenced by their

Box 1. The tolerance niche in relation to other niche concepts

Our conceptualization of the tolerance niche is characterized by conditions that enable survival of individuals, but preclude a species from having self-sustaining populations. Consequently, these are conditions explicitly defined as those that exist beyond the boundary of the fundamental niche. This conceptualization of the tolerance niche is different from the current sporadic usage in the literature of 'tolerance range' and 'tolerance niche' (e.g., [52,53]), and from Shelford's [54] conceptualization of 'toleration', which all pertain to the full range of conditions that a species can survive, including those conditions in which species have self-sustaining populations. Likewise, our conceptualization of the tolerance niche is distinct from the 'habitat niche', which is defined as 'the physical and chemical limits tolerated by the mature plant in nature' [55], and is also known as the 'adult niche' or 'adult-growth niche' [34], because these niche concepts include conditions in which populations are self sustaining. Finally, our conceptualization of the tolerance niche is distinct from the 'population persistence niche' [56], which considers those places where populations are self sustaining only if they are above some threshold density (i.e., such that Allee effects are alleviated), and different from the 'population niche' [57], which considers conditions where populations can be found, regardless of whether they are self sustaining.

Ultimately, the aim of the tolerance niche is to complement the modern conceptualization of the realized and fundamental niches in the context of global change. Its motivation, therefore, is not unlike that for the 'potential niche', which is defined as the intersection between the fundamental niche and the environmental conditions present in a time period of interest [58]. Furthermore, although the realized and fundamental niche concepts can be frustrating in their imprecision and simplified nature [19], they also provide a conceptual framework that continues to be widely used and modified (e.g., [59]). Indeed, we believe that it is the simplicity of these concepts and their usefulness as conceptual tools that have allowed these ideas to remain so influential. Nevertheless, in the context of rapid global change, we believe that there is a need for a broader consideration of conditions in which individuals of a species can survive; this information can help to improve forecasts of species range dynamics and inform conservation practice.

capacity to survive climatic conditions found outside their realized niches. This capacity is important because decadal variation in climate over the remainder of this century is expected to create conditions that are intermittently unsuitable for populations shifting to new locations. Species that cannot survive in newly colonized areas when conditions occasionally exceed those of the realized niche will be hindered in their response to the underlying directional changes in climate, because their range shifts may be knocked back repeatedly by unfavorable climatic oscillations. By contrast, species that can persist *in situ* under climatic conditions that temporarily limit population growth will be better able to geographically track changes in climate over time, that is, exhibiting the 'ecological ratchet' effect [34]. How such dynamics manifest will depend on dispersal ability, biotic interactions, and whether climatic oscillations exceed the fundamental and tolerance niches of species.

Characterizing the tolerance niche could inform the application of climate adaptation strategies, including *in situ* conservation efforts and managed relocation. Conservation efforts *in situ* typically attempt to reduce stressors other than climate change, for example, by removing invasive species [35], but could also involve efforts to reduce stressors that are indirectly associated with climate change, for example, by removing native competitors or predators that expand their distributions, as a consequence of climate change, into areas where species of concern are located [36]. The tolerance niche informs *in situ* conservation because such efforts will be more feasible when a target species can tolerate the physical conditions it experiences in a given location following changes in climate (i.e., the conditions at a site remain within the tolerance niche). In the case of managed relocation [37–39], the size and placement of the tolerance distribution could help to identify areas that are currently climatically suitable only for the survival of translocated individuals, but that are likely to support positive population growth in the future, as climate conditions transition from the tolerance to the fundamental or realized niche. Although likely controversial, such an approach might be crucial for slow-growing, long-lived species, such as trees, which might otherwise lag dangerously behind rapidly shifting climatic conditions. Consequently, characterizing the tolerance niche would inform the potential scope and scale of managed relocation.

