

# Unifying niche shift studies: insights from biological invasions

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**Assessing whether the climatic niche of a species may change between different geographic areas or time periods has become increasingly important in the context of ongoing global change. However, approaches and findings have remained largely controversial so far, calling for a unification of methods. Here, we build on a review of empirical studies of invasion to formalize a unifying framework that decomposes niche change into unfilling, stability, and expansion situations, taking both a pooled range and range-specific perspective on the niche, while accounting for climatic availability and climatic analogy. This framework provides new insights into the nature of climate niche shifts and our ability to anticipate invasions, and may help in guiding the design of experiments for assessing causes of niche changes.**

## Niche shifts during invasions: setting the scene

How climate determines the distribution of species is a classic question in ecology, closely tied to Hutchinson's [1] concept of the environmental niche, and still a major research topic [2,3]. Although, for some species, it has become possible to determine the fundamental climatic niche based on physiological information and a mechanistic understanding (e.g., [4]), for most species only the realized climate niche can realistically be estimated through empirical studies [5]. With global change, it has become increasingly important not only to describe species' climate niches but also to understand whether these can change rapidly (niche shifts; see Glossary) or not (niche conservatism) between different geographic areas or time periods [6] (Figure 1). The primary approach to investigating climatic niches in space and time has been to analyze climatic conditions across a species' distributional ranges and/or over time [7].

As already understood by Charles Elton [8], biological invasions offer a unique opportunity to study how species colonize new environments [9–11], and whether they retain

their climatic niche in a new range [7]. Addressing this question has proved important in recent years as a test of our capacity to use climate matching to assess invasion risks by exotic species at transnational scales [12,13], in particular when using ecological niche models (ENMs), which rely heavily on climatic niche conservation between native and exotic ranges [6,7,14]. Do a majority of species retain their native climatic niche when introduced elsewhere? The answer to this question is fundamental because it informs both theoretical and applied ecology, but approaches have diverged and findings have remained largely controversial so far (Table S1 in the supplementary material online) [6,7].

Evidence exists both for and against climatic niche conservatism during invasions. A recent large-scale survey of 50 Holarctic terrestrial plant invaders concluded that climatic niche shifts are rare overall between the native and invaded ranges, and therefore models can usefully predict invasion in the exotic range [15]. The same conclusions were reached for birds [16] and other groups ([6]; Table S1 in the supplementary material online). But the assumption of niche conservatism was also challenged by evidence of climatic niches shifting during invasions (e.g., [17–21]; Table S1 in the supplementary material online), potentially hampering predictions in the new range. Contrasting evidence of niche dynamics during invasions, and particularly of the frequency of niche shifts (i.e., of centroid and/or limits; Figure 1) among various taxonomic groups, thus coexist in the literature (~50% shifts/42% no shifts, and 8% no conclusion in Table S1 in the supplementary material online). This contrasting evidence may, however, correspond to different types of niche changes, biological and/or methodological study contexts, data types, species characteristics, or methods being used [6,22–25] (Table S1 in the supplementary material online), which confounding effects prevent sound interpretation of the possible mechanisms behind niche changes. Unification of the analytical context and metrics used, and a well-balanced comparison across different species, taxonomic groups, environmental spaces, and geographic areas [7,9], may contribute to reconcile conflicting evidence that observational studies of biological invasions requires.

Here, we build on a review of niche changes reported in empirical invasion studies (Table S1 in the supplementary material online) to formalize a new framework that unifies the analytical context (Box 1, Figures 1 and 2), clarifies the

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\*A.G. and C.K. led the study and all coauthors contributed to the review writing. A.G., O.B., and B.P. developed the figures. B.P., C.K., and C.D. prepared Table S1 (in the supplementary material online).

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## Glossary

**Accessible range:** the geographic locations within a given area that are accessible to a species given its current distribution and the timescale considered in the study. It is thus conditional upon spatial configuration and the species' dispersal ability [27,28].

**Analog climate:** a combination of climate factors found in one area or time period that is within the envelope of climatic conditions found in a different area or time period used for comparison [38]. Contrary: 'non-analog climate'.

**Available environment:** the set of environmental conditions that exist in a given area [29] (Box 3). Synonyms: 'realized environment' (whole range, not species specific), 'background environment'.

**Ecological niche model (ENM):** also called species distribution or habitat suitability models; multivariate models fitting the niche of species by relating distribution observations with environmental variables measured at the same sites, and projected over a whole study area [2,5].

**Exotic niche:** the niche measured based on a species' distribution in the exotic range. Synonyms: 'naturalized niche', 'adventive niche', 'invaded niche', or 'invasive niche' (for invasive species).

**Exotic range:** the geographic range where a species is not native. Synonyms: 'naturalized range', 'adventive range', 'invaded range' (for invasive species).

**Exotic species:** a species present in a region where it is not native, mostly due to human actions that enabled it to overcome biogeographic barriers [54]. Synonyms: 'alien species', 'non-native species', 'non-indigenous species', 'introduced species'.

**Fundamental niche:** the envelope of environmental (abiotic) conditions allowing populations to sustain themselves in an  $n$ -dimensional environmental space. It depicts the ecophysiological requirements of species [27]. Synonyms: 'physiological niche'.

**Native niche:** the niche measured in the native range.

**Native range:** the complete geographic area where an exotic species is native.

**Niche–biotope duality:** the reciprocal correspondence between the niche conditions in multidimensional environmental space and the physical locations that a species actually occupies in geographic space (derived from [14]).

**Niche centroid:** the mean niche position in  $n$ -dimensional environmental space.

**Niche conservatism:** the tendency for species to retain their niche in space and time. Synonyms: 'niche stability'.

**Niche envelope:** the envelope of conditions in multivariate environmental space defining a species' niche. The boundary of the envelope can be defined in many different ways (e.g., percentiles; [22]).

