

Most invasive species largely conserve their climatic niche

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Edited by Susan P. Harrison, University of California, Davis, CA, and approved August 6, 2020 (received for review March 6, 2020)

The ecological niche is a key concept for elucidating patterns of species distributions and developing strategies for conserving biodiversity. However, recent times are seeing a widespread debate whether species niches are conserved across space and time (niche conservatism hypothesis). Biological invasions represent a unique opportunity to test this hypothesis in a short time frame at the global scale. We synthesized empirical findings for 434 invasive species from 86 studies to assess whether invasive species conserve their climatic niche between native and introduced ranges. Although the niche conservatism hypothesis was rejected in most studies, highly contrasting conclusions for the same species between and within studies suggest that the dichotomous conclusions of these studies were sensitive to techniques, assessment criteria, or author preferences. We performed a consistent quantitative analysis of the dynamics between native and introduced climatic niches reported by previous studies. Our results show there is very limited niche expansion between native and introduced ranges, and introduced niches occupy a position similar to native niches in the environmental space. These findings support the niche conservatism hypothesis overall. In particular, introduced niches were narrower for terrestrial animals, species introduced more recently, or species with more native occurrences. Niche similarity was lower for aquatic species, species introduced only intentionally or more recently, or species with fewer introduced occurrences. Climatic niche conservatism for invasive species not only increases our confidence in transferring ecological niche models to new ranges but also supports the use of niche models for forecasting species responses to changing climates.

Bayesian inference | biological invasions | niche breadth | niche dynamics | species distribution models

Recent times are seeing the resurgence of the ecological niche as a focus for ecological and evolutionary studies (1–3). As a key concept linking species distributions and environmental conditions, the ecological niche has been widely applied to reconcile diverse topics that could not be previously considered in one framework (4, 5). Assessing species niches and their dynamics can help elucidate patterns of species distributions and global diversity (4, 6), rates of specialization and extinction (3, 7), mechanisms underlying sympatric and allopatric speciation (8, 9), and species adaptations to different environmental conditions (10, 11). In the Anthropocene, species are shifting distributions in an unparalleled magnitude, and the ecological niche is a promising concept to develop better tools for conserving biodiversity and informing management strategies (1, 9). Central to this area are ecological niche models (ENMs), which have been used for predicting potential invasion risks and future extinction rates by quantifying species niches based on the relationships of species distributions and environmental predictors (2, 10). One key assumption for applying ENMs is that species niches change very slowly across space and time (i.e., niche conservatism), so that species occupy similar environmental conditions in new geographical ranges or time periods (12, 13).

Niche conservatism was once thought to be common at different spatial and temporal scales (4, 5). Recently, a number of studies reported changes in niche breadth and/or position (i.e., niche shift), sparking a widespread debate whether niches are conserved through ecological and evolutionary time spans (2, 3, 14). Support for the niche conservatism hypothesis exists in some birds (e.g., ref. 15), fungi (e.g., ref. 16), plants (e.g., ref. 13), and mammals (e.g., ref. 17), whereas niche shift has been reported in some reptiles (e.g., ref. 18), insects (e.g., ref. 19), aquatic invertebrates (e.g., ref. 20), freshwater fishes (e.g., ref. 21), and marine fishes (e.g., ref. 22). In addition, Rolland et al. (6) reconstructed ancestral and present niches for 11,465 terrestrial species and found significantly faster rates of niche shift in endothermic vertebrates than ectothermic vertebrates. Due to the conflicting conclusions of previous studies and because these mostly tested the niche conservatism hypothesis solely for species within one taxonomic group (2, 14), it is hard to obtain a general pattern of niche dynamics across clades. This situation also reduces the confidence in applying ENMs to predict species distributions in new space or time (2, 13) and limits our ability to forecast species responses to upcoming climate changes (10).

Understanding niche dynamics is pivotal to developing effective conservation strategies (2, 11, 23), and biological invasions represent a unique opportunity to study whether species conserve niches in a short time frame and how species respond to rapidly changing environments (18, 24). Invasive species have been massively introduced to new areas, yielding separate datasets of native and introduced distributions across the globe (2, 4,

Significance

There has been a widespread debate whether the ecological niche of species is conserved across space and time. This niche conservatism hypothesis is of high practical relevance for conserving biodiversity. Here, we synthesized empirical evidence on this hypothesis for invasive species to investigate how their climatic niche changes between their native and introduced ranges. Our results supported the hypothesis overall, but we also found important differences among taxa with different characteristics and for different types of data. Our findings are not only relevant for predicting spatial distributions of invasive species in their exotic ranges but also for forecasting species responses to changing environments in the Anthropocene.

Author contributions: C.L. and J.M.J. designed research; C.L., C.W., and J.M.J. performed research; C.L. analyzed data; and C.L., C.W., W.X., and J.M.J. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at <https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2004289117/-DCSupplemental>.

First published September 3, 2020.

22). In the process of colonizing new habitats, invasive species either maintain, expand, or contract their niche space as a consequence of changes in the realized niche (i.e., the set of all biotic and abiotic conditions in which a species is observed in nature) and/or the fundamental niche (i.e., the set of all abiotic conditions under which a species is inferred to maintain positive population growth in the absence of biotic interactions) (12, 25). Changes in realized and fundamental niches are two non-mutually exclusive processes (12, 26). When being introduced to new ranges, invasive species often face new biotic interactions (e.g., competition and predation) and dispersal limitations (e.g., geographical barrier and habitat fragmentation), leading to a change in the realized niche but not per se in the fundamental niche (18, 27, 28). However, a number of invasive species have been found to evolve rapidly in their new ranges, resulting from genotype sorting, genetic recombination, interspecific hybridization, or natural selection (12, 29–32). The evolution of environmental tolerance or the development of appropriate characters can facilitate species adaptation to exotic environmental conditions, causing changes in both realized and fundamental niches (2, 4). Although there is an increasing interest in exploring how species change niches during invasion processes (e.g., refs. 13, 18, 19, 23), pervasive disputes exist in the conclusions of niche conservatism and the patterns of niche dynamics (2, 12).