Niche syndromes inform extinction risks and management options

The relations among the realized, fundamental, and tolerance components of the niche inform potential differences in species vulnerabilities to climate change. We define these relations as 'niche syndromes' and provide six generalized examples in Figure 1. We focus in these examples on dynamics at large geographical scales and on the simplified case of two pertinent climate variables, in which we primarily vary one of them (mean annual temperature). Although many other, more complex syndromes are conceivable, we describe these simplified cases to illustrate the utility of this approach. Furthermore, we show cases here in which there is a relatively strong initial correspondence between the size and relative placement of the realized, fundamental, and tolerance niches in environmental space and the size and relative placement of the realized, fundamental, and tolerance distributions in geographical space. In such a setting, if climate warms substantially and a species is unable to evolve *in situ* or shift its geographical range, then over time its realized distribution (although static in geographical space) will shift relative to its realized niche space, as depicted in each panel of Figure 1. In such cases, species with tightly nested niche components (Figure 1A), or those with realized and fundamental niches situated close to the edge of their tolerance niche relative to the directionality of climate change (Figure 1C), will be at risk of extinction following only modest changes in climate. To survive, such species will have to shift their geographic distributions or evolve *in situ* to keep pace with changing conditions. Species whose tolerance niches provide a buffer (Figure 1B) relative to the direction of climate change might experience a delay in how quickly a risk of extinction manifests, because previously established individuals might be capable of persisting for many years. Species that have a large fundamental niche relative to their realized niche (Figure 1D–F) will vary in their extinction risk depending on the relative position of these niche components, the specific mechanism responsible for differences between niche components, and the length of their life spans. For example, species whose realized distributions shift into previously unoccupied fundamental niche space (Figure 1D) might not be impacted at all if their previous absence from those conditions were due to dispersal limitation. By contrast, if species were previously limited from those portions of their fundamental niche by biotic interactions, then they could be at risk of extinction. For weak interactions, for example, with a competitor, this risk might take many decades or longer to play out, because the competitor in question would need to shift its own distribution into the realized distribution of the focal species, and then competitively displace the species of interest (e.g., [40]). By contrast, when strong interactions, for example, with a virulent pathogen, have excluded the focal species from portions of the fundamental niche, the risks from climate change could manifest quickly, so long as climate change leads the interacting species to rapidly shift its distribution into the realized distribution of the focal species. Finally, a species whose realized distribution is shifted by climate change into conditions characterizing its tolerance niche (Figure 1E) might go extinct relatively quickly or slowly depending on the dynamics of biotic interactions, but also on its life span. All else being equal, species with longer life spans will be able to persist for a greater period of time; for example, trees that cannot reproduce, but which could continue to grow, might persist in place for centuries (e.g. [41]).

Niche syndromes also inform the management options that are available in response to climate change. In particular, they can help to indicate when no management action is warranted, when conserving species *in situ* is practical, and when managed relocation efforts of different geographic scales are compatible with reducing risks of extinction (Figure 1). For example, no conservation action is warranted if climate change shifts the realized distribution of a species into its fundamental niche space and its previous

