Niche syndromes, species extinction risks and management under climate change

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Abstract

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 in 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, i.e., 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]. Better understanding 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. The fundamental niche was envisioned to encompass the full set of physical conditions and resources required to allow 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

Hutchinson [17], the distinction between the realized and fundamental niche has been expanded to include not only limitations imposed by 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, i.e., to consider species' realized and fundamental distributions.

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 might 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, in spite of 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 occurs 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 our 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 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, as their range shifts may be knocked back repeatedly by unfavorable climatic oscillations. In 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, i.e., exhibiting the 'ecological ratchet' effect [34]. How such dynamics manifest will depend on dispersal ability, biotic interactions, and whether climatic oscillations exceed species' fundamental and tolerance niches.

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, e.g., by removing invasive species [35], but could also involve efforts to reduce stressors that are indirectly associated with climate change, e.g., 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. While likely controversial, such an approach might be crucial for slow-growing, long-lived species, like 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 relationships among the realized, fundamental and tolerance components of the niche inform potential differences in species vulnerabilities to climate change. We define these relationships 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. Further, 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 (Fig. 1a), or those with realized and fundamental niches situated close to the edge of their tolerance niche relative to the directionality of climate change (Fig. 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 (Fig. 1b) relative to the direction of climate change might experience a delay in how quickly a risk of extinction manifests, as previously established individuals might be capable of persisting for many years. Species that have a large fundamental niche relative to their realized niche (Fig. 1d,e,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 (Fig. 1d) might not be impacted at all if their previous absence from those conditions were due to dispersal limitation. In 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, e.g., with a competitor, this risk might take many decades or longer to play out, as the competitor in question would need to shift its own distribution into the

focal species' realized distribution, and then competitively displace the species of interest (e.g., [40]). In contrast, when strong interactions, e.g., 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 lead the interacting species to rapidly shift its distribution into the focal species' realized distribution. Finally, a species whose realized distribution is shifted by climate change into conditions characterizing its tolerance niche (Fig. 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, e.g., 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 (Fig. 1). For example, no conservation action is warranted if climate change shifts a species' realized distribution into its fundamental niche space and its previous absence from that space was due solely to dispersal limitation (one of three possibilities in Fig. 1d). *In situ* conservation will be most practical when the future occurrence of a species is projected to remain within its fundamental (Fig. 1d) or tolerance niche (Fig. 1e). Managed relocation could be conducted at different distances away from the location of historical populations. In general, the further a species' realized niche 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., 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, e.g., 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 (Fig. 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 (Fig. 1c). Finally, niche syndromes, in combination with species' life-spans, help to inform how rapidly risks from climate change might manifest and therefore provide insight to the degree of urgency for particular management actions.

Generating Empirically-Based Hypotheses Regarding Niche Syndromes

While relationships among niche components must exist, we do not know which syndromes are most common because these relationships have never been widely mapped for any group of species. There are, however, reasons we might suspect that particular syndromes or particular pair-wise relationships 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 these species' realized and tolerance niche are closely aligned. In 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 it is therefore not surprising that many species restricted to the Southeast suffer no frost damage when grown in the Northeast [44], suggesting broad mismatches between the cold-margin of species realized and tolerance niches. 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 relationships among niche components have not previously been widely characterized, data is 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. While 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, while 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, e.g., physiological experiments allow the boundaries between realized and tolerance niches to be compared, e.g. [45]. Further, a large amount of data exist 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 in the past decade in efforts to study niche conservatism [e.g., 21,22,24], but these efforts could be extended to more explicitly compare 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, e.g. 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 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, e.g., 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, like 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 relationships among the realized, fundamental and tolerance niches of an individual species (Fig. 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 species' tolerance niche; in practice, however, some of these conditions might actually 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 rely solely upon conditions observed within the native distribution of species [e.g., 3]. We believe that conclusions reached from such research (including our own work) runs the danger of being deeply misleading whenever the conditions realized within a species current distribution represent only a small portion of the conditions in which that species can actually survive or even thrive. Fortunately, there are many paths forward that can reduce these concerns – we outline three 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 fully characterize the fundamental niche 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 enormous, e.g., around 2500 botanical gardens globally grow nearly a third of all known flowering plants [47]. Third, we must begin to describe the relationships among niche components for as many species as possible. This will allow 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 time-frame in which those risks are likely to manifest, and develop adaptation strategies in the context of continued global change.

Acknowledgements

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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 allow 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 relationships 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

a species' realized distribution (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, e.g. planted through horticulture, that survive ambient conditions but do not establish self-sustaining populations

Tolerance niche: 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

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

Our conceptualization of the tolerance niche is characterized by conditions that allow survival of individuals, but preclude a species from having self-sustaining populations (see glossary). 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 than the current sporadic usage in the literature of 'tolerance range' and 'tolerance niche', e.g. [52,53], and different than 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], as 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 than 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 compliment 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]. Further, 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 there is a need for a broader consideration of conditions in which individuals of a species can survive - information that can help to improve forecasts of species range dynamics and inform conservation practice.

Figure Legends

Figure 1. Niche syndromes: implications for extinction risk and conservation management

The solid colors show the relationship 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 dashed 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 (Fig. 1a-c, f) or to remain within the fundamental niche (Fig. 1d) or tolerance niche (1e), 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. The top panels **(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 allow 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

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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.

Figure 2. The distribution of *Aesculus parviflora* in the eastern USA.