A key factor for varying conclusions in previous studies might be the highly diversified techniques used for testing different assumptions and assessing niche dynamics for invasive species (1, 7, 14, 33). Guisan et al. (2) reviewed the techniques and classified them into three approaches. The ordination approach directly compares native and introduced niches in a two-dimensional (2D) environmental space constructed by two synthetic axes calibrated from associated environmental variables (33). The ENM approach assesses niche dynamics based on the predictability of ENMs that are calibrated using environmental and species distribution data in one range and transferred to the new range (7). The univariate approach estimates changes in niche breadth and position along an individual environmental variable across the landscape where species occur (14). However, conflicting conclusions regarding niche conservatism are frequently reported for different approaches (2). For example, Guo et al. (34) applied the ordination, ENM, and univariate approaches for the globally introduced *Phragmites australis* and found ambiguous results, supportive as well as contradictory to the niche conservatism hypothesis, with conclusions highly depending on the approach.

Although no technique is considered most appropriate in all contexts (5), the COUE scheme (a unified terminology representing Centroid shift, Overlap, Unfilling, and Expansion) developed by Broennimann et al. (33) and improved by Petitpierre et al. (13) has become the gold standard to address niche conservatism (2, 23). This scheme not only inherits the convenience and robustness of the ordination approach but also overcomes the biases introduced by spatial resolution and sampling efforts (2, 33). Further, the COUE scheme is informative about linking the binary pattern (i.e., niche conservatism is either observed or not) and the continuous process (i.e., the magnitude of niche shift is measured) of niche conservatism in one framework (2, 5, 35). To test the niche conservatism hypothesis as a process, the COUE scheme first constructs a 2D environmental space from two synthetic axes associated with all environmental variables using a principal component analysis (PCA). The global environmental space of species is then split into three components (Fig. 1): stability (S) represents the environmental space occupied in both native and introduced ranges, unfilling (U) represents the environmental space only occupied in the native range, but also available in the introduced range, and expansion (E) represents the environmental space only occupied in the

introduced range, but also available in the native range (2, 13). To account for the difference in sampling strategies and efforts, a kernel density function is applied to smooth the density of occurrences in the native and introduced environmental space, respectively (13, 33). The magnitudes of S and E are weighted by the occurrence density in the introduced range, whereas the magnitude of U is weighted by the occurrence density in the native range (33). Only expansion is suitable to characterize the magnitude of niche shift, because unfilling reflects the potential environmental condition that species may further colonize in the introduced range after a certain lag time (13, 15, 18). The COUE scheme allows for testing the niche conservatism hypothesis as a binary pattern using two statistical methods, namely the niche equivalency test and the niche similarity test (33). The former determines whether native and introduced niches are significantly equivalent to each other via randomly reallocating species occurrences between two ranges, and the latter determines whether native and introduced niches are more similar to each other than expected by chance via randomly reallocating species occurrences in one range.

Although many studies have addressed the question whether species conserve their niche during contemporary biological invasions, a comparison of findings across studies has only rarely been carried out (but see ref. 2), and we are not aware of a single study that synthesized findings of niche dynamics to investigate the underlying mechanisms. Therefore, we performed a synthesis of studies that tested the niche conservatism hypothesis and assessed niche dynamics for invasive species (12). We focus on the realized niche, because all studies included here quantified the change between native and introduced niches using only distribution data compiled in the field. Among studies, the vast majority (91.9%) of predictor variables used for assessing species niche were climatic (see *Materials and Methods* for more details),

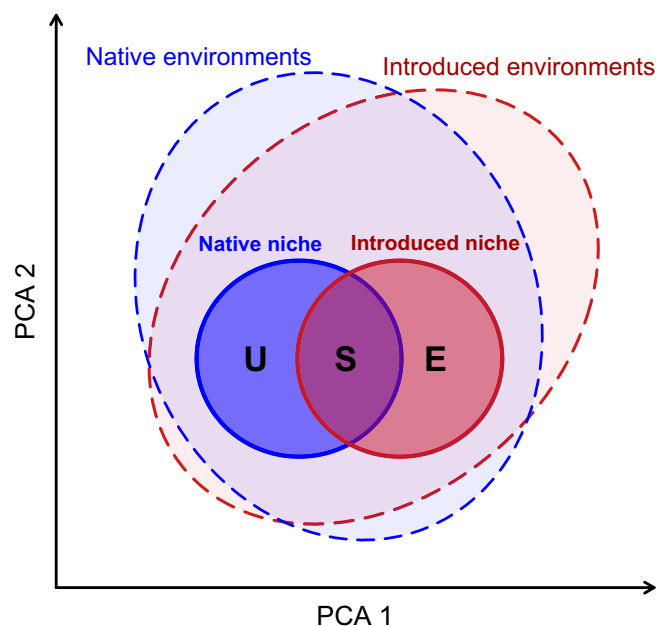


Fig. 1. Schematic representation of the decomposed global niche using the COUE scheme. Dotted lines show available environments in the native range (light blue) and invaded range (light red), and the overlap shows the analogous environments present in both ranges. Filled blue and red circles show the native and introduced niches that represent the environmental space occupied in the native and introduced ranges, respectively. Stability (S) represents the environmental space occupied in both native and introduced ranges. Unfilling (U) and expansion (E) represent the environmental space only occupied in the native and introduced ranges, respectively.

which can be largely attributed to both the crucial role of climatic factors in shaping species distributions and the increase in publicly available climate data (6, 19, 26).