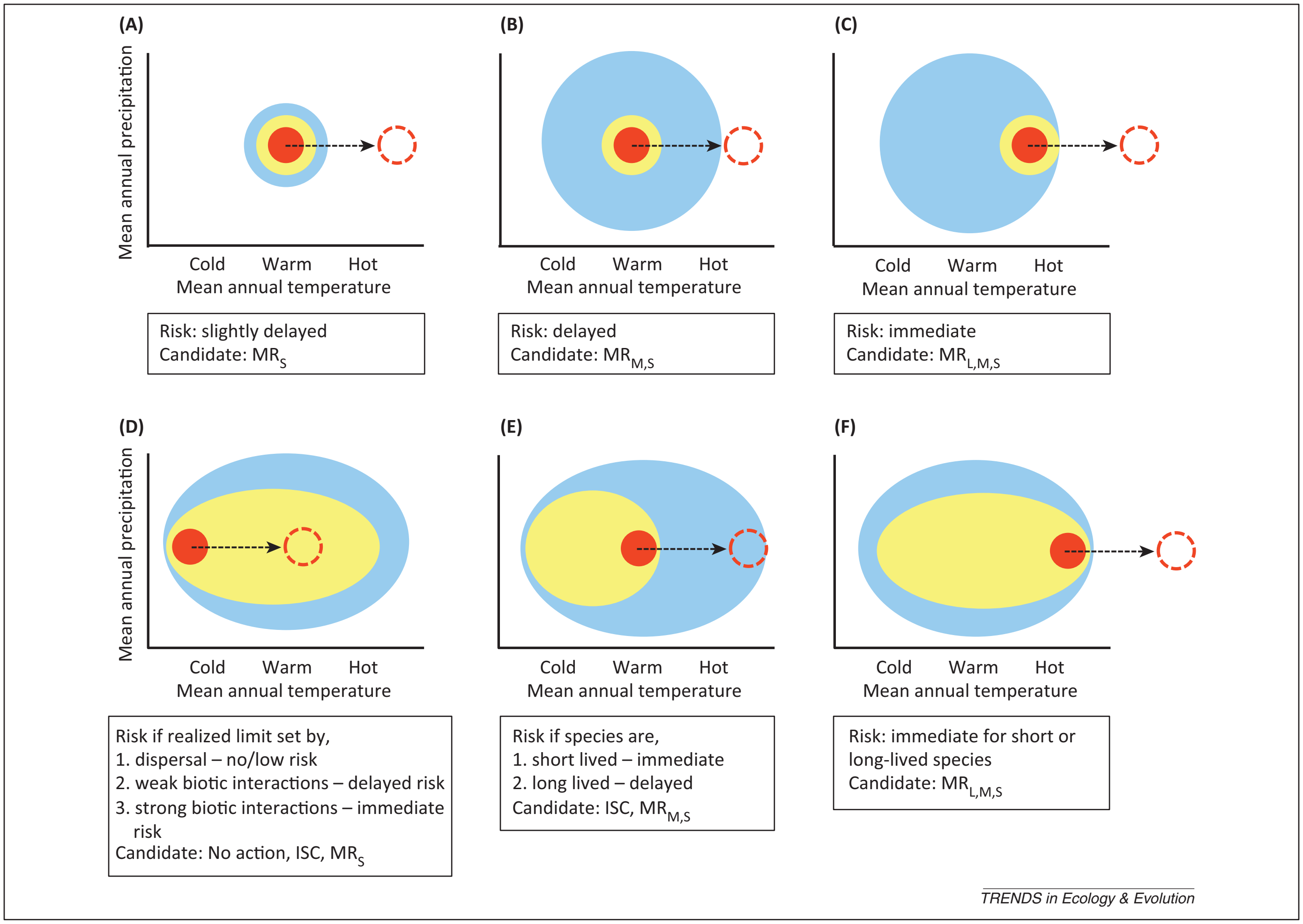

Figure 1. Niche syndromes: implications for extinction risk and conservation management. The filled colors show the relation among the realized (red), fundamental (yellow), and tolerance (blue) niches, under the simplified scenario in which niche space within a region corresponds with the spatial arrangement of the realized, fundamental, and tolerance distributions at some initial point in time. Each panel considers situations in which a species does not evolve or shift its geographic distribution to track climate change, such that the climatic conditions it experiences within its realized distribution change over time, in the direction of the arrow, to a point in which the realized distribution (depicted by the broken circle) is no longer synchronous with realized niche conditions. Such climatic shifts could cause the geographic locations where a species has occurred historically to be completely beyond any component of its niche **(A–C,F)** or to remain within the fundamental niche **(D)** or tolerance niche **(E)**, but beyond the historical realized niche. Species are classified as candidates for alternative management approaches: no action, *in situ* conservation (ISC), and managed relocation over short (MR$_S$), medium (MR$_M$), or long (MR$_L$) distances from realized niche conditions. (A–C) consider long-lived species whose realized distributions are limited by dispersal from establishing populations in the fundamental niche or individuals in the tolerance niche. The immediacy of extinction risk for species with these niche syndromes is determined by the time that elapses before environmental conditions pass beyond their tolerance niche boundaries. MR conducted over short distances could be used to move species beyond particular geographic barriers, whereas translocations over longer distances could enable long-lived species to establish in places that are currently unsuitable for maintaining self-sustaining populations, but which are anticipated to become suitable in the future with continued warming. (D) If the mismatch between the realized and fundamental niche is due to dispersal limitation, warming climate should pose no risks to persistence where species currently occur. If the discrepancy is due to biotic interactions, then extinction risks will be delayed by the speed at which interacting species shift their distributions with climate change and the time necessary for these interactions to result in population decline. If these interactions are strong, as can be the case with predation, then risks could be realized quickly. (E) Long-lived species (such as trees) might persist for centuries, whereas extinction of short-lived species would occur more quickly, barring other modes of persistence (e.g., long-lived soil seed banks). ISC that mitigated particular stressors could facilitate long-term persistence. (F) Species with this syndrome would be at immediate risk from climate change, but would have large amounts of fundamental niche space that are potentially suitable for MR.