**Niche expansion:** proportion of the exotic niche non-overlapping with the native niche.

**Niche overlap:** the intersection of two niches in  $n$ -dimensional environmental space.

**Niche shift:** a change in the centroid (see above) or limits of the niche envelope in environmental space. Synonyms: 'niche change'.

**Niche stability:** proportion of the exotic niche overlapping with the native niche.

**Niche unfilling:** proportion of the native niche non-overlapping with the exotic niche.

**Non-analog climate:** see 'analog' climate.

**Ordination:** statistical approach used to represent the arrangement of a series of objects described by multiple descriptor variables into a reduced multi-dimensional space which axes represent combinations of the initial variables (see 'principal component analysis').

**Potential niche:** the intersection between the fundamental niche and the realized environment [3,29].

**Principal component analysis (PCA):** a classical ordination approach (see above).

**Rare climate:** climatic conditions poorly represented overall within an area during a given time period.

**Realized niche:** the environmental (abiotic) niche of a species as quantified from field observations, that is, the fundamental niche modulated by biotic exclusions, population dynamics (such as source–sink dynamics), and dispersal limitations [14,27]. Synonyms: 'ecological niche'.

**Schoener's D:** the most common measure of niche overlap [22,33].

role of the niche–biotope duality (Box 2) [3,14], and helps to identify potential factors influencing niche change between ranges. The central idea of this framework is to decompose a niche comparison between native and exotic ranges into its three basic components: niche unfilling, niche stability, and niche expansion (Box 3, Figure 2) [15]. We present these elements and discuss them along with the importance of taking into account the available environment, distinguishing analog from non-analog climatic conditions

between ranges (Box 4), and accounting for niche factors and niche dynamics at finer resolution. We conclude with recommendations on using the proposed framework for future niche change studies.

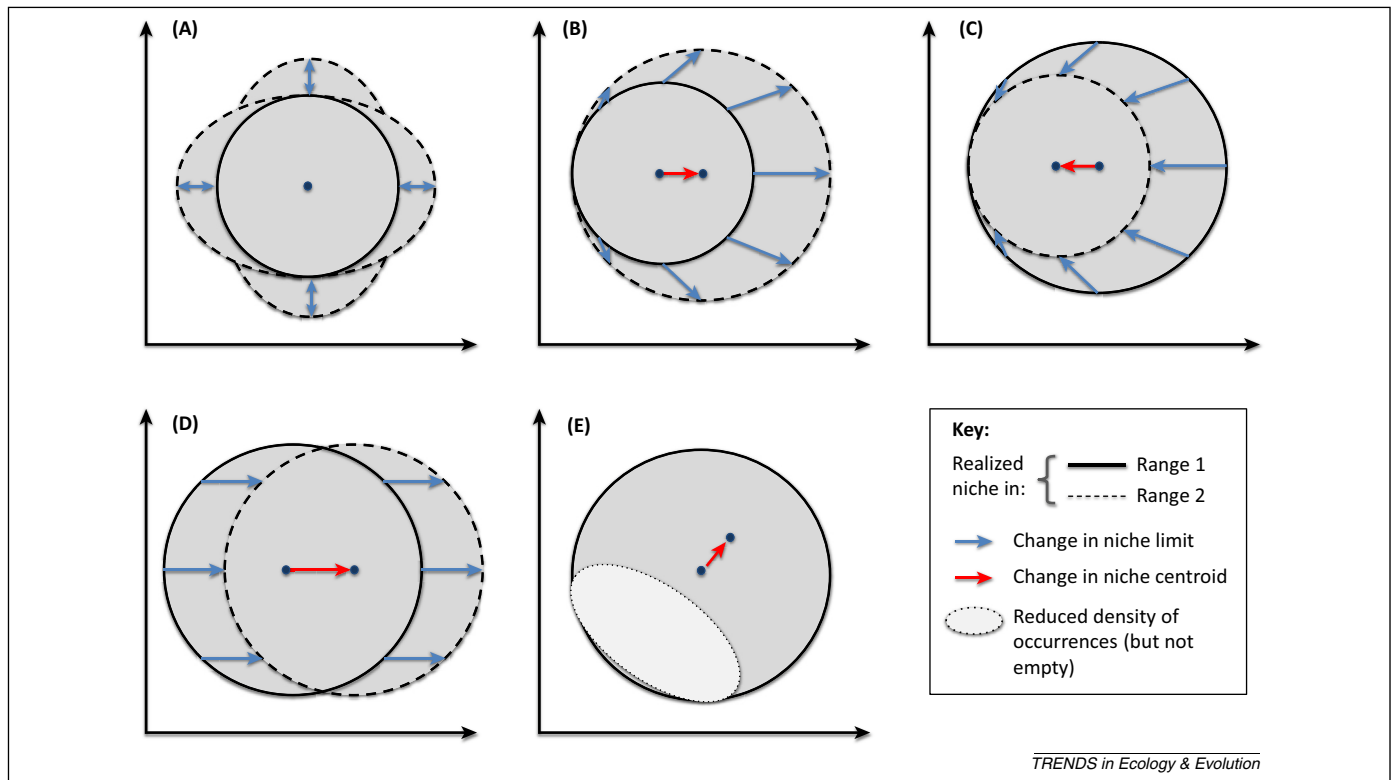
## Niche changes and associated metrics

### *Which niche is measured from field observations?*

The realized climatic niche quantified from field observations is determined by biotic constraints on the fundamental ecophysiological niche, population dynamics (e.g., source–sink dynamics), and dispersal limitations (i.e., accessibility; Box 2) [26–28], but it is also constrained by the availability of the environment in the areas (Box 4) at the timescale considered in the study (i.e., some conditions can be available at one time in one area, but not earlier or later) [23,29]. A change in this realized niche can thus result from adaptive evolution occurring in the colonized range [10,30] or from changes in biotic interactions, dispersal limitations, or from preadaptation to conditions not available (anymore) in the initial range at the time of the study but available in the colonized range [7]. Hereafter, we consider a niche shift as any change of the realized niche, that is, the niche as measured by climatic characteristics at sites of species occurrence in the field. It thus implicitly includes any potential change of the fundamental niche, although with such empirical data, a change caused by evolution of physiological tolerance cannot be differentiated from a change due to other factors [17,25].