Our study addresses two overarching questions: 1) Do invasive species conserve their climatic niche between native and introduced ranges, and 2) are there strong differences in the magnitude of niche shift between species of different taxonomic groups and habitats, and between different types of data used in existing studies? To answer these questions, we first reviewed all studies testing the niche conservatism hypothesis and then conducted quantitative analyses using data from studies applying the COUE scheme. Specifically, data about three metrics (E, S, and U) were compiled for each species to estimate the changes in breadth and position between native and introduced climatic niches. To better understand the response of invasive species to exotic climatic conditions, we applied Bayesian hierarchical models to investigate how species characteristics, introduction history, and parameters of niche estimation affected niche dynamics.

Results

Study Composition. We found remarkable differences in focal organisms and niche approaches among studies (*SI Appendix, Fig. S1*). Most studies focused on plants (38.4%) or terrestrial ectotherms (33.7%), rather few on aquatic species (16.3%), and even fewer on terrestrial endotherms (11.6%). Although our dataset covers 13 taxonomic groups, most studies (69.8%) only included one species (*Dataset S1*). There were 25 studies applying more than one approach, with ordination approach being the most common overall (80.2%), while only four studies applied the hypervolume approach (i.e., climatic niche was compared in a multidimensional space constructed by three or more predictors). Of 22 techniques identified, the COUE scheme was most widely used across studies (60.5%) and the frequency was even higher (70.3%) if only considering studies published after 2012, the year of its development. Thirteen criteria were adopted for concluding on niche conservatism, with the largest number of studies (37.2%) based on the match between the occupied native and introduced environmental space (Match env; *Dataset S1*).

Synthesis of Studies. The niche conservatism hypothesis was rejected in most studies (62.8%) and for most species (59.5%). Among groups of organisms, the highest rates of rejection were found in aquatic species (78.6% of studies; 71.1% of species) and

the lowest in terrestrial endotherms (40.0% of studies, 44.8% of species; *SI Appendix, Table S1*). The approach with the lowest rejection rate across studies was the ENM approach (61.8%); across species it was the ordination approach (49.6%). For species assessed by two or more studies, the proportion of species with contrasting conclusions among studies was remarkably high (74.0%). Even within studies, the inconsistency of conclusions remained high if species were assessed in different continents (41.9%), by different techniques (35.0%), or by different criteria (36.2%). For species assessed by the COUE scheme, rejection rate was extremely high for the niche equivalency test (99.1%), whereas it was 51.7% for the niche similarity test.

Scenarios of Niche Changes. We found a continuum of changes between native and introduced climatic niches, from highly conserved niches to considerably expanded niches (Fig. 2). The change in niche breadth was measured using the ln-transformed ratio of the breadth of the native niche to that of the introduced niche (breadth ratio), and the change in niche position was measured using Sørensen's similarity index calculated based on the occupied environmental space of native and introduced niches (niche similarity). Changes in niche breadth and position occurred most frequently under scenarios representing a larger native niche (65.4%; Fig. 2 *A, B, E, and F*) and similar niches (72.3%; Fig. 2 *A–C and D*). In the most frequent single scenario (32.8%; Fig. 2*B*), the native niche was larger than but not completely containing the introduced niche, and the two niches had a similar position. Interestingly, the scenarios where the native niche completely contains the introduced niche contributed to 20.5% of all cases (Fig. 2 *A and E*), whereas the opposite scenarios where the native niche is a subset of the introduced niche were much less frequent (7.1%; Fig. 2 *D and H*). Corresponding climatic niche changes were also found in each group of organisms (Fig. 3). The scenario of a larger native niche and of similar niche positions was the most prevalent, whereas the scenario of a smaller native niche and of dissimilar niche positions occurred least frequently.

Niche Similarity between Continents. The assessments of climatic niche dynamics were not evenly distributed among continents (Fig. 4), with most assessments focusing on species native in a continent of the Northern Hemisphere (66.8%; Asia, Europe, and North America) and species introduced to a well-developed

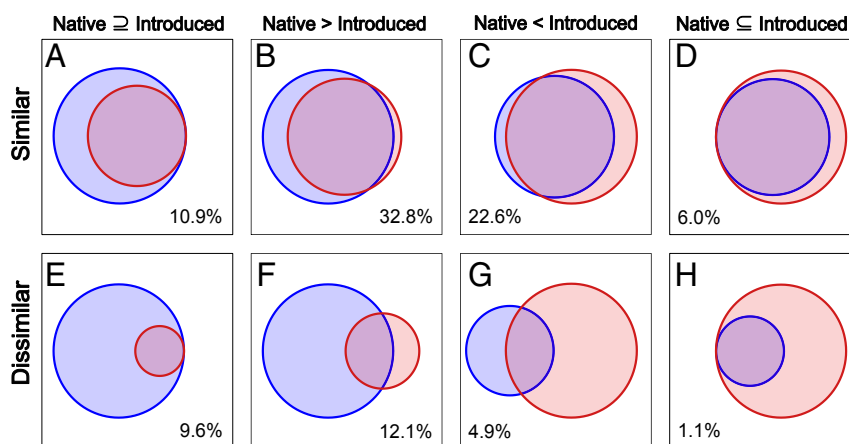


Fig. 2. Eight simplified scenarios of changes in breadth and position between native and introduced climatic niches. In the 2D environmental space, the native niche (blue circle) could be containing (*A and E*), larger than (*B and F*), smaller than (*C and G*), or belonging to (*D and H*) the introduced niche (red circle). Two niches can occupy similar (*A, B, C, and D*) or dissimilar (*E, F, G, and H*) positions. The breadth and similarity of native and introduced niches are averaged across all species under each scenario, with the percentage showing the frequency of the scenario. Niche breadth is quantified using dynamic data from studies that estimate niche dynamics using the COUE scheme, and niche similarity is quantified using Sørensen's similarity index. The breadth of the smaller niche is set as a proportion of the larger niche for better visualization.

