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Niche dynamics in space and time

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Niche conservatism, the tendency of a species niche to remain unchanged over time, is often assumed when discussing, explaining or predicting biogeographical patterns. Unfortunately, there has been no basis for predicting niche dynamics over relevant timescales, from tens to a few hundreds of years. The recent application of species distribution models (SDMs) and phylogenetic methods to analysis of niche characteristics has provided insight to niche dynamics. Niche shifts and conservatism have both occurred within the last 100 years, with recent speciation events, and deep within clades of species. There is increasing evidence that coordinated application of these methods can help to identify species which likely fulfill one key assumption in the predictive application of SDMs: an unchanging niche. This will improve confidence in SDM-based predictions of the impacts of climate change and species invasions on species distributions and biodiversity.

Introduction: The fundamental challenge facing predictive application of niche-based species-distribution models

The assumption that the niche of a species might remain unchanged [1–4], or change only slowly over hundreds to millions of years (i.e. niche conservatism; see Glossary) [5–7], currently influences the study of species distributions and has generated considerable debate [8]. This is because pervasive niche-conservatism is used as a justification for applying species distribution models (SDMs; see Glossary) [9,10] to predict species distributions in space and across time. In this way, authors assume slow or absent change in the niche to study species diversification and geographical distributions [11–15], to forecast species extinction and biodiversity loss in response to climate change [16–18] and to predict the establishment and spread of invasive species [19–21].

In reality, there is little basis for evaluating whether the assumption of an unchanging niche holds when predicting changes in species distributions in space and time. If niches of species are not static, then they can expand, contract or shift. These niche dynamics, if they occur over the time period or area of interest, probably invalidate conclusions based on the application of niche-based SDMs. One crucial issue in developing an evaluative framework for niche dynamics is resolving which niche concept(s) is most pertinent for the application of SDMs [22].

Niche-based SDMs are discussed and applied in the context of Hutchinson's niche [23] — defined by a combination of environmental characteristics (i.e. his 'hypervolume') — in which populations of a species can maintain a positive net growth rate. Hutchinson further distinguished between the fundamental environmental niche (see Glossary), which is genetically and physiologically determined, and the realized environmental niche (see Glossary), which includes, additionally, constraints arising from interspecific competition (Figure 1) [24,25]. The distinction between realized and fundamental niches is important for describing and understanding niche dynamics. This is because a niche-shift (see Glossary) could result from changing ecological processes influencing the realized niche as when, for example, an exotic species experiences release from natural enemies in the new environment. Alternatively, a niche-shift could involve both the realized and fundamental niches if, for example, the genetically-determined environmental tolerances of a species were to respond to selection during range expansion (Figure 1).

Ideally, predictions of species distributions (e.g. in a modified climate or different area) should, first, be based on a quantification of the fundamental niche and, second,

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Glossary

Allopatric speciation: speciation following the division of a large population into at least two new populations that are separated by a geographic barrier.
Brownian motion model: niche attributes of a species or clade are affected by genetic drift or selection in directions that are random and vary independently over time.
Climatic niche: an aspect of the environmental niche that is defined by limits in climatic variation. Outside of this niche, a population cannot maintain a positive net rate of population increase (e.g. owing to excessively low minimum winter temperature, insufficient growing season precipitation, etc).
Directional selection: occurs when natural selection favors phenotypic values that tend to lie either above or below the mean phenotypic value in a population.
Environmental niche: all environmental conditions that meet the physiological requirements of a species necessary for positive population growth rates (compare fundamental and realized niches, described below).
Founder effect: the tendency for the few individuals that disperse and found a new population to carry only a small, and potentially unrepresentative, portion of the genetic variation that exists in their population(s) of origin.
Fundamental niche: the requirements of a species to maintain a positive population growth rate, disregarding biotic interactions.
Niche: the requirements of a species to maintain positive population growth rates (see fundamental and realized niche).
Niche conservatism: the tendency for related species to have similar fundamental and/or realized niches; also, the tendency for the niche of a species to be little changed over time (i.e. to exhibit temporal autocorrelation).
Niche shift: any change in the position of either the fundamental or realized (Hutchinsonian) niche of a species.
Niche stasis: lack of any kind of change in the niche. Applies to either the fundamental or realized niche.
Null model: a model in which purely random processes create observed patterns; it is used in constructing a null hypothesis for statistical testing.
Phylogenetic signal: the tendency for more closely related species to have more similar characteristics.
Realized niche: the portion of the fundamental niche in which a species has positive population growth rates, given the constraining effects of biological interactions, such as competition.
Species distribution model (SDM): a model that describes or predicts the probability of the presence or absence of a species across environmental gradients or in a specified geographical area.