 (a) The map shows the native range, locations where the species is naturalized or adventive, and

a non-exhaustive sampling of locations where this species is grown in botanical gardens or sold

commercially 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 (see

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 this species

can tolerate or in which it can form naturalized populations. Native and naturalized/adventive

distributions are from BONAP.org and plants.usda.gov. Botanical garden distributions were

provided by BGCI, PlantSearch Database (7-18-12) 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 Mitchell et al. [55].
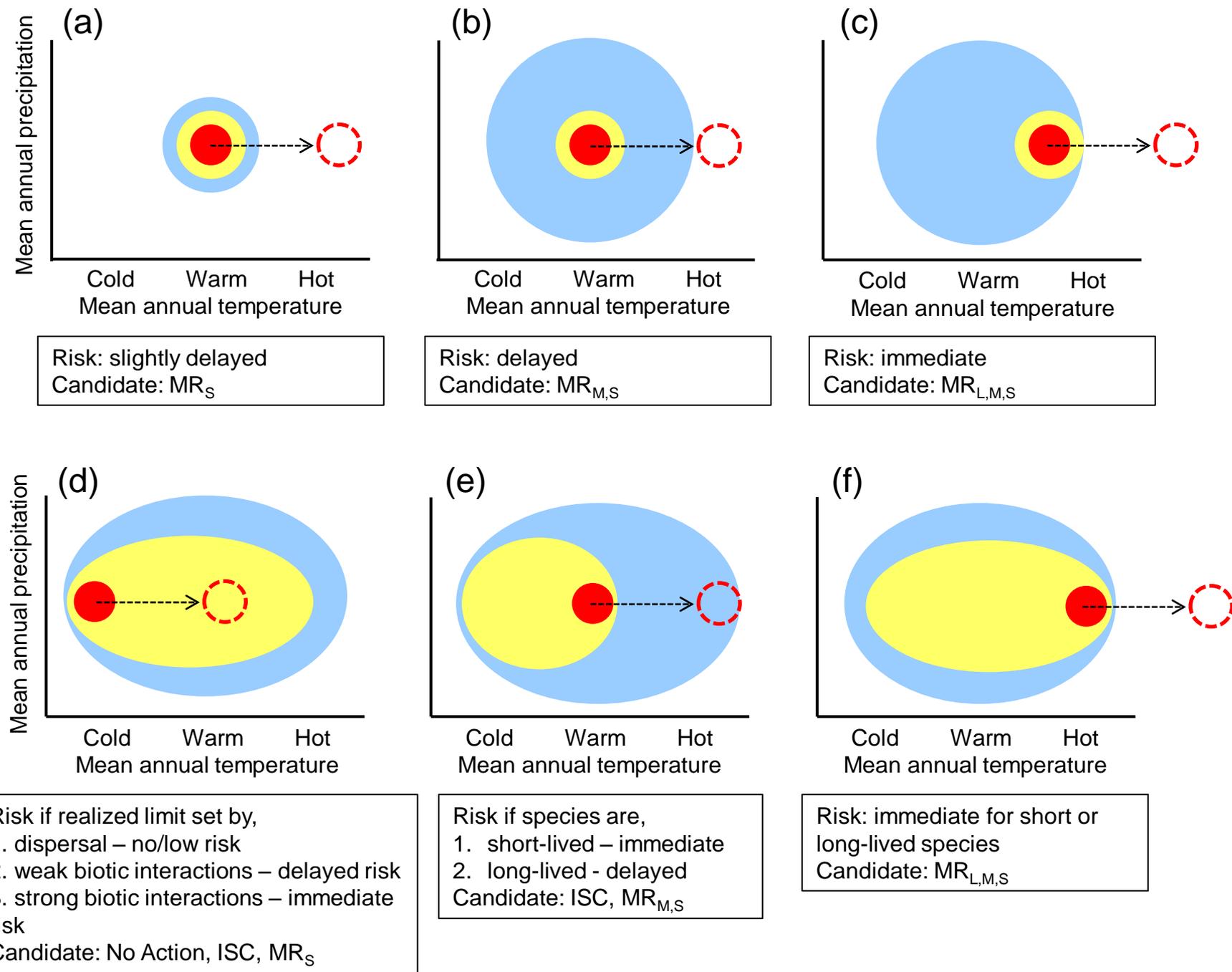
Figure 1

(a)

Mean annual precipitation

Cold   Warm   Hot
Mean annual temperature

Risk: slightly delayed
Candidate: MR_S

(b)

Cold   Warm   Hot
Mean annual temperature

Risk: delayed
Candidate: $MR_{M,S}$

(c)

Cold   Warm   Hot
Mean annual temperature

Risk: immediate
Candidate: $MR_{L,M,S}$

(d)

Mean annual precipitation

Cold   Warm   Hot
Mean annual temperature

Risk if realized limit set by,
1. dispersal – no/low risk
2. weak biotic interactions – delayed risk
3. strong biotic interactions – immediate risk
Candidate: No Action, ISC, MR_S

(e)

Cold   Warm   Hot
Mean annual temperature

Risk if species are,
1. short-lived – immediate
2. long-lived - delayed
Candidate: ISC, $MR_{M,S}$

(f)

Cold   Warm   Hot
Mean annual temperature

Risk: immediate for short or long-lived species
Candidate: $MR_{L,M,S}$

Figure 2

(a)

(b)

Mean Annual Precipitation (cm)

Mean annual temperature (ºC)

■ = native distribution
■ = naturalized distribution
● = botanical garden
▲ = commercial nursery