### *Two main approaches to quantifying niche changes*

Two main approaches have been used so far to compare niches between ranges, based on direct observations or on model predictions [22] (Figure 3, Table S1 in the supplementary material online). The first approach uses observations directly and compares the difference in environmental attributes of the sites where the species occurs between the native and exotic ranges in environmental space. This comparison can be done either through univariate (e.g., [19]) or multivariate tests (e.g., in a reduced principal component analysis, PCA, space [17]; Figure 3A). Such a direct approach does not rely on any underlying model that relates the occurrences to the environment. The approach can be considerably improved by calculating smooth densities of species occurrences in a gridded environmental space, as a way to avoid unrealistic 'holes' in a niche due to low sampling effort [22] (see also [31,32]). The second approach relies instead on the outcomes of ENMs [2] (also called species distribution models, SDMs [5]), and compares the overlap of reciprocal predictions of geographic distributions (i.e., predicting the invaded distribution with the model fitted in the native range, and vice versa), usually comparing in the exotic range the two predictions by the models fitted in each range [18,33,34] (Figure 3B). Specialized software has been developed for niche comparisons based on the ENM approach (ENMTool [34]). Comparative analyses with virtual species, for which distributions and niche overlap are known, showed that the first approach (ordination) quantified niche overlap more accurately overall than the second (ENM) [22]; however, the ordination approach provides a mathematically less formalized representation of the niche



**Figure 1.** Theoretical scenarios of realized niche changes in space (e.g., following invasions) or time (e.g., under climate change). Change of: (i) the niche envelope (expansion or contraction) without change of the niche centroid, due to symmetric niche change, that is, in two opposite (A) or all directions in climatic space; (ii) the niche centroid with expansion (B, C) or displacement (D) of part of or the whole niche envelope; or (iii) the niche centroid only, due to a change of the density of occurrences within the same niche envelope in climatic space (E). The latter case would result in stability (no change) in Figure 2. Observed changes are likely to be combinations of these cases.

and is less able to optimize the weighting of the different environmental factors based on their relevance for a species' ecology. The ENM approach is particularly useful to assess ENM transferability between ranges [35]. Thus, although both approaches have strengths and weaknesses [22], comparisons of niche change results between studies (meta-analyses) should preferentially include those based

on ordinations, and at least make clear which approach was used (Table S1 in the supplementary material online).

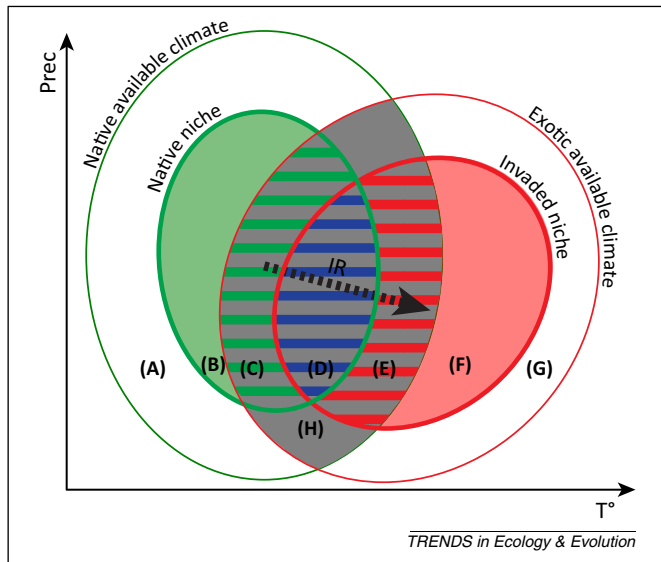
#### *Different components of niche change: centroid shift, overlap, expansion, and unfilling*

From either of these approaches, different niche change metrics can be calculated, at two levels of analyses – pooled ranges and range specific (Box 3). The most commonly used metrics so far measure either a shift of the niche centroid,  $C$  (mean position; e.g., using Euclidean distance [17]), or a change in the overlap,  $O$ , between the two niches (e.g., using Schoener's  $D$  [33] or minimum convex polygons [36]), and they are usually calculated in relation to the entire realized niche between two ranges (i.e., pooled; Box 3). However, a niche change detected in one of these two ways can result from multiple situations (Figure 1): (i) a change of the niche envelope (overlap  $\neq 1$ ) due to symmetric niche expansion or contraction (hereafter called 'unfilling' in the case of invasions, because it corresponds to a part of the native niche that was not filled) in climatic space, thus not shifting the niche centroid (Figure 1A); a species may expand both to warmer and colder conditions in a way that the average temperature-related niche position remains stable as it is observed for common spotted knapweed invading North America (*Centaurea stoebe*, Figure S1A in the supplementary material online); (ii) a change of the niche centroid with displacement of the niche envelope (Figure 1B–D) due to niche unfilling (e.g., black cherry tree invading

#### **Box 1. The analytical context for quantifying niche shifts**

Assessing niche change between ranges is generally done by considering a species native in one area (its native range) and invading another (or several other) biogeographically separated area (the exotic range; e.g., [15]). This context could similarly apply to the same species in two (or more) time periods (e.g., [49]). Regions large enough to include the entire (or large parts of) native and exotic species' geographic distributions are usually considered for comparison. The choice of these areas will strongly condition the niche–biotope duality (Box 2), and thus the available environments (Figure 2 in main text, Box 3), and ultimately the quantification of niche changes [3,25]. Optimally, the studied ranges should encompass the species' complete geographic distribution in the native and introduced ranges that could potentially be reached by a species given its dispersal ability, that is, the accessible areas [28]. In practice, we recommend defining areas with ecological relevance, such as biomes or ecoregions, and using species data (atlas or occurrences) well representing the focal species' range. The full multidimensional set of environmental conditions observed in one area/time period is the realized environment (Boxes 2 and 3) [29,56], and the envelope of conditions where the species is observed represents its realized environmental niche (Box 2) [3,57].