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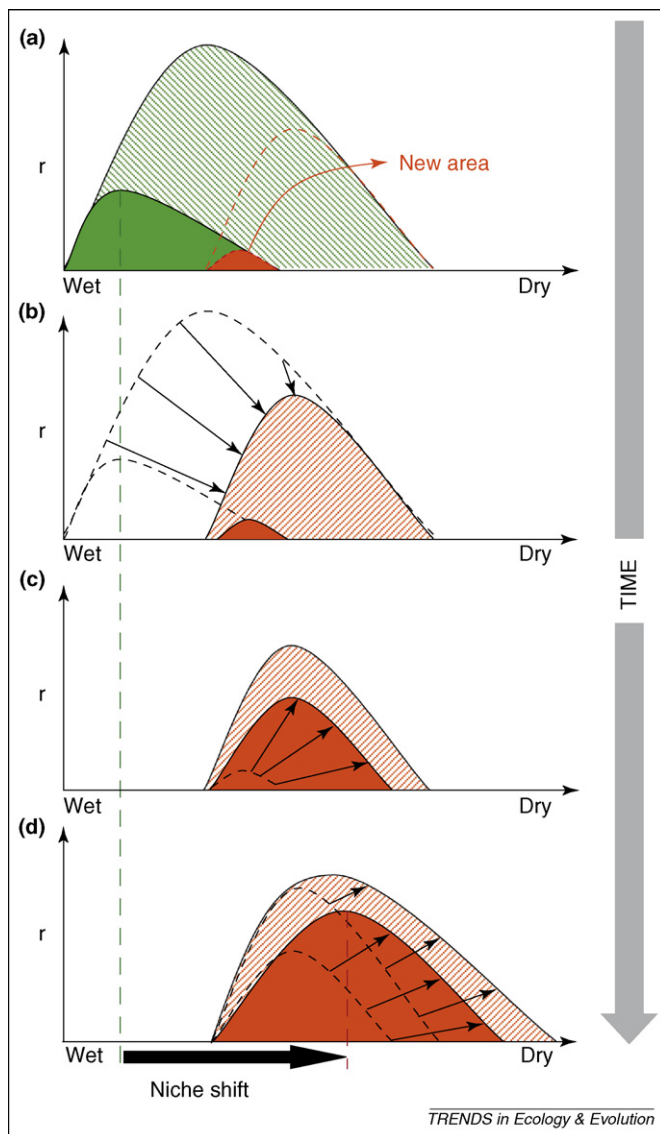[*] These authors contributed equally.

Figure 1. The relationship between fundamental and realized niche during a founder event and subsequent niche expansion along one environmental axis (relative moisture availability). There are four snapshots in time, which progresses from the top panel to the bottom. In each panel, the rate of increase of populations (r, on the y-axis) is shown as a function of location along a moisture gradient (on the x-axis). (a) The realized niche (dark green) of the species in comparison with its fundamental niche (light green), the reproductive rates that would occur in the absence of competitors. The dashed green line indicates the moisture optimum in relation to the original realized niche of the species. A collection of individuals from one end of the moisture gradient, together defining a realized niche (red area) and a fundamental niche (dashed red line), disperse to establish populations in a new area with similar conditions. (b) In the new area, populations of the species establish somewhere within the original realized and fundamental niches (red and light red areas, respectively), which are small in comparison to those of the species in its original range (change in fundamental niche shown by black arrows). (c) In the newly colonized area, the species expands (black arrows) its use of habitats (i.e. its realized niche) to portions of the fundamental niche that were not occupied in the original range, which might happen because of competitive release in the new area. (d) With time, directional selection acts to favor individuals that tolerate drier conditions than those potentially tolerated by the first colonists. This happens because populations now experience conditions that were not within the realized niche in the original range. Thin black arrows indicate the evolution of the fundamental niche and expansion of the realized niche in the invaded range. The cumulative shift in realized niche is also shown.

manipulative experiments, SDMs must be fitted with field observation data. However, observed distributions of species include effects of biotic interactions and for this reason only provide information on the realized environmental niche. Any change in biotic interactions might alter the realized niche [26] and affect the accuracy of predictions of species distributions.

However, even if one could estimate the fundamental niche, the main issue remains that using SDMs to project species distributions in space and time assumes, potentially uncritically, that neither the fundamental nor the realized niche changes [26]. Recent findings suggest that niche shifts do occur in previously unrecognized situations, owing to ecological processes changing the realized niche, and/or evolutionary processes altering the fundamental niche [6,27,28]. Furthermore, we still cannot predict which species will be affected by niche changes, nor is it clear under which ecological conditions or over what time periods these niche changes will be observed. Thus, it is crucial that we better understand the conditions that determine the range of niche dynamics — from rapidly changing niches (Box 1) to completely static niches (Box 2;

be constrained by the effects of biotic interactions. Given that the fundamental niche can only be estimated using costly manipulative experiments in the field and/or under controlled conditions, these estimates have only been conducted for a few species. In the absence of data from

> **Box 1. The case for rapid change of environmental niche**
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> Support for rapid niche shifts is found in diverse fields of ecology and evolution. Some theoretical models of speciation suggest rapid niche change [81]. For example, whereas strong differences in per capita survival and reproductive output between habitats (i.e. source-sink dynamics) favor niche stasis [82,83], weak differences, temporally correlated variation in fitness, and gene flow from source to sink might promote niche expansion [82]. The effects of dispersal and selection interact to determine whether the species niche (and range) contracts or expands rapidly [65] (reviewed in [84]).
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> Evidence for rapid niche shifts comes from empirical studies of invasive species ecology [35,36], phylogenetic analysis [12,14,70] and community ecology [24], and the occurrence of host shifts by pathogens is well documented [60,85]. Insects can expand the range of habitats they occupy and evolve increased dispersal rates in response to climate change [86]. Niche shifts can also occur during invasion of new geographical areas by plants [27,36,79] and animals [35], and have happened in less than 100 years [35]. Niche shift might be a factor that enables successful invasion by exotic species [36].
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> Niche shifts have also been studied experimentally. Invasive exotic species can undergo rapid adaptation and population differentiation, as shown in field [71] and laboratory [76] experiments. For example, Wright *et al.* [77] examined the occurrence of a California annual plant, *Collinsia sparsiflora*, in an area of patchy serpentine soils. They used five environmental variables in SDMs [10] to predict species distribution, survival of experimental plants and flowering performance. Their models predicted the flowering performance of experimental plants and two nearby populations from serpentine soil, and four additional serpentine species. The models did not, however, predict the performance of two non-serpentine populations of *C. sparsiflora* in serpentine soils, thus suggesting a niche shift. Wright *et al.* [77] also showed that the models performed well in predicting plant performance when competitors were removed (i.e. predicting the fundamental niche), suggesting that the fundamental and realized niches of the species were similar. Another experimental study, on *Pinus contorta* in British Colombia, demonstrated that populations are locally adapted to climatic conditions (i.e. they differ in their fundamental niche), but that competitors exclude most individuals from optimal environments within each local population (i.e. limited to their realized niche) [82]. Taken together, these studies show that rapid niche shift can occur in a variety of species and habitats.