absence from that space was due solely to dispersal limitation (one of three possibilities in Figure 1D). *In situ* conservation will be most practical when the future occurrence of a species is projected to remain within its fundamental (Figure 1D) or tolerance niche (Figure 1E). Managed relocation could be conducted at different distances away from the location of historical populations. In general, the further the realized niche of a species lies from the ‘cool’ margin of its fundamental niche (so long as there is a general correspondence between environmental and geographical space), the greater the geographic distance a species could be moved (e.g., Figure 1D–F). In some cases, where only dispersal limitation had precluded occupation of geographically distant portions of the fundamental niche, populations might establish readily after planned introduction. In other cases, however, active management might be necessary following translocation, for example, to counter the effects of antagonistic species interactions at recipient locations. Additionally, the existence of a tolerance niche beyond the cool margin of the fundamental niche (Figure 1B,C) could facilitate the managed relocation of species to areas that will become climatically suitable for population persistence in the future. This approach would offer a broader range of potential recipient locations and longer-term solutions for species imminently threatened by extinction in their current distributions (Figure 1C). Finally, niche syndromes, in combination with the life spans of species, help to inform how rapidly risks from climate change might manifest and, therefore, provide insight into the degree of urgency for particular management actions.

Generating empirically based hypotheses regarding niche syndromes

Although relations among niche components must exist, we do not know which syndromes are most common because these relations have never been widely mapped for any group of species. There are, however, reasons we might suspect that particular syndromes or particular pair-wise relations between niche components are commonly repeated. For example, many animals that inhabit lowland tropical areas appear to occupy conditions that are close to their thermal maxima [42], suggesting that the warm-margin boundaries of the realized and tolerance niches of these species are closely aligned. By contrast, many temperate tree species appear to tolerate conditions warmer than those in their realized niche [40]. Among European trees, those with small geographical distributions are largely restricted to glacial refugia, suggesting that their current distributions are constrained by dispersal limitation [43], in which case there might be large mismatches between realized and fundamental distributions. Similarly, in the USA, many plant species show a signature of dispersal limitation following glacial retreat (e.g., [16]) and, therefore, it is not surprising that many species restricted to the southeastern USA suffer no frost damage when grown in the northeastern USA [44], suggesting broad mismatches between the cold margin of the realized and tolerance niches of these species. Ultimately, determining whether particular niche syndromes are common and understanding when they are likely to occur will only be possible once we have constructed empirically based hypotheses that characterize the niche components of a large number of species.

Although relations among niche components have not previously been widely characterized, data are available now to begin to do so for a large number of species. The realized niche can be characterized from native distributions, which are well documented for many species. Although the fundamental and tolerance niches are more difficult to characterize fully, important aspects of their size, shape, and positioning relative to other niche components can be hypothesized based on available data. These working hypotheses, although imperfect, can be improved as additional data become available, but will generally be useful even when knowledge about them is incomplete. Knowing, for instance, that a species can tolerate conditions 5 °C cooler than the cold margin of its realized niche could inform selection of candidate sites for managed relocation, even if it was uncertain whether even colder temperatures could be tolerated. Data are also available in many cases to compare pairs of niche components, for example, physiological experiments enable the boundaries between realized and tolerance niches to be compared (e.g. [45]). Furthermore, a large amount of data exists for comparisons of the realized niche and previously unoccupied portions of the fundamental niche, which can be explored by examining the niche space occupied by species that have naturalized beyond the bounds of the conditions realized in their native ranges. Such comparisons have become common over the past decade in efforts to study niche conservatism (e.g., [21,22,24]), but these efforts could be extended to compare more explicitly differences between the realized and fundamental niche. Given the thousands of naturalized species globally [46], such data are clearly plentiful.