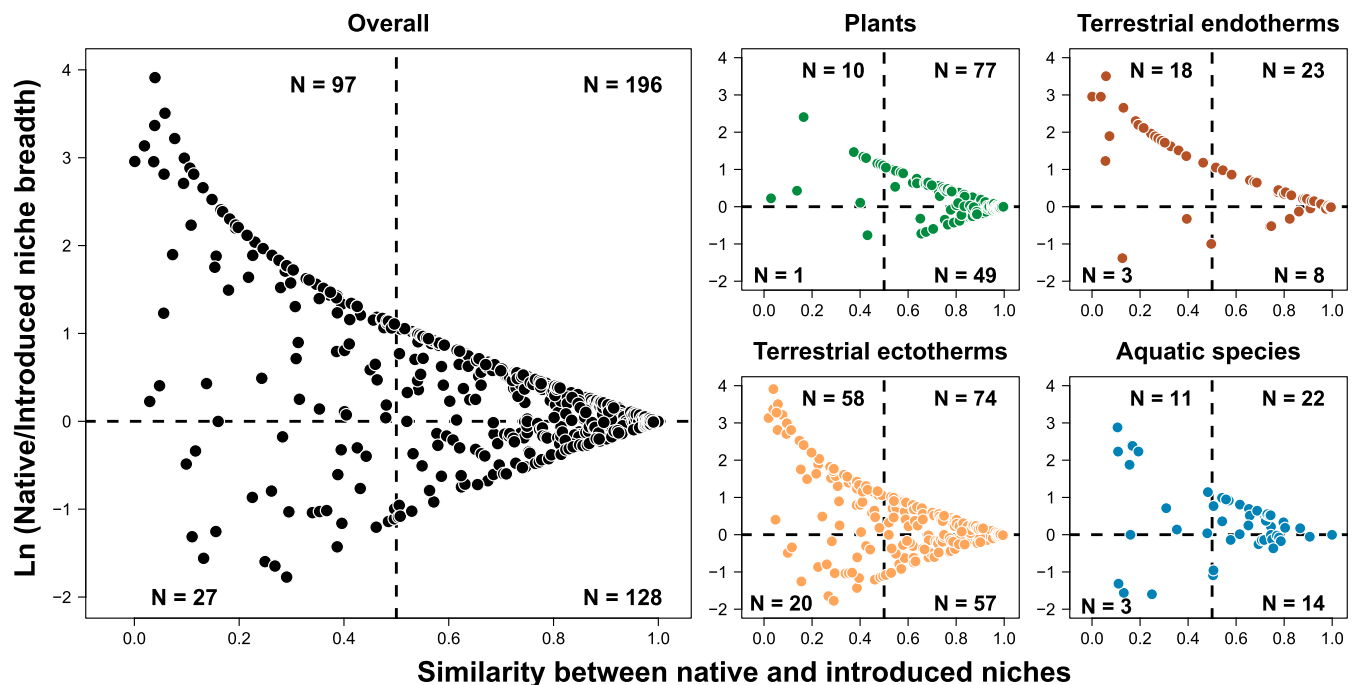


Fig. 3. Relationships between niche similarity and breadth ratio for all species (overall) and for each group of organisms. Niche similarity is quantified using the Sørensen similarity index, and breadth ratio is the ln-transformed ratio of the breadth of native niche to that of the introduced niche. In each panel, points with breadth ratio larger than 0 indicate that the native niche is larger than the introduced niche, and niche similarity larger than 0.5 indicates the two niches occupy a similar position in the environmental space. The numbers of points in each corner are shown in each panel.

continent (74.1%; Australia, Europe, and North America). A higher niche similarity was found for species introduced from Europe to North America (0.87 ± 0.06 ; mean niche similarity \pm 95% confidence intervals) and to Oceania (0.83 ± 0.04). By contrast, niche similarity was lower for species that were native in more than one continent and introduced to Europe (0.41 ± 0.19) and for species introduced from Asia to North America (0.42 ± 0.19).

Assessment of Niche Changes. The generality of a larger native climatic niche and similar niche positions was further supported by the breadth ratio being markedly larger than 0 (0.42; hereafter, mean effect sizes are represented by the mean of Bayesian posterior values) and similarity being larger than 0.5 (0.65; Fig. 5). These results demonstrate that the native niche was overall 1.52 times larger than the introduced niche, and invasive species colonized similar climatic conditions in native and introduced ranges. More than half of the global niche was in the zone of stability (0.53), confirming the tendency of species to occupy similar climates in both ranges. Unfilling contributed to one third of the global niche (0.33), more than twice as much as expansion (0.14), meaning that invasive species still had larger potential to occupy exotic climates in the introduced range but only limited capacity to expand into new climatic space. This conclusion was also supported by findings from the original studies, which reported very limited niche expansion (<10%) for most species (54.9%; Dataset S1).

There were clear differences among groups of organisms (Fig. 5). Plants showed the lowest breadth ratio (0.23) but the largest niche similarity (0.82), indicating that invasive plant species occupied a relatively larger introduced climatic niche but preferred climates similar to those in the native range. Plants also had much lower unfilling (0.22) than the other three groups, indicating the reduced climatic space left for their future colonization. Much lower niche similarity was found for terrestrial

endotherms (0.49) and aquatic species (0.51). Expansion of terrestrial ectotherms (0.18) and aquatic species (0.18) were about two times larger than that of plants (0.09) and terrestrial endotherms (0.08), indicating their stronger capability to colonize new environments.

Influence of Factors. Close associations were found between climatic niche dynamics and groups of organisms (Fig. 6). Compared to plants, terrestrial animals (i.e., endotherms and ectotherms) had much larger breadth ratios, demonstrating their relatively narrower introduced climatic niches. Aquatic species showed much lower niche similarity but larger expansion, suggesting their stronger capability to colonize new environments. Additionally, terrestrial ectotherms and aquatic species had larger unfilling, indicating that the suitable environments for their colonization were not well-occupied.

Climatic niche dynamics were also related to the intentionality and year of species introduced to new areas (Fig. 6). Niche similarity was higher for species introduced both intentionally and unintentionally but lower for species only intentionally introduced. The year of introduction was positively associated with breadth ratio but negatively with niche similarity. This meant that species with less residence time had a relatively smaller introduced niche and lived in more different climates in the introduced range compared to the native range. Species introduced intentionally or more recently had larger unfilling, indicating larger climatic conditions left for their further colonization.