see Glossary). Unfortunately, evidence for the occurrence of niche shifts is mixed and debated (Table 1).

The combination of niche-based SDMs, environmental data from the field, and phylogenetic information can help us to better define both the timescales over which shifts of the realized niche occur and which species are most likely to experience them. Additional empirical data on the life history characteristics, ecological circumstances and evolutionary histories that are associated with particular dynamics of species niches will also improve confidence in the predictions supplied by niche-based SDMs. Here, we examine how recent studies in ecology and phylogenetics have contributed to our understanding of the conditions, patterns, processes and timescales surrounding niche dynamics. We build on recent theoretical and empirical studies of niche change and stasis across different timescales to illustrate the observed variability in niche dynamics. Recent work has relied increasingly on the implementation of alternative models to guide hypothesis testing and has emphasized the need to identify factors that might affect the detection and quantification of niche shifts. These advances provide new understanding of niche dynamics that could help us to identify the conditions under which either niche stasis is a supportable assumption or the potential for niche shifts appears large. This in turn will improve our ability to assess the risk of establishment and invasion by exotic species, and to develop justifiable confidence in predictions of species response to climate change.

Niche conservatism meets phylogenetics

The use of the term niche conservatism in the literature is inconsistent. Niche conservatism has been used to signify that niches appear to be statistically correlated over time [12,17,29], and that the fundamental niche has a tendency to resist evolution [15]. This latter definition is similar to phylogenetic inertia, in which species have not evolved to reach ecological optima because of the lack of heritable variation or the presence of evolutionary constraints that prohibit occupation of some areas of niche space. The term is also similar to phylogenetic signal (see Glossary), in which trait variation among species remains associated with phylogenetic relationships [30]. Thus, niche conservatism might be assigned to various patterns resulting from niche dynamics. For example, stasis of the fundamental and realized niches (e.g. through stabilizing selection and competitive dominance, respectively), phylogenetic signal (e.g. owing to finite rates of random divergence of the fundamental or realized niche of species over time) and evolutionary constraints [30] could all be considered as niche conservatism. Nonetheless, these relationships remain vague until it is possible to identify the amount of niche change expected over time owing to random processes. Because of these terminological, conceptual and operational difficulties, we suggest that the terms 'niche stasis', 'niche shift' and 'phylogenetic signal' be used predominantly, to minimize confusion in studying niche dynamics.

How does species distribution modelling contribute to understanding niche dynamics?

The use of SDMs has been suggested as a tool with two particular applications: for identifying niche characteristics in natural systems and at spatial scales that make experimentation infeasible [10]; and for studying niche dynamics [8]. One way to model and test for niche shifts in response to climate change or speciation events is to predict past species distributions from models fitted under current climate conditions [11,17,31,32] (i.e. hindcasting), or similarly to forecast current distributions from models fitted using historical records [33,34]. Some hindcasting studies claim support for minimal niche change using a null hypothesis of change to randomly distributed, independent niches [17,29]. Nonetheless, methods to estimate the amount of niche change to be expected owing to random processes and to examine species data for deviation from random niche divergence have not been fully developed.

Niche-based SDMs have been used to demonstrate rapid niche changes during invasions by exotic species, for example fire ants (*Solenopsis invicta*) [35] and spotted knapweed (*Centaurea maculosa*, Figure 2) [36]. By contrast, the invasive Argentine ant (*Linepithema humile*) in North America shows little evidence of niche shift [37]. These examples of using SDMs to compare niche properties between species' native and invaded ranges (over tens to a few hundreds of years), and niches between the present and the late Pleistocene (over thousands of years [17,29]), show that change in the realized niche can occur over different timescales (Box 1; Table 1). Thus, SDMs can contribute to detecting niche shifts that occur in a species over time or between populations separated in geographic space. This is accomplished by fitting models with occurrence data on the species at one time or in one part of its range, then evaluating the performance of the models when they are projected in time (as in hindcasting) or in

Table 1. Studies of niche conservatism or shift 1996–2007, showing the lack of association between the frequency of or propensity for niche shift and any particular ecological conditions, morphological characteristics or evolutionary history