**Figure 2.** Schematic 2D representation of the indices of niche change (unfilling, stability, and expansion) presented in [15] (see definitions in Box 3). Unbroken thin lines show the density of available environments (Box 4) in the native range (in green) and in the invaded range (in red). The gray area shows the most frequent environments common to both ranges (i.e., analog environments). The green and red thick lines show the native and the invaded niches, respectively. Niche unfilling ( $U$ ), stability ( $S_p$ ), and expansion ( $E$ ) are shown with green, blue, and red hatched surfaces, respectively, inside analog environments. The definition of a niche shift using the change of niche centroid only (inertia ratio, IR) is shown with a thick broken arrow. In this context, the uppercase letters represent similar features in both graphs: (A) available conditions in the native range, outside of the native niche and non-analog to the invaded range. (B) Conditions inside of the native niche but non-analog to the invaded range. (C) Unfilling, that is, conditions inside of the native niche but outside the invaded niche, possibly due to recent introduction combined with ongoing dispersal of the exotic species, which should at term fill these conditions. (D) Niche stability, that is, conditions filled in both native and invaded range. (E) Niche expansion, that is, conditions inside the invaded niche but outside the native one, due to ecological or evolutionary change in the invaded range. (F) Conditions inside of the invasive niche but non-analog to the native range. (G) Available conditions in the invaded range but outside of the invasive niche and non-analog to the native range. (H) Analog conditions between the native and invaded ranges.

Europe, *Prunus serotina*, Figure S1B in the supplementary material online) and/or expansion (e.g., desert false indigo invading Europe, *Amorpha fruticosa*, Figure S1C in the supplementary material online) in the invaded range; or (iii) a change of the niche centroid only, without niche expansion or unfilling, due to a change of the density of occurrences within the same niche envelope in climatic space (Figure 1E). The latter case can result from changes in competition, limited dispersal, or availability of environmental conditions in the exotic range that reduce the density of species occurrences in some part of the niche space [25], changing the position of the centroid with only a weak impact on the niche limits, as shown for pinweed invading North America (*Erodium cicutarium*, Figure S1D in the supplementary material online). Thus, a shift of the niche centroid between the native and the exotic range (Figure 1B–E) can provide a first indication that a niche change occurred, but it is not sufficient to interpret its exact nature. And, reciprocally, an absence of a shift of the niche centroid does not mean that no niche shift occurred.

New indices were thus required to decompose niche comparisons to reveal two distinct components of niche changes: ‘expansion’ and ‘unfilling’ (Box 3, Figure S1 in the

supplementary material online) [15]. ‘Unfilling’ ( $U$ ) most commonly corresponds to the proportion of the native niche non-overlapping with the exotic niche, and ‘expansion’ ( $E$ ) refers to the proportion of the exotic niche non-overlapping with the native niche. These indices, as just defined, measure changes that are relative to one of the ranges (native or exotic), but they can also be measured with regard to the entire species distribution, where native and exotic ranges are pooled (Box 3). The pooled versions of  $E$  and  $U$  ( $E_p$  and  $U_p$  in Box 3) thus inform us about the species niche dynamic at the global scale of the study, but convey less information about our ability to predict species invasions from the native range (Box 3).  $E$  and  $U$  (and equivalently  $E_p$  and  $U_p$ ) are recently published indices [15] that can easily be calculated from the same two main approaches previously described [22], but provide much more information than simple overlap or centroid changes. Studies that found overall niche conservatism for invaders consistently relied on such a complete set of niche change metrics (Table S1 in the supplementary material online). Later, we will refer to the whole set of niche change metrics as the COUE scheme (Box 3).