The parameters of niche estimation also demonstrated strong influences on observed climatic niche dynamics (Fig. 6). Niche similarity was higher when niche dynamics were assessed at a coarser scale or using more introduced occurrences. Breadth ratio was positively correlated with the number of native occurrences, implying that native niche was observed to be relatively larger when more native occurrences were available. Smaller expansion was found for more native and more introduced

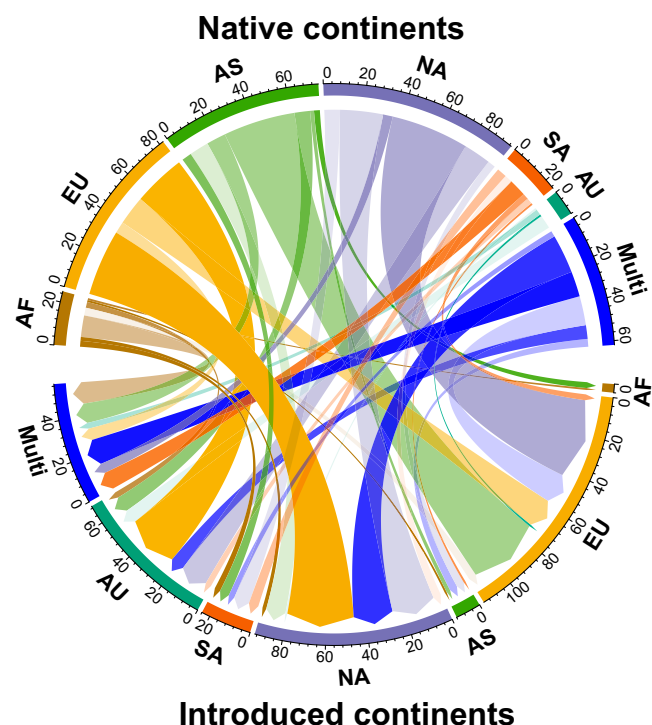


Fig. 4. Niche similarity for species introduced between and within continents. Segments with different colors represent the native continents (upper half) and the introduced continents (lower half): AF, Africa; AS, Asia; AU, Australia; EU, Europe; NA, North America; SA, South America; Multi, More than one continent. The width of each arrow represents the number of species that are introduced from the native to introduced continents. The transparency of each arrow represents the averaged niche similarity across all species between corresponding native and introduced continents, with darker colors indicating higher similarity.

occurrences and smaller unfilling for more introduced occurrences. However, we did not detect a clear relationship between the number of predictors and any of five metrics.

Influences of factors differed among groups of organisms and were stronger for plants and terrestrial ectotherms than terrestrial endotherms and aquatic species (*SI Appendix*, Fig. S2). The year of introduction was the only factor associated with niche dynamics for all groups, however with contrasting directions among groups. For example, the associations between the year of introduction and unfilling were negative for plants but positive for terrestrial ectotherms. With longer residence time, plants demonstrated lower expansion, whereas aquatic species showed higher expansion. Close associations of niche dynamics with the number of introduced occurrences were found in three groups: if niche dynamics were estimated with more introduced occurrences, higher niche similarity was found in plants, terrestrial endotherms and aquatic species and smaller breadth ratio in plants and terrestrial endotherms.

Discussion

Synthesizing previous conclusions of climatic niche conservatism found that most studies rejected the niche conservatism hypothesis. However, rejecting this hypothesis was probably an artifact because markedly contrasting conclusions were drawn for the same species assessed by two or more studies, or even within a study by different techniques and different criteria. These results echo the concern that the dichotomous conclusion of niche conservatism is strongly sensitive to techniques, criteria, or just author preferences (2). For example, ENM approaches

are highly dependent on the predictive performance of transferred models in new ranges. However, model transferability is susceptible to environmental novelty, spatial autocorrelation, and sample bias, and poor transferability might result from insufficient sample sizes, collinearity of predictors, or model overparameterization rather than the shift of species' climatic niche between two ranges (2, 24). Univariate approaches have been criticized for spuriously concluding niche shifts because climatic niches are probably conserved in particular axes but shifted in others (14, 21). The niche equivalency test might actually reflect statistical significance rather than meaningful ecological differences, because this test is very sensitive to sample sizes and the climatic condition of background regions (14). Otherwise, the niche conservatism hypothesis would be rejected for nearly all invasive species in our study, given 99% of the assessments reported that climatic niches were not equivalent between native and introduced ranges.

By contrast, when consistently analyzing data of climatic niche dynamics estimated from the standard COUE scheme, we observed only limited changes in niche breadth and position, supporting the niche conservatism hypothesis. Climatic niche conservatism was further confirmed by stability as the largest component and expansion as the smallest component of the global niche. Indeed, it can be argued that only niche expansion, that is, an increased occupancy of environmental space in the exotic range that is also available in the native range, should be interpreted as niche shift (discussed above and see refs. 15, 18). By overcoming the bias of different methodologies, our quantitative analyses revealed that most invasive species largely conserve their climatic niche.