Topic	System	Conclusions	Refs
Character divergence	Theoretical	Character displacement among prey species is enhanced with some forms of predation	[57]
	Darwin's finches	Food resource and bill morphology change result from competition in a drought year	[58]
Host shift	Insect pest	Insipient speciation involves genotype–environment interaction	[59]
	Viruses and African carnivores	Related viruses find hosts in dogs (*Canis familiaris*), lions (*Panthera lio*) and others	[60]
	Tephritid fruit flies	Hybrid speciation event is associated with host shift	[61]
	Butterflies (*Papilio*)	Host shift is supported by change in predation regime	[62]
Niche conservatism	Theoretical	Niche conservatism is due to higher fitness of individuals in source habitats than in sinks	[63,64]
	Beech (*Fagus*)	Niche conservatism suggested by reciprocal modelling of beech in North America and Europe	[4]
	Plants and mammals	Conservatism supported by non-random association of occurrences with projected range	[17,29]
	Birds, mammals, butterflies	Niche conservatism displayed by sister taxa with adjacent distributions	[3]
	Theoretical	Gene flow crucial to determining local adaptation and range changes	[65]
	Plant communities	Niche conservatism is shown by correlation in range size for disjunctive congeners	[38]
	Argentine ant	Similarity between ants in native and introduced ranges revealed by niche modelling	[37]
	Plankton diversity	Diversity in tropics explainable by higher speciation rates and niche conservatism	[66]
Niche conservatism and shifts	Sundews (*Drosera*)	Niche shifts shown by clades, described by ancestral climate envelope reconstruction	[50]
Niche shift	Plant phenology	Radiation to new habitats is often accompanied by altered phenology	[67]
	Copepods	Niche shifts are adaptive responses to environmental variability	[68]
	Plant invasions	Ecological and evolutionary processes change during successive stages of plant invasions	[27]
	Genus *Arabidopsis*	Recently evolved species show greater changes in range and climatic characteristics	[69]
	Invasive species	Niche shift shown by lack of reciprocal predictability between native and invaded ranges	[35,36]
	Plant communities	No phylogenetic signal in comparison of occupied plant niches suggests niche shifts	[70]
	Introduced plant	Introduced populations rapidly adapt to conditions at local latitude	[71]
	Pinus contorta	Populations vary in optima of fundamental niche	[72]
	Bivalves	Shifts supported by species origin in warm waters and adaptation to polar regions	[73]
	Oaks (*Quercus*)	Niche characteristics and habitat occupancy suggest phylogenetic over-dispersion	[39,49]
Niche shifts and speciation	Dendrobatid frogs	Divergence in climatic niche occurred during speciation of Ecuadorian frogs	[11]
Niche size	Edaphic conditions	Niche size is maintained by gene flow and strong selection	[74,75]
	Invasive plant/laboratory	Plasticity and niche evolution both contribute to invasive ability	[76]
	Edaphic conditions	Modelling of niche affected by ecotypic variation in soil chemistry tolerance	[77]
Phylogenetic and ecological relatedness	Lizards (*Anolis*)	No relationship exists between clade phylogeny and climate or habitat niches	[12,40]
	New World warblers	Niche conservatism occurs in recently diverged species, shifts at deeper branches	[41]
	European plants	Niche positions explained by phylogenetic distance and taxonomic levels	[78]
	Aphelocoma jays	Pervasive niche shifts unrelated to phylogenetic distance	[14]
Range limits	Theoretical	Niche limits and demographic process interact to influence range limits	[79]
Species richness gradients	New World Birds	Niche conservatism, extinction in basal clades explains species richness gradient	[80]

geographic space (as with invasive species). Furthermore, these empirical results suggest that the uncritical assumption of niche stasis, so as to allow prediction using SDMs, appears to be questionable at best. New approaches are thus needed to keep predictive modelling from being at the mercy of an untested and understudied assumption. These approaches include consideration of phylogenetics and evolutionary models so as to improve understanding of niche dynamics.

How can phylogenetics contribute to understanding niche dynamics?

In the absence of extensive phylogenetic data, comparisons of characteristics of the realized niche in one species over time, or among putative sister-species, have used the criterion of non-random association of pairs of niche measurements to conclude that species niches show limited divergence over time or maintain a phylogenetic signal [3,17,29,38]. These comparisons of realized niches are of
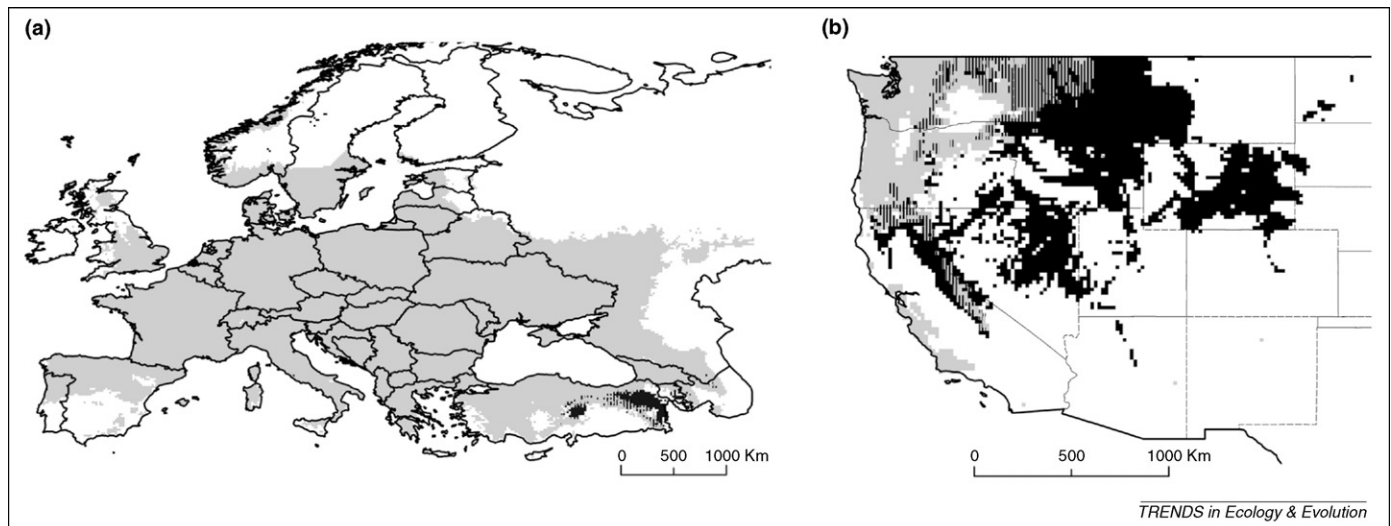
Figure 2. Niche shift in an invasive plant, spotted knapweed (*Centaurea maculosa*). The distribution of spotted knapweed was modeled with eight modeling techniques, and consensus predictions are shown (six of eight models). **(a)** The modeled distribution of spotted knapweed in Europe. Here, the gray area indicates predicted presence when the models have been calibrated with occurrence data from the European range. When this 'European model' is projected to the western United States **(b)**, the predicted range of the species is shown again in gray. However, when the models are calibrated with occurrence data from the USA, the species is predicted to occur in the black area. Projection of the 'United States' model to Europe (a) leads to predicted presence, shown also in black. The gray and black hatched areas in both panels show that there is little area that both models predict as being occupied by the plant and, thus, provide a spatially explicit representation of a shift in the species realized climatic niche. Adapted with permission from [36].