#### Dealing with available and non-analog climates between ranges

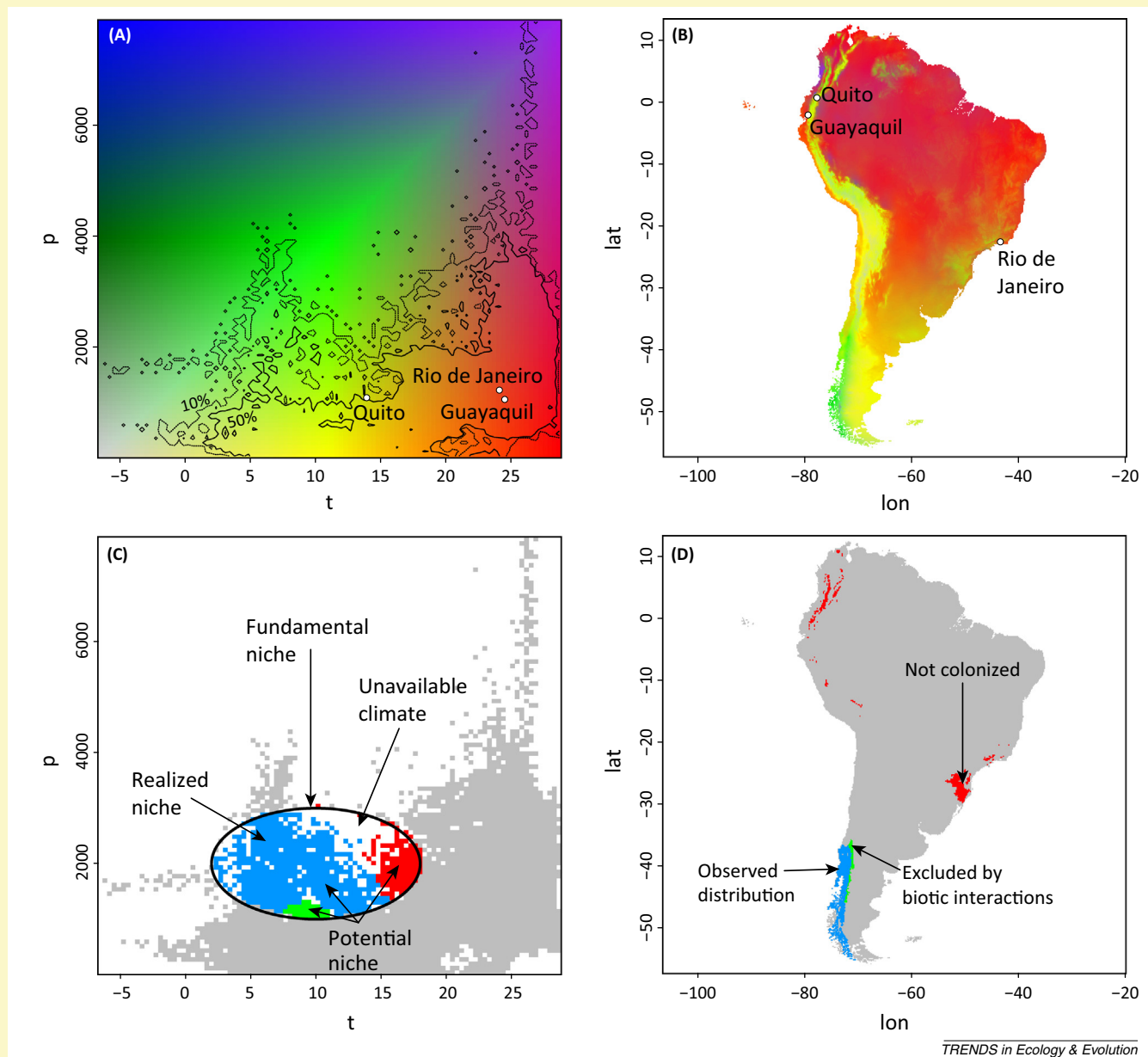
The availability of climatic conditions in geographic space matters when quantifying niche changes between ranges. Owing to the niche–biotope duality (i.e., the correspondence between environmental and geographic spaces; Box 2), some conditions common in the exotic range may be rare in the native range (or the converse; Box 4) so that, without correction, one may detect niche shifts (measured with centroid change or overlap of percentile envelopes) only because these conditions are more or less available in one range than in the other [3,25]. Accounting for environmental availability is thus necessary and has been done so far in two ways. First, niche change metrics can be corrected by the distribution of the available environment, either by comparing the overlap between native and exotic niches with the overlap between native and exotic ranges [23], or by transforming species densities in the environmental space into species ‘occupancies’ (i.e., the ratio of density of species to the density of available environment [22]; see also [37]). Second, niche metrics can be calculated only within the most common environments shared between native and exotic ranges (say within the shared portion of the 75th percentiles encompassing the prevailing conditions in each range [15]). Removal of rare climates is, however, likely to have a strong impact on the results (with either approach) when the two ranges show important differences in climate availability. In this case, we advise comparing analyses across a range of percentiles (say 75%, 80%, 85%, 90%, 95%, and 100%) in order to see how the quantification of niche change can be affected by various levels of trimming (see supplementary material online in [15]) and to understand the implications (specific to each case study) for the interpretation of niche changes.

An extreme case of climate non-availability is when climate conditions exist only in one of the two ranges (Box 4) [38]. These non-analog climates represent a severe problem when calculating niche change metrics, because

### Box 2. Hutchinson's niche–biotope duality

It is important to recall the niche (environmental space) versus biotope (geographic space) duality framework described by G.E. Hutchinson [14]. This duality means that there is no direct match between the topology of the niche space and the geographic distribution of a species (Figure 1). The same combination of climate factors (colors in Figure 1A) can occur in one or several localities in geographic space (same colors in Figure 1B), and locations close in environmental space can be far apart geographically and vice versa [3]. For instance, in South America, the cities of Quito and Guayaquil are close to each other but climatically far away, whereas Guayaquil and Rio are geographically far but climatically close (Figure 1). Interpretation of niches and distributions of species thus requires careful screening of both spaces jointly (Figure 1A,C vs Figure 1B,D), with special attention to issues of dispersal limitations, biotic

interactions, and available environmental conditions [14]. Blank areas in Figure 1C represent environments that are not available within the geographic range considered (here South America). The intersection of the available environment and the fundamental (i.e., physiological) limits of a species define its potential niche [3,29]. Parts of this potential niche can be unoccupied by the species because of dispersal limitations (i.e., red areas in Figure 1C,D) or exclusion by biotic interactions (i.e., green parts in Figure 1C,D). As the potential niche rests on the hypothetical quantification of the fundamental niche [58], whereas we focus mainly on the realized niche here, we do not expand further on this concept. For a full theoretical development of the concepts and definitions of niches and distributional areas, with formal abbreviations, see Soberón and Nakamura [3] and Peterson *et al.* [2].



**Figure 1.** (A–D) Hutchinson's duality framework, inspired by Soberón and Nakamura [3] and Soberón and Peterson [25]. The fundamental niche ellipse pictured in (C) is theoretical (artificially created) and could not be derived from field observations.

### Box 3. Metrics to quantify and decompose niche changes: the COUE scheme

The niche space of an exotic species can be classified into three categories: niche space occurring only in the exotic range (i.e., expansion,  $\varepsilon$ ), in both exotic and native range (i.e., stability,  $\sigma$ ), and only in the native range (i.e., unfilling,  $\nu$ ). Niche comparisons can then be made at two levels: (i) relative to the entire niche of the species, pooled from the two ranges (pooled ranges approach); or (ii) relative to the native or exotic ranges separately (range-specific approach). **Table 1** presents a unified terminology (COUE, an acronym based on its main components, centroid shift, overlap, unfilling, and expansion, as defined below) for niche comparisons and related metrics of niche changes.