Two mechanisms could be responsible for the conserved climatic niche of invasive species. First, preadaptation to recipient ecosystems is a crucial premise of successful invasions (13, 36). Species introduced to climates similar to those in their native

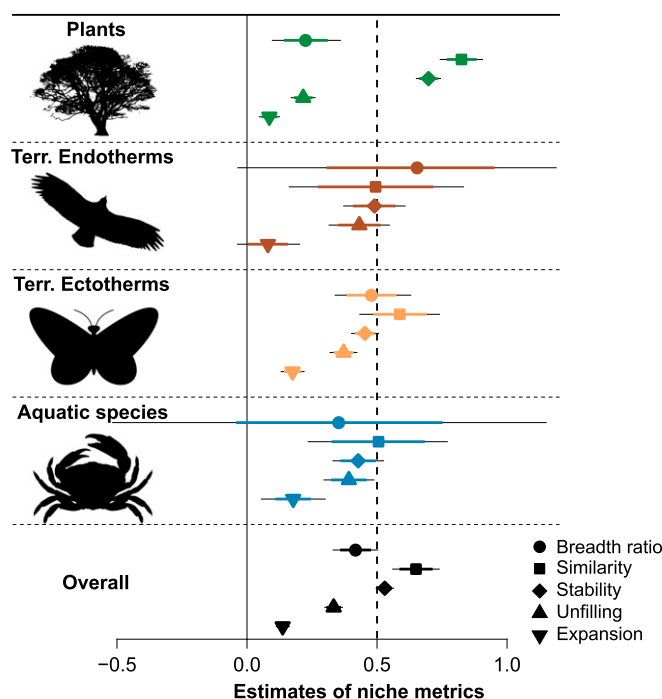


Fig. 5. Estimates of five niche metrics for all species (overall) and for each group of organisms. Breadth ratio is the ln-transformed ratio of the breadth of native niche to that of the introduced niche (compare Fig. 4), and similarity is the niche similarity between two niches quantified using Sørensen's similarity index. Means of 12,000 Bayesian posterior values are shown with 80% credible intervals (CI) (colored thick lines) and 95% CI (thin lines).

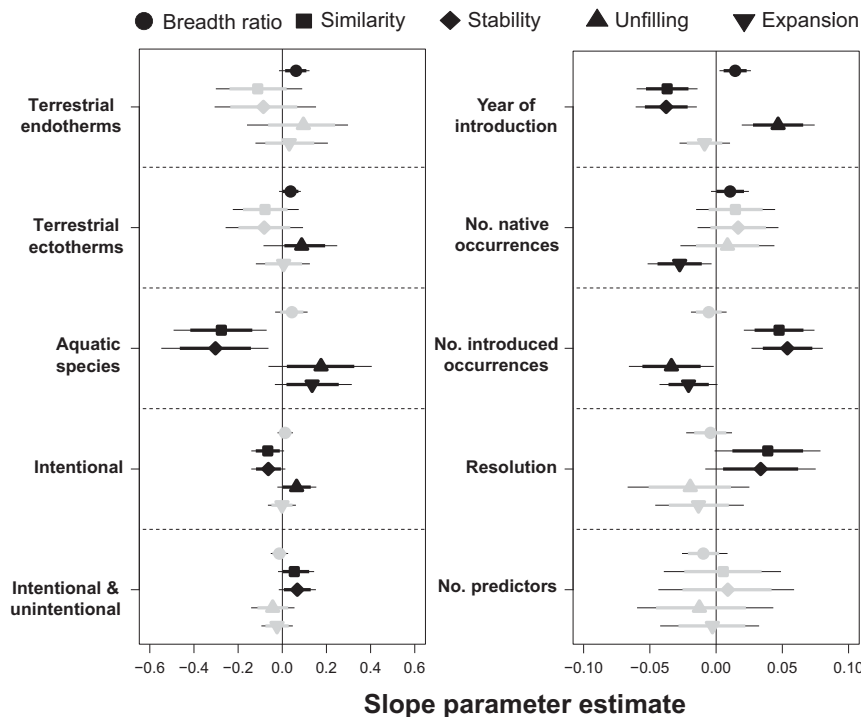


Fig. 6. Relationships between five niche metrics and seven factors for all species. The reference categories selected for assessing relative effects of categorical factors are plants and introduced unintentionally. Standardized effect sizes of each factor are represented by the mean of 24,000 Bayesian posterior values estimated with 80% credible intervals (CI; thick lines) and 95% CI (thin lines). Points are filled if the 80% CI does not overlap with zero and gray if the CI includes zero.

ranges are more likely to establish self-sustaining populations, thus reducing the possibility of niche shift in the exotic climate. Second, sources of invasive species may consist of populations from particular lineages in the native range and only reflect a subset of the native climatic niche (9, 37). Idiosyncratic species introductions can impede genetic admixture of introduced populations, consequently preventing invasive species from expanding their niche in new ranges (4, 37).

Despite the lower magnitude, niche expansion still contributes to more than 10% of the global niche, implying that at least some invasive species can quickly occupy novel climatic conditions in a short time frame. This pattern is particularly striking for those species for which the introduced niche completely contains the native niche, such as the cane toad (*Rhinella marina*) and the white clover (*Trifolium repens*). Rapid evolution in the fundamental niche might be an important driver of such considerable niche expansion (12, 27). Indeed, a number of studies have reported that invasive species can rapidly evolve to better adapt to various climatic pressures in the introduced range (29, 30, 38). For instance, cane toads displayed an ability to colonize both highly arid and cold climates after being introduced to Australia in 1935. One key mechanism for their colonization success is the up-regulation of genes associated with dispersal ability and metabolism (30). Adaptive evolution is also crucial for the successful invasion of white clover in North America, where it rapidly established latitudinal clines in cold tolerance (38). Moreover, the rate of adaptive evolution can be accelerated by an enhanced fitness of individuals at the invasion front (30), a good match between genetic provenance and recipient climate (29), increased genetic variation due to different source populations (18) and multiple introductions (32), and hybridization of closely related species (31). Since many invasive species represented in our dataset were introduced to their exotic ranges

relatively recently, we expect that some of them will demonstrate greater niche evolution with time elapsing and even remarkable genetic divergence among intraspecific populations. Hence, assessing niche changes for invasive species should be regarded as a conservative way to understand niche evolution (12). More experimental evidence is required for better understanding the relationship between rapid evolution and niche changes (2, 23).