limited use in detecting niche change because they involve only relative differences among pairs of species. Also, given enough time, niche stasis is not the null expectation for evolution of the fundamental niche [30]. Furthermore, the possibility of parallel directional selection (see Glossary), the arbitrariness of taxonomic levels and the lack of knowledge of how much change should be expected given the amount of elapsed time make broader interpretation of simple among-species comparisons difficult.

In contrast to comparisons of species pairs, comparisons based on combining phylogenetic methods with empirical data on environmental niche characteristics might contribute to a better understanding of niche dynamics by providing a framework in which different patterns of distribution of niche characteristics on tree nodes are expected (e.g. [39,40]), based on underlying ecological and evolutionary mechanisms (Box 3). For example, a distance matrix that is derived from niche characteristics of species can be compared with a matrix of phylogenetic distances among the species by using a Mantel test or similar randomization. The presence or absence of significant correlation between corresponding elements of the two matrices is interpreted as the presence or absence of phylogenetic signal in the trait (e.g. [12,40,41]). Nonetheless, this approach reduces a phylogeny to a distance matrix that, while providing a measure of the concordance between ecological and phylogenetic distances, omits information on the timing and distribution of niche changes on the tree.

In the presence of significant correlation between phylogenetic distance and distance among environmental niche values of species, the question becomes whether there is more or less niche similarity than expected, given the amount of genetic change that has occurred. To address this, phylogenetic analysis, using information contained in tree topology, can be applied to characteristics of the realized niche in a similar way to how it is applied to analyze the evolution of morphological characters (e.g.

[11,42]). At the same time, interpretation of the analysis should recognize that niche characteristics observed in the field, as with morphological characteristics of specimens, are influenced by both genetic and environmental factors.

How can evolutionary models contribute to inference on niche dynamics?

The application of evolutionary models of character change supports our understanding of niche dynamics by helping us to choose among particular evolutionary processes that might have influenced patterns of niche change. For example, random evolution of a character (e.g. an aspect of the environmental niche of a species) over time can be modeled by the Brownian motion model, a null model (see Glossary) of character evolution in which direction and degree of change vary randomly over time and for which there are no additional constraints [43]. The resulting among-species distribution of the magnitude and direction of character change is Gaussian (bell-shaped), with a single expectation of no change and a finite standard deviation. This process results in among-species variance in character values (e.g. niche metrics) that increases with the square root of elapsed time [43].

A family of models, of which Brownian motion character-change is a special case, incorporates the possibility that selection can act, in addition to random effects, as a source of character differences among species [44]. Selection in these models can include both directional and stabilizing selection through a series of hierarchical models that include one or more terms for ecological optima for extant species, in addition to a term for Brownian motion [45]. Parameter estimation is possible through the use of likelihood methods, whereas a model comparison approach can determine which model of character change is most supported by the data [45]. For example, Losos *et al*. [40] failed to reject a Brownian motion model in favor of constrained evolution affecting the realized niche (Box 4).

Box 3. A case study: Florida oak niches

Niche shift and niche stasis are unlikely to be a simple dichotomy. A recent study by Cavender-Bares *et al.* [39] addressed the distribution of species niches and how this varied at different levels of a phylogeny. The authors used ecological, physiological and phylogenetic information to address the co-occurrence of 17 oak (*Quercus*) species that dominate forests in north Central Florida [39]. The authors developed a phylogeny for these species using sequences from two nuclear genes, and evaluated the physiological and physical characters of each species as seedlings (in laboratory experiments) and as adults (in the field). At the community level, they measured ecological habitat characteristics, including soil moisture and fire return interval, and used them to describe niche overlap among species. They then tested for phylogenetic signal by randomizing the phylogenetic distance scores among species. By comparing species co-occurrence frequencies and niche overlap at different levels of phylogenetic resolution, Cavender-Bares *et al.* identified clades at multiple phylogenetic levels in which niche overlap and co-occurrence were either more or less extensive than expected on the basis of a randomization test.