Centroid shift measures the change in mean niche position (and thus mean intensity) in the pooled ranges space, and thus no range-specific counterpart exists here. At the pooled range level, niche stability ( $S_p$ ) measures the proportion of niche assessed from the pooled native and exotic occurrences (possibly transformed into ENM predictions or densities in the environmental space, **Figure 3** in main text) present in both native and exotic ranges. This is similar to the niche overlap ( $O$ ) assessed through Schoener's  $D$  or Hellinger's  $I$  [22,33]. The non-overlapping parts of the two niches ( $1 - S_p$ ) can then be decomposed into global ratios of expansion ( $E_p$ ) and unfilling ( $U_p$ ) based on the pooled ranges. Decomposing niche changes relative to the pooled species distribution is informative about the magnitude of niche changes at the global scale (i.e., relative to the entire realized niche of the species), but may not be informative about niche changes specific to either exotic or native ranges (as used, e.g., in [15]). For example, the exotic niche can be very small relative to the entire pooled niche but entirely located in environments different from the native niche, in which case  $E_p$  would be very small, although the entire invaded niche is distinct from the native niche and would hardly be predictable from the native range data. It is, however, possible to quantify a ratio of expansion ( $E$ ) and unfilling ( $U$ ) relatively to the exotic or native niches only, that is, at the range-specific level. These are informative about the relative importance of changes in each exotic and native niche. In turn, niche stability can be assessed from the perspective of native or invaded niches separately, depending on whether it complements the relative expansion or relative unfilling ratios ( $S_n = 1 - U$ ;  $S_e = 1 - E$ , respectively).

**Table 1. Unified terminology for niche comparisons and related metrics of niche changes**

Niche change component	Absolute component	Metric	
		Pooled ranges	Range specific
Centroid shift	–	$C$	–
Expansion	$\varepsilon$	$E_p$	$E$
Stability	$\sigma$	$S_p$ ( $\approx O$ )	$S_n$ , $S_e$
Unfilling	$\nu$	$U_p$	$U$

no insight on the biology of the species in these non-analog climates can be learned from a comparison between ranges. This is because colonization of portions of environmental space not present in the native range cannot be unambiguously considered as resulting from niche evolution in the exotic range, and the interpretation of these situations thus remains speculative [23,25]. A scientifically more rigorous approach to assess niche expansion, therefore, is to restrict the analyses to the shared, analog climatic conditions between the native and exotic ranges (e.g., [15]), and to provide measures of expansion in non-analog situations separately [32]. Studies that restricted their analyses to analog environments found niche conservatism to be dominant among invader species (**Table S1 in the supplementary material online**). Complementary

### Box 4. The available climate and the analog/non-analog issue

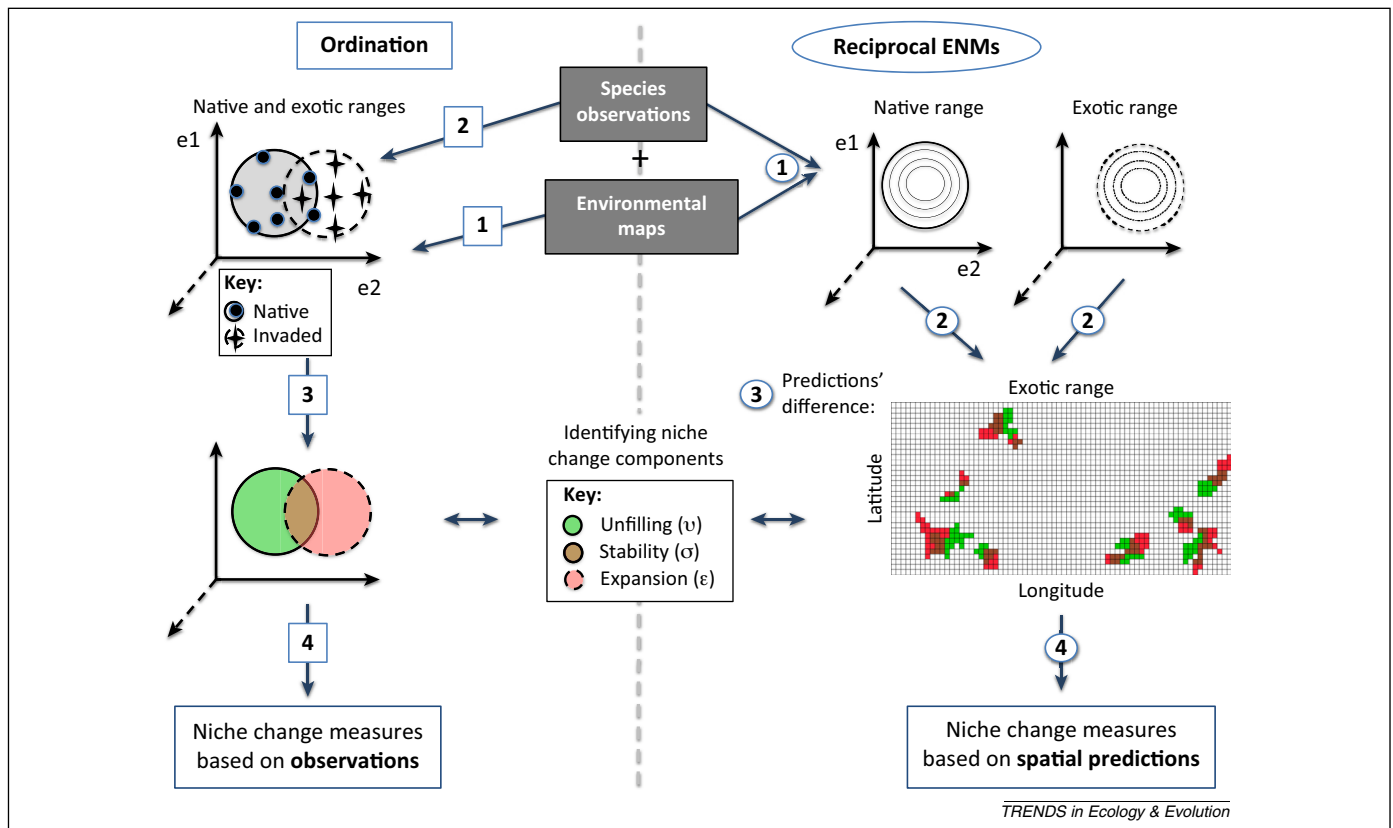
The available environment is a subset of all possible environmental combinations (**Box 2**). The existence of non-available environments constrains niche shape and size [29]. For instance, places with very warm summer temperature (say  $>40^\circ\text{C}$ ) and very cold winter temperature (say  $<-20^\circ\text{C}$ ) do not currently exist on Earth (see **Figure 1** in [29]). When comparing the available environment in two areas, some habitats in one area (or time period) may be much more frequent or rare than in the other area (or time period), or some specific conditions found in one range may be totally absent from the other range. For instance, some very dry conditions of Western North America are not found in Western Europe [17] and tropical conditions of the Tertiary in Europe are not observed anymore [59]. Conditions similar in two ranges or two time periods are called 'analog' and those differing 'non-analog' [38,39] (or 'non-overlapping backgrounds' in [25]). Non-analog environments in an invaded range, or in the future, typically represent situations outside the range of values considered to quantify the native niche and not experienced by the species before invasion, and therefore lead to difficulty in interpreting niche shifts [15] and predicting species distributions [39]. Tools are available to define areas in the exotic range with climates analog to the native range. The simplest approach is to define a bounding box that encloses all the conditions present in the native range (e.g., BIOCLIM; [61]). Any pixel in the exotic range outside of the bounding box range can be considered non-analogous. A more refined approach is the MESS analysis (Multivariate Environmental Similarity Surfaces) [60], an index of similarity reporting the closeness of a point described by a set of climate attributes (e.g., a pixel in the exotic range) to the distribution of these attributes within a population of reference points (e.g., the native range).