The finding of conserved climatic niche for invasive species has prominent implications for predicting future invasion risks. First, the tendency of species to occupy similar climates increases our confidence of transferring ENMs to new geographical ranges (3, 5), as model transferability has been reported to be positively correlated with the overlap between native and introduced climatic niches (13, 15). Second, the large magnitude for unfilling suggests that invasive species are often not in equilibrium with exotic climates and there are still suitable habitats remaining for their future spread (17, 19). To develop cost-effective strategies on managing invasions, more attention should be paid to surveilling and controlling the spread of invasive species into climatic conditions that are occupied in their native range but (not yet) colonized in their introduced ranges (2, 4).

Variations in niche dynamics among groups of organisms partly explain contrasting conclusions of climatic niche conservatism among taxonomic groups. Plants remarkably differed from other groups and showed the lowest breadth ratio and the highest niche similarity. For them, climatic conditions are assumed to be the primary factor determining their invasion success (13, 39), leading to invasive plants occupying more similar climates between ranges. Aquatic species are more difficult to detect in the field. Their lower detection probability might hamper the inference of their environmental space and reduce observed niche similarity (22).

Pronounced influences of intentionality and residence time on climatic niche dynamics highlight the importance of considering introduction history to understand biological invasions (13, 23, 36, 39). Higher niche similarity for species introduced both intentionally and unintentionally is probably related to increased propagule pressures associated with more pathways. Elevated propagule pressures could facilitate the introduction of species to more sites with suitable climates and increase the overlap of climatic space occupied in native and introduced ranges. If species are only introduced via intentional pathways, their distributions are very likely constrained within the regions with higher human activities, leading to a larger unoccupied climatic space in the introduced range and lower niche similarity (23, 36). Close associations between the year of introduction and niche dynamics strongly support the notion that biological invasion is an ongoing process (13). The positive relationship between niche similarity and residence time contrasts with previous empirical findings that species with longer residence time undergo a stronger niche shift (e.g., ref. 18). Larger native niche and unfilling for species with less residence time together reveal the important impacts of dispersal limitation on species colonization (13). Because recently introduced species do not have enough time to spread to nearby regions, their occupied climatic space in the introduced range would be much smaller than species introduced earlier, whereas the unoccupied climatic space would gradually decrease in the process of colonization (13, 15). In addition, plant invaders showed lower niche expansion with increased residence time. This counterintuitive result might be explained as follows: Compared to other organisms, plants are easier to sample in the field, and thus online repositories include many data on the spatial distribution of plant invaders. In their introduced ranges, however, many observations are compiled from sink habitats, where species can survive but cannot establish self-sustaining populations (28, 40). Therefore, the number of observations from those environments may decrease with time, resulting in the smaller magnitude of niche expansion for species introduced earlier.

Climatic niche dynamics are also affected by the data used for estimation. A larger native niche with more native occurrences implies that generalist species with a larger range have a more conserved niche than specialist species (18). This is because generalists can live in a broader range of climatic conditions in the native range, resulting in a relatively larger native niche (40). Increased niche similarity with the number of introduced occurrences means that species with larger introduced ranges occupy more similar climates with their native populations. A lack of correlation between niche metrics and the number of predictors should not be interpreted as a negligible role of dimensionality on niche dynamics, because the COUE scheme has already synthesized all environmental variables to two PCA components (2, 33). PCA can effectively avoid the statistical issues arising from excessive predictors (e.g., multicollinearity and overparameterization), thus reducing the impacts of dimensionality on niche estimation (14, 24, 33).

Our study has two important caveats. First, we were unable to evaluate the relative magnitude of changes in fundamental versus realized niches (27, 28). For most species, the degree to which the fundamental niche is represented by the realized niche is unknown (12, 25). Evolution in physiological traits and environmental tolerances can trigger changes in both the fundamental and realized niche (2, 10). By contrast, varying biotic interactions change the realized niche, but not the fundamental niche, in the short term (9, 28). The second limitation of our study is related to the COUE scheme. While the scheme provides a robust framework to control for biases of field observations, unexpected errors might appear if there are remarkable differences in sampling coverages and intensities across a species' range (40). We are also unable to estimate niche changes for species without overlap between native and introduced

niches. It would be optimal to assess niche dynamics in an environmental space that is standardized by the density of pooled occurrences between the native and introduced ranges.

Anticipating species responses to increasing anthropogenic stressors is a major task of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (41). We confirm that invasive species largely conserve their niches in exotic climates (4, 5). This general pattern of climatic niche conservatism is critical to forecast species responses to future climatic conditions (12, 13). As a consequence of global warming, the next decades might see tremendous appearances of novel climatic conditions (41, 42). Rates of climatic niche evolution have been reported to be dramatically slower than projected climate changes (26), and our study confirms that climatic niches only shift slowly. In the future, there will probably be massive alterations in species distributions and community compositions because species are either able to track suitable climatic conditions within their niches or otherwise disappear (5, 10, 26). Extinction risk might be higher for plants and terrestrial endotherms due to their limited capability of expanding niches. However, close associations of species characteristics with niche dynamics offer important information on predicting species responses to changing climates (2, 12, 23). Incorporating management strategies with estimated niche dynamics would be insightful for optimizing limited resources and prioritizing species and regions for conservation (10, 18, 20).

Materials and Methods

Study Compilation. To most comprehensively compile empirical studies that tested the niche conservatism hypothesis and/or assessed niche dynamics for invasive species, we applied two search strategies following the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) guidelines (ref. 43 and *SI Appendix, Fig. S3*). First, we searched the Clarivate Analytics' Web of Science database in December 2018 with the query TS = ((Introduce* OR inva* OR alien OR nonnative OR nonnative OR exotic OR naturaliz* OR nonindigenous OR nonindigenous) AND Niche). We then screened the titles and abstracts of all publications returned by the search to filter out irrelevant studies. Second, we screened the reference sections of relevant publications to find additional articles. Third, after scanning the titles and abstracts of 7,304 articles, we found 171 articles potentially relevant to our study. Fourth, we screened the full texts of each relevant article and excluded studies that neither made conclusions on niche conservatism (i.e., conserve or shift) nor estimated niche dynamics using the COUE scheme. Finally, 86 studies were retained encompassing 434 invasive species (*Dataset S1*).