Cavender-Bares *et al.* found that species niches were over-dispersed among the major clades in the oak phylogeny, indicating that niche shifts occurred extensively within oak clades and that species within clades were less ecologically similar than would be expected by chance (Figure Ia) [39]. Nonetheless, species niche distribution within subclades at intermediate phylogenetic resolution showed greater levels of over-dispersion than occurred either at the species level or in the basal oak clades. Furthermore, the authors suggested that a negative correlation between phylogenetic distance and differences in soil moisture preferences hints at niche convergence among distantly related species. In contrast, consideration of wider taxonomic and environmental scope revealed phylogenetic signal (Figure Ib).

Other studies that used phylogenetic information identified patterns of ecological differences in terms of evolutionary relatedness. For example, patterns in North American wood-warblers (Parulidae) suggest the presence of phylogenetic signal in niche traits in recent speciation, but niche shifts deeper in the evolutionary pasts of the clades [41]. In addition, the combination of niche-based distribution models and molecular phylogenies of dendrobatid frogs to estimate ancestral states of niche dimensions suggests niche divergence and complementarity in association with speciation [11]. Thus, recent studies have documented substantial niche shifts, but niches do not seem to be widely divergent in some cases, with the degree of shift varying with phylogenetic level within a clade.
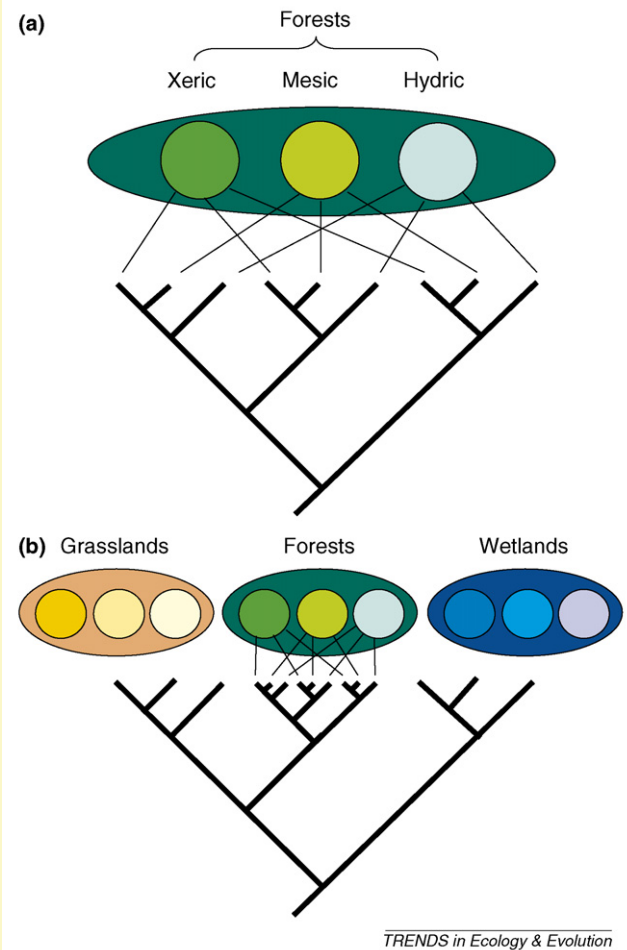

Figure I. Detecting a phylogenetic signal in the environmental niches of oaks (*Quercus*) depends on environmental variation and phylogenetic tree size. **(a)** Niche shifts are shown by the over-dispersed pattern of the occurrence of related species in relation to the moisture differences among types of forest (xeric, mesic and hydric); there is no phylogenetic signal. **(b)** With larger environmental and taxonomic scope, phylogenetic signal in habitat preference is observed when comparing clades at deeper levels on the expanded phylogenetic tree. Dryer conditions occur towards the left of the figure and wetter conditions to the right, both among the three habitat types (grasslands, forests and wetlands) and within each of these groups. Redrawn with permission from [49].

Other methods to detect non-Brownian evolution (e.g. by detecting that potential environmental niches are filled non-randomly in association with speciation events) are also possible by correlating phylogenetic contrasts with the height of the nodes at which the contrasts are assembled. A significant correlation leads to rejection of the Brownian motion model because trait evolution occurs systematically throughout the tree [46].

How have environmental niche data, phylogenetics and evolutionary models been combined?
The combination of niche modelling and the use of phylogenetic methods has demonstrated shifts of realized environmental niche that are associated with speciation and ecological diversification. For example, Knouft *et al.* [12] examined the degree to which phylogenetic similarity parallels similarity of realized climatic niches (see Glossary) of Cuban *Anolis* lizards. The authors recognized that a negative correlation between evolutionary distance and niche similarity would suggest that niches tend to show phylogenetic signal, perhaps similar to Brownian motion evolution. They used a phylogenetic tree of 11 Cuban *Anolis* species to calculate the sum of the branch lengths between pairs of individuals, each representing a distinct species, and determined the niche similarity of the species in terms of climatic niche dimensions. The authors found no significant correlation between niche similarity and phylogenetic distance, indicating no detectable phylogenetic signal in the characteristics of the climatic niche.