The taxonomic group most amenable to immediate and robust study of all three niche components is plants. Plants are widely naturalized, but also widely planted horticulturally, for example, in botanical gardens and nurseries [47,48], providing data that can inform hypotheses regarding the bounds of the tolerance niche. Clearly, horticultural data must be considered carefully, but they do offer a largely untapped reservoir of information [49–51]. For instance, climate tolerance inferences based on the distribution of highly selected cultivars would be suspect, whereas data from wild type individuals would offer increased confidence, and wild-collected individuals planted in botanical gardens would offer the most confidence. The outer boundaries of the tolerance niche would be informed by those plants that require continued assistance to survive, which could be determined through discussion with nursery and botanical garden staff, and from evidence on plant survival in trial gardens (e.g. [44]). The boundary between the tolerance and fundamental niche will often be difficult to determine with horticultural data alone, but hypotheses about such boundaries could be made, for example, in cases where species can be successfully grown but are unable to produce fertile offspring. Data from horticultural plantings that related survival or reproductive success to interannual variation in environmental conditions could also be particularly useful in determining niche boundaries. Ultimately, however, similar to all types of evidence that inform any niche boundary, horticultural data can be useful for informing hypotheses, but will rarely be definitive in isolation from other data sources.

Here, we provide an example of how several disparate types of data (from the native, naturalized, and horticultural ranges) can be brought together to form hypotheses about the relations among the realized, fundamental, and tolerance niches of an individual species (Figure 2). In this example, we have taken a conservative approach, relative to understanding extinction risk from climate change, by considering niche space known only from horticultural plantings (and not from native or naturalized distributions) as characterizing the tolerance niche of the species; in practice, however, some of these conditions might be within the fundamental niche, a determination that could be informed with additional data on plant reproduction and fitness. Ultimately, this example is but one of thousands of possible comparisons, but is sufficient to illustrate that large mismatches among niche components could occur and emphasizes the need to better understand how common such patterns are in nature.

Future research on the niche at large scales in response to global change

The predominate focus of current research on the niche and on forecasting efforts relies solely upon conditions observed within the native distribution of species (e.g., [3]). We believe