Data Compilation. We performed an extensive collection of information available in each study. Techniques used for testing the niche conservatism hypothesis were divided according to statistical methods (*SI Appendix, Table S2*). Besides classifying techniques into the three approaches outlined above (2), we also considered the recently developed Hypervolume approach that follows the idea of Hutchinson's *n*-dimensional hypervolume (44). Here species niche is estimated and compared in a multidimensional space directly constructed by three or more predictors (45). Criteria to conclude on niche conservatism were divided according to the tested assumptions and the relied metrics (*SI Appendix, Table S3*). Species were classified into four main groups of organisms: plants, terrestrial endotherms (birds and mammals), terrestrial ectotherms (amphibians, insects, and reptiles), and aquatic species (algae, corals, crustaceans, fishes, and molluscs). We followed the authors' definition of the native and introduced continents for each species. The intentionality of introduction of each invasive species followed the classification in Saul et al. (46): 1) intentional, 2) unintentional, or 3) both intentional and unintentional. Data of the year of introduction in each introduced continent was collected from each study and supplemented from the Global Alien Species First Records Database (47). We considered four parameters with available data in all studies for estimating niche dynamics: resolution, number of predictors, and number of occurrences in the native and introduced ranges (hereafter, native occurrence and introduced occurrence, respectively). Predictor variables included climate (91.9%), topography (3.7%), marine environments (2.0%), land use (1.0%), vegetation type (0.8%), and soil characteristics (0.6%). Of the climatic variables, 57.5% were temperature- or energy-related, 41.3% were water-related, and 1.2% were integrated water-energy variables; 56.2% of climatic variables were

extremes, 24.6% were measures of seasonality or other variability, and 19.2% were means (Dataset S1).

In addition to the authors' overall conclusion on niche conservatism (which is mainly related to climatic niche, as indicated in the previous paragraph), in each study we also recorded all conclusions for different species included, for populations in different introduced continents, for different techniques, and for different criteria. Climatic niche shift was concluded if the niche conservatism hypothesis was rejected either in one continent, by one technique, or by one criterion. To quantify the consistency of conclusions, we selected species that were assessed two or more times at each of four levels: in different studies (48 species), in one study but in different introduced continents (74 species), in one continent but by different techniques (60 species), and by different criteria of one technique (94 species). For each level, the proportion of species with the same conclusion was used as the proxy for consistency.

For those studies that estimated niche dynamics using the COUE scheme, we collected data for the three metrics E, S and U, respectively. We requested the data from the authors if they were not available in the study or online. We only kept the 30 studies that assessed dynamics between native and introduced niches in analogous environments (i.e., environmental conditions present in both native and introduced ranges), because species colonization in nonanalogous environments cannot separate the consequences of niche shift from the nonavailability of environments (2). Conclusions of the niche equivalency and niche similarity tests were also compiled.

Metrics of Niche Dynamics. The quantitative analyses focused on estimating overall changes in breadth and position between native and introduced climatic niches, because niche breadth can represent the range of environmental space occupied by species (3), and niche position is so far the most commonly used metric to test the niche conservatism hypothesis (2). In this step, we addressed to what extent niches are conserved by interpreting niche shift as a continuous process (5), because species distributions in the introduced range only reflect a snapshot of the ongoing colonization (13). Niches were considered as conserved if either niche expanded slowly, that is, the native niche was larger than the introduced niche (12), or niche position changed slowly, that is, the native and introduced niches occupied similar positions in the environmental space (27).

For the COUE scheme, magnitudes of E and U are estimated relatively to the occurrence density in the introduced and native range, respectively (<https://github.com/cran/ecospat>). Despite S representing the overlap in environmental space between native and introduced niches, its magnitude is estimated relatively to the occurrence density in the introduced range and is directly calculated as the complement of niche expansion (i.e., $1 - E$). To transform metric values to the same scale, we calculated the magnitude of U relatively to the occurrence density in the introduced range as follows:

$$U_T = \frac{S}{1 - U_O} \times U_O,$$

where U_O is the original U value reported in the study and U_T is the transformed U value. Since the magnitude of U can be rescaled only if the occurrence density is the same in S for the native and introduced niches, we compared the occurrence density in S between native and introduced niches using simulated distribution data of virtual species. We applied simulations because it was impossible to obtain species distribution data for all studies included. Our simulations showed that the occurrence density in S was very close for native and introduced niches (80% credible intervals estimated from 12,000 Bayesian posterior values largely overlapped), and the conclusion was robust to different niche attributes and sample sizes (SI Appendix, Supplementary Information Text and Fig. S4). We divided E, S, and U_T by their sum to calculate their relative contributions to the global niche. Four species with no shared environments between two ranges ($S = 0$) were excluded because the U_O value could not be transformed. In total, we compiled 448 sets of metric values for 293 species.

The breadth of the native niche (B_N) and introduced niche (B_I) were expressed by the environmental conditions occupied in the native and introduced ranges as

$$B_N = S + U_T$$

$$B_I = S + E,$$

which allows us to estimate the broadening or contracting of species niche between two ranges using the ln-transformed ratio of the breadth of the native niche to that of the introduced niche (breadth ratio, BR) (28):

$$BR = \ln\left(\frac{B_N}{B_I}\right).$$

Therefore, if the breadths of the native and introduced niche are the same, $BR = \ln(1) = 0$; if the breadth of the native niche is twice the breadth of the introduced niche, $BR = \ln(2) = 0.69$; and if the breadth of the native niche is only half of the breadth of the introduced niche, $BR = \ln(0.5) = -0.69$. The relative niche position in the 2D environmental space is expressed as the similarity between native and introduced niches (45), rather than the distance between niche centroids. Niche similarity (Sim) is quantified using Sørensen's similarity index (48):

$$Sim = \frac{2S}{B_N + B_I}.$$

Sim ranges from 0 to 1, representing cases where the two niches are totally