In another example, Graham *et al.* [11] used climatic variables, species occurrence data, niche modelling and a phylogeny to describe the relationships among niches of species in three clades of dendrobatid frogs in Ecuador. Because the authors' methods hinged on reconstruction of the ancestral climate niche, and given that these reconstructions are error-prone [47], the authors tested for directionality in the evolution of pairs of sister species by comparing the phylogeny of the frogs (a maximum

likelihood tree) with what might be produced if trait evolution were to follow a Brownian motion model. They failed to reject the adequacy of invoking a Brownian-like evolutionary process to explain among-species differences in niche traits. They also found, however, that sister species generally showed niche divergence along gradients of moisture and seasonality.

Is scale important in studying niche dynamics? A caveat

Recent studies have shown that the scale of investigation, be it spatial, temporal, environmental or phylogenetic, is important in studies of niche dynamics. The effects of scale (e.g. in studying the climatic niche) can be tied to the spatial resolution at which climatic information or species distribution data are available (Figure 3). In some cases, data will thus need to be collected and/or analyzed at multiple resolutions and extents. For instance, Broennimann *et al.* [36] showed that rapid niche change was detectable when both native (European) and invaded (North American) ranges of an exotic plant were compared (Figure 2). The temporal period in their study was only 120 years, but the geographical extent was large, encompassing Europe and the western United States. Similarly, the statistical power to detect phylogenetic signal within a clade depends on tree size and the taxonomic inclusiveness of the study [48,49]. In their biogeographical study of native vegetation in northern Florida, Cavender-Bares *et al.* [49] (Box 3) found that phylogenetic signal was more evident when more environments and a larger phylogenetic tree were used to examine the phylogenetic structure
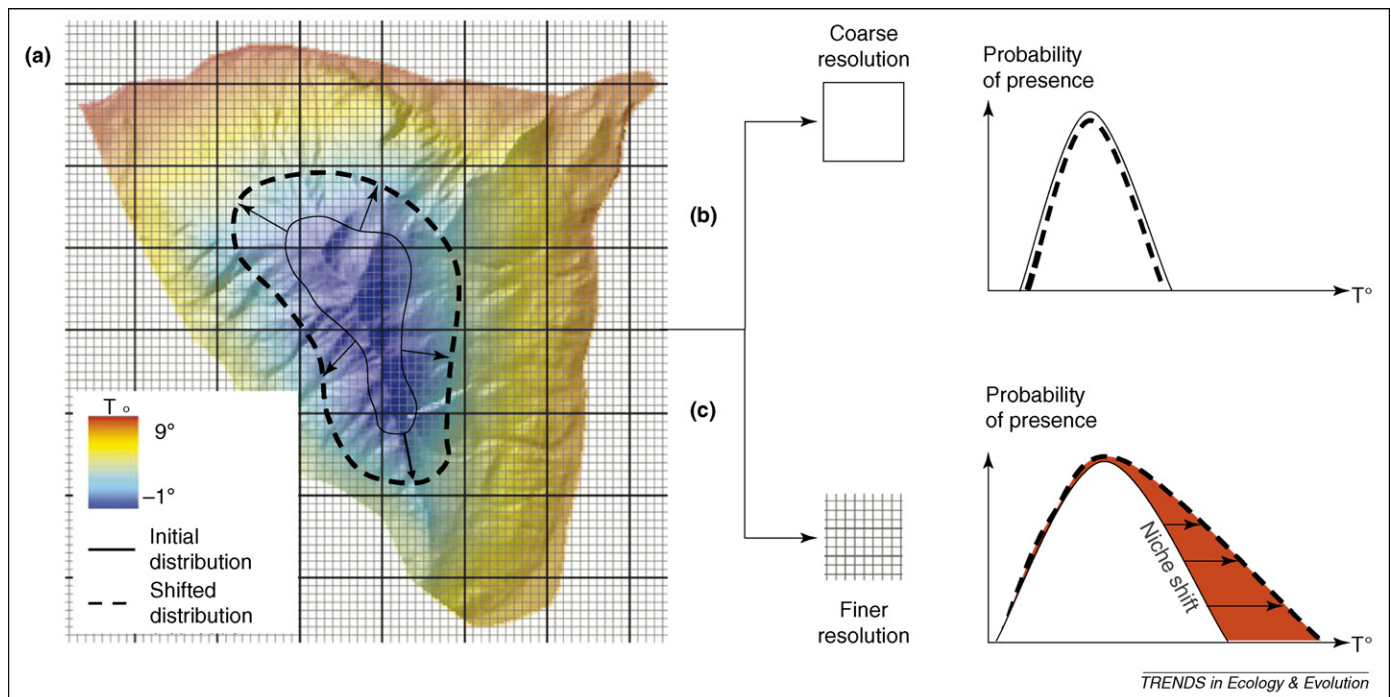

Figure 3. Effect of sampling resolution on detecting an environmental niche shift. **(a)** A hypothetical gradient of annual mean temperature is shown by color shading on a mountain peak. The realized niche of a hypothetical plant shifts to include warmer temperatures, with a corresponding expansion of the distribution of the plant to lower altitudes. The initial and expanded distributions of the species are shown by solid and dashed lines, respectively. Large and small cells (squares) show a difference in spatial resolution (in this case, 10x) of data on species occurrence and local temperature, as might be obtained from a sampling program. **(b)** When temperature variation (and/or species presence) is expressed at a coarse resolution, both initial and shifted niches result in estimated species distributions that show identical probabilities of species presence as a function of temperature. **(c)** Expression of spatial variation at a finer spatial resolution enables detection of the niche shift, shown by the increased probability that species will be present at higher temperatures (i.e. lower elevation).

of oak (*Quercus*) and other plant communities (Box 3, Figure I).