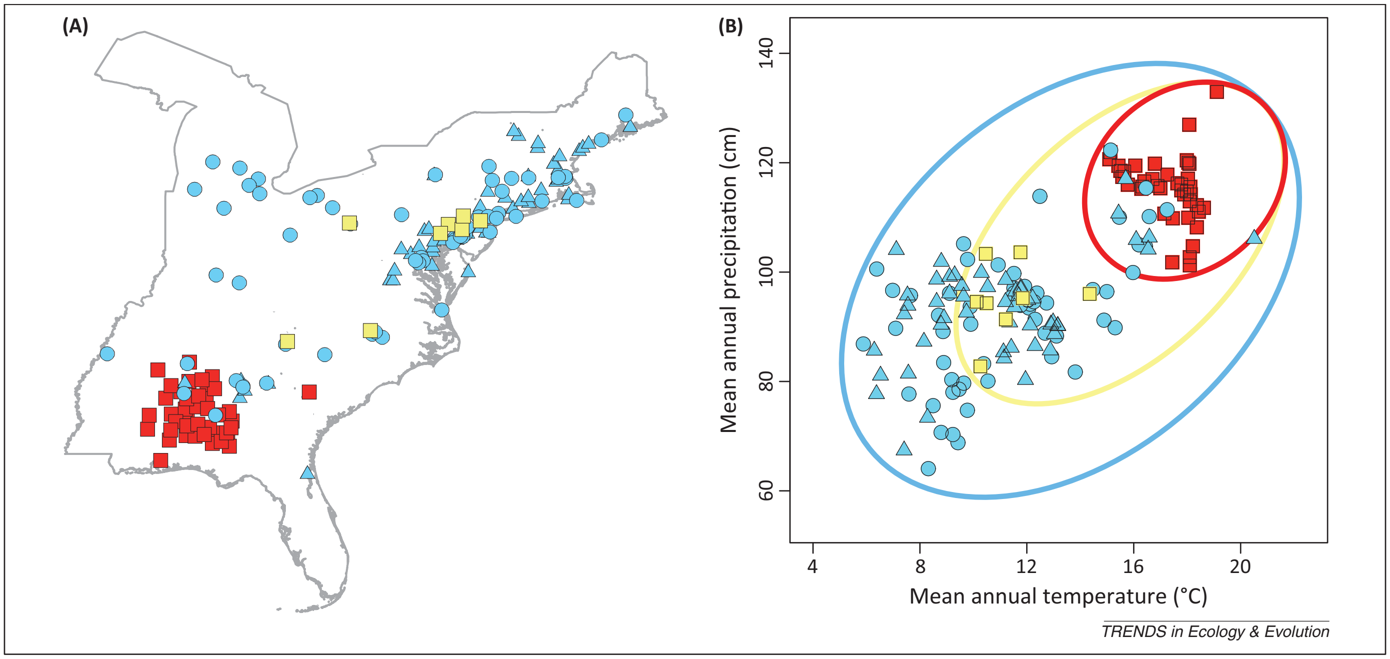

Figure 2. The distribution of the bottlebrush buckeye *Aesculus parviflora* in the eastern USA. **(A)** The map shows the native range (red squares), locations where the species is naturalized or adventive (yellow squares), and a nonexhaustive sampling of locations where this species is grown in botanical gardens (blue circles) or sold commercially (blue triangles) across the eastern USA. **(B)** The graph illustrates the niche space, in terms of mean annual temperature and precipitation, occupied by this species. The red, yellow, and blue circles represent hypotheses for the boundaries of the realized, fundamental, and tolerance niches, respectively (see main text for more details regarding these hypotheses). Although niche space is characterized here with just two climate variables, more complex characterizations would continue to show that the realized niche of this species represents only a small portion of the climatic space that this species can tolerate or in which it can form naturalized populations. Native and naturalized and/or adventive distributions are from The Biota of North America Program (http://www.bonap.org) and the Plants Database of the US Department of Agriculture (http://www.plants.usda.gov). Botanical garden distributions were provided by the PlantSearch Database of the Botanic Gardens Conservation International (BGCI) (accessed 18 July 2012) and from inquiries to individual gardens. Commercial nursery occurrences were determined by searching species lists available online from individual retailers. Climate data are described in [60].

that conclusions reached from such research (including our own work) runs the danger of being deeply misleading whenever the conditions realized within the current distribution of a species represent only a small portion of the conditions in which that species can survive or even thrive. Fortunately, there are many paths forward that can reduce these concerns, three of which we outline here. First, we can and should characterize portions of the fundamental niche that exist beyond the realized niche. Although we are not currently in a position to characterize the fundamental niche fully for species, by using naturalized species we can map out large portions of this space, not for all species, but for the thousands that have become naturalized worldwide. Second, we should characterize the tolerance niche for as many species as possible. There are limited data to do this for most animal species, but the available data for plants are numerous, e.g., approximately 2500 botanical gardens globally grow nearly one-third of all known flowering plants [47]. Third, we must begin to describe the relations among niche components for as many species as possible. This will enable us to determine whether particular syndromes are associated with particular geographical contexts (such as areas that were affected by Pleistocene glaciations) or particular species traits (such as range size or dispersal syndrome), or interactions between geographic context and species traits (such as small ranged species in areas that were formerly glaciated). Accomplishing this offers the potential for important new insights for ecology, evolution, and biogeography, as well as for the development of a predictive framework for niche syndromes. This in turn would greatly advance our ability to forecast extinction risks, understand the timeframe in which those risks are likely to manifest, and develop adaptation strategies in the context of continued global change.

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