experimental approaches would then be needed to determine whether, for instance, expansions in non-analog conditions may represent a change of the fundamental niche [7]. This issue is particularly important because non-analog climates not only occur across space but will also occur over time due to climate change [38]. This is also the reason why projections of ecological models in non-analogous climates are considered unreliable [23,39]. Still, colonization of non-analog climates in the exotic range may represent relevant situations to consider from a management perspective, calling for separate ENM projections in both analog and non-analog climates in the invaded range (through fitting ENMs with pooled data from the native and exotic range [40]).

### What other factors could affect the quantification of climatic niche changes?

#### Range unfilling in the native range

Geographic range unfilling (not to be confused with niche unfilling) – that is, when a species does not occupy all the geographic locations that have suitable conditions within its climatic niche – can occur in the native range as a result of non-equilibrium situations, such as ongoing post-glacial recolonization during the Holocene [41], and can potentially affect the quantification of niche change. This problem is also known as the 'accessible area' issue [28]. But geographic range unfilling does not necessarily lead to niche unfilling in environmental space. For instance, it was shown that range unfilling can nonetheless translate into complete climatic niche filling for some tree species in Europe [42]. Range unfilling particularly affects niche quantification if the climates present in the unfilled geographic space are rare and/or not well represented – or



**Figure 3.** The two approaches commonly used to quantify niche changes between ranges (Box 1). Ordination is based on the observations directly, whereas the ecological niche model (ENM) is based on predictions ([22]; Box 1). Steps for ordination are (numbers in squares): 1. Definition of the reduced multidimensional environmental space. 2. Plot of the observations from each range in this space. 3. Comparison of the niche defined from observations in each range. 4. Calculation of the niche change metrics (Box 3). Steps for ENMs are: 1. Fit of ENMs by relating field observations to environmental variables. 2. Projections of the ENMs in geographic space. 3. Compute difference in the projections. 4. Calculation of the niche change metrics (Box 3). See main text for discussion of the respective strengths and weaknesses of the two approaches.

even absent – in other parts of the range. However, published analyses generally calculate range filling based on a geographic projection of the realized niche at the time of the study (e.g., [41]), and thus these documented cases of range unfilling cannot translate into niche unfilling. But range unfilling measured in other ways – for example, field common garden experiments located beyond a species' current geographic and climatic range [43–45] – may reveal niche unfilling.

#### *Biased or incomplete sampling of species distributions*

Another issue relates to the type and quality of species distribution data. Although it is important to cover an entire species' niche to assess niche change without bias, its complete native and exotic distribution ranges need not necessarily be considered. Because of the niche–biotope duality [3,14] (Box 2), the climatic niche of a species might well be fully captured even if only a part of its geographic distribution is sampled. However, and similarly to the issue of range unfilling, when geographic truncation leads to environmental truncation [46], niche change studies based on both ordinations and ENMs (Figure 3) should be considered with care, because their conclusions will only be applicable to the climate space investigated and within analog climatic combinations between the two ranges. In these situations, approaches based on ENMs [2,5] (Figure 3) may be less reliable for spatial predictions, as they rely heavily on fitted species–environment response curves that could be biased [46,47]. In addition to environmental truncation, bias or

errors in the geographic sampling of the distribution of a species may also bias measures of niche change. For instance, coarse atlas distribution data may portray a species in areas where it does not exist, whereas occurrence data (e.g., from herbaria) may under-represent or omit areas where the species occurs, both possibly affecting niche quantification.