Variation in choice of scale thus influences our ability to identify niche shifts, to determine their prevalence within a phylogeny, and to evaluate their magnitude. These results suggest that multi-scale studies of niche shifts, using both phylogenetic trees and niche-based SDMs, will help us to identify clades that are especially prone to shifts in environmental niche. Multi-scale studies will also produce empirical guidance regarding the scales at which studies of environmental niche need to be conducted to describe adequately niche-shift prevalence and magnitude.

What can we conclude regarding the dynamics of the environmental niche?

Understanding niche dynamics is a prerequisite to predicting patterns of biodiversity in future climates or in areas distinct from where models are fitted. However, neither niche stasis nor rapid niche shift prevail in current studies (Table 1). It would be helpful to know whether niche shifts are likely to occur in the case of biological invasions, and whether niche stasis predominates in the case of climatically induced range shifts within a region. However, the necessary data for these conclusions do not exist. In the case of biological invasions, a strong founder effect (see Glossary) followed by genetic drift, directional selection or hybridization might occur frequently, but sufficient studies to support this possibility have not yet been conducted. Clearly, studies that combine phylogenetic and ecological data show that closely related species can frequently diverge along one or more environmental gradients [11,14,39,49]. Nonetheless, the degree to which niche dynamics might affect predictive modelling is not yet known, which should weaken confidence in the conclusions of studies relying on SDMs to predict effects of climate change or species invasions. The most important action that can be taken to boost this confidence is to collect the data necessary to identify biological factors, both current and historical, that are associated with patterns of niche dynamics.

What remains to be done?

The patterns of niche dynamics over time need rigorous study. Sufficient empirical work is needed to conduct meaningful meta-analyses of correlates of niche dynamics. Confidence in the use of niche-based SDMs for prediction will increase markedly with a general understanding of how environmental conditions influence rates of niche change, the spatial and temporal variability of these rates, their variation with time-span under consideration, focal clade, the life-history variability of the component species in the clade, and phylogenetic tree size. For example, we speculate that clades that have high rates of polyploidy, species with strongly bimodal dispersal distances, and ample genetic variation within species are more prone to rapid niche shifts than are clades where these characteristics are absent. Similarly, the realized niche of competitively dominant species might be unlikely to change over any timescale. Other possibilities could be suggested, and supportable hypotheses should be tested.

There is an additional need for comparative studies that identify both the groups of species that are characterized by environmental niche stasis or shifts, (e.g. [50]) and the attributes that these species share. Similarly, the question of which characteristics of the realized niche need to be measured should be addressed. One could, for example, first estimate a variety of modeling parameters that describe niche traits (e.g. environmental limits, estimated environmental optima, niche position etc.) and then analyze whether and how use of these parameters affects discernable phylogenetic patterns of niche change. Probably, models that describe the realized niche using variables that are closely related to functional and physiological species characteristics will provide more meaningful ecological and evolutionary information than do models using other variables.

Increasing refinement of alternative hypotheses, such as alternative models of the evolution of the environmental niche, are likely to contribute to understanding evolutionary and ecological factors associated with patterns of niche dynamics. Furthermore, alternative models for character change have recently been developed in both phylogenetics [51–53] and quantitative genetics [54]. These methods enable one to identify trends in niche dynamics, for example, clade propensities for experiencing stabilizing and/or directional selection, the contribution of random evolution to niche dynamics, and the existance of evolutionary stable lineages within portions of clades. These approaches have yet to be applied to environmental niche-related characters, in general, and specifically to characteristics of the climate niche. New studies can attempt to identify lineages in which niche shifts are either overwhelmingly small or unlikely, such as lineages with a strong phylogenetic signal, evidence of a long history of stabilizing selection, and maintenance of niche characteristics in spite of wide geographical separation of species distributions. Species identified in these studies will be good candidates for more confident predictions of their response to climate change.

The relative contributions of directional and stabilizing selection to among-species variation in niche characteristics can now be analyzed with new tools [55]. By helping us to choose species with conservative evolutionary histories, these analyses will provide additional confidence in predictions made with SDMs. By contrast, estimating the propensity for niche change, and the historical rate and magnitude of niche change in clades could help us to identify lineages in which the probability of future niche change is great relative to other lineages. Studies that put trait variability into a phylogenetic context are likely to identify lineages with a propensity for niche change and, for example, identify species that might become invasive when introduced to new areas. To do this, we require greater understanding of the relationship between the rate of niche change over phylogenetically meaningful time spans and the rate of niche change over a hundred to several hundred years. This will help us to predict the frequency of niche shifts and other niche dynamics over the short term. The interpretation of phylogenetic data in the context of rapid niche change might involve the use of calibrated trees for which the actual rate of niche change could be calculated. These areas remain open for investigation.

Finally, although observed changes in environmental niche might be due to evolution of the fundamental niche, currently there is no method to evaluate the relative influence of fundamental and realized environmental niches to niche variation arising from either speciation or change within a species over time. We suggest that innovative combination of phylogenetic methods and physiological experimentation to model the fundamental niche (e.g. [56]) could answer, if only partially, the question of the relative importance of changes in the fundamental and realized niches in observed patterns of niche dynamics.

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