#### *Beyond macroclimate: microclimate and non-climatic factors*

Climate is often seen as the main factor driving species distributions at large scales [5], and most global-scale studies of niche changes in native [48–50] and exotic species [15,17,19,20,36] looked at changes in macroclimate (i.e., the coarse and large-scale climate that usually determines biomes). This primary role of macroclimate does not prevent finer climatic characteristics or other abiotic factors from affecting species distributions, such as the restriction to specialized habitats (e.g., mountain microclimates, stream banks, or particular soil types) that must generally be characterized at a finer spatial grain (e.g., 1 km × 1 km) than that typically used in macroclimatic studies. Niche changes may be particularly observed in non-climatic components (such as soils) of a species' niche. For instance, Bertrand *et al.* [51] showed that a shift of the climatic niche centroid can be observed when soil variables are included in the analyses. When shaping the distribution in the native range, these microscale factors could thus result in the detection of apparent



macroclimatic niche expansion in the exotic range for two reasons: (i) part of the native macroclimate might not be occupied by the species due to spatial correlation with factors that hinder its occurrence [51]; or (ii) a species might occur under conditions in the native range that, within the coarse cells of macroclimatic maps, are scattered and marginal (and thus smoothed and hindered in niche analyses based on mean values within coarse cells), but are dominant in the exotic range and thus only revealed there in the niche quantification, causing an apparent niche shift.

However, these factors will only modify measures of macroclimatic niche change if: (i) their geographic distribution matches a restricted portion of the climatic niche in the native or exotic range, and (ii) this restricted portion is the one that shows niche change. In this regard, studies at a finer resolution (e.g., microclimate) and/or including non-climatic factors would be useful for a more detailed understanding of niche dynamics in invaded ranges. But to be complementary to the strict macroclimatic niche studies conducted so far, findings based on macroclimate alone should be presented and compared with findings when microclimatic and non-climatic components are added (as for analog/non-analog climates), so that their relative effect can be properly assessed (e.g., [51]).

### **Towards a unifying framework: concluding remarks and remaining challenges**

There has recently been a great diversity of studies examining climate niche change in exotic species (Table S1 in the supplementary material online), some reporting dramatic niche changes [17,18,20,36]. However, how many shifts occur in analog versus non-analog climates, and whether these only occur in specific taxonomic groups or habitats, remains to be investigated. Among 36 studies including around 180 species, approximately 50% of the species showed a niche shift overall, with a higher prevalence among plants than animals, and a majority of the studies reporting niche shifts included only one or a few species (Table S1 in the supplementary material online). It might therefore be that studies reporting a shift (rather than no shift) were preferentially published, especially considering that the only two studies that concluded overall niche conservatism among a large number of invader species used an ordination approach, relied on the most complete set of niche change metrics, and accounted for environmental availability (Table S1 in supplementary material online). Therefore, conclusions on niche shifts probably strongly depend on the organisms, methods, and data used, and generalization about the frequency and drivers of niche shifts can only be based on a standardized and rigorous approach for quantifying niche shifts within each group. This could ultimately allow concluding if there are identifiable trends among niche shifts, or if niche changes are very idiosyncratic (i.e., species specific). To promote such standardization in future studies, we recommend:

- using as much as possible, within a same taxonomic group, the same set of variables used in previous studies on the same group, so that proper comparisons can be ensured; this does not additionally prevent testing niche changes with other sets of variables, if thought to be more meaningful to picture species' niches in the group considered;
- disentangling all possible situations of niche change through measures of niche unfilling and expansion in complement to centroid shift and overlap metrics, at the two possible analytical levels (COUE scheme; Box 3);
- correcting these niche change metrics to account for the density of occurrences and the available environment in both ranges (or time periods);
- assessing whether niche metrics change when excluding rare climates along a range of percentiles, and when considering analog and non-analog environments separately; this will ensure retaining all the necessary information for further interpretation and comparison of results from different studies.

We suggest three important remaining challenges for studies of realized niche changes during biological invasions. (i) Assessing climatic niche changes at finer scales and in combination with other non-climatic factors, such as differences in soils [51], biota, and disturbances between the native and exotic range. High-resolution data are becoming increasingly available and standardized to be comparable across large spatial areas. They constitute avenues to provide complementary answers to questions on macroclimate niche changes, and to improve our ability to predict and anticipate invasions. (ii) Assessing invasions in non-analog environments have been poorly addressed so far. Because these situations cannot be predicted from the native range with static approaches, and thus their interpretations remain speculative, they require mechanistic approaches (e.g., [4]) or experiments (see below). It is however a promising field of investigation that may deliver invaluable insights on colonization processes in non-analog situations while also improving assessments of biodiversity under future climate changes [38]. Retrospective studies that examine the details of invasion success and failure into particular non-analog climates, relative to the native climatic niche, could inform us of possible predictors of invasion into non-analog climates (e.g., for niche-based spatial predictions) [32]. (iii) Although correlative niche shift studies of exotic species may guide experimental studies [9], a dual approach has been rare so far (but see [52]). Experimental studies on populations found in geographic areas where niche expansion occurred in the exotic range are needed to rigorously identify the related ecological or evolutionary causes, for example, through rapid evolution [10,43], increased phenotypic plasticity [53], or biotic interactions (e.g., enemy release) [30]. Similarly, information about unfilling can help identify interesting model systems [9] for studying why some habitats and landscapes are more resistant to invasions, for example, due to dispersal limitations [28] or abiotic or biotic resistance [54].

We expect that systematic use of this framework will substantially advance generalization about niche change,



not only in invasion studies (including pests and diseases) but also in studies of niche conservatism between disjoint distributions (e.g., arctic–alpine) [55] or across time in response to global change [49].

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### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.tree.2014.02.009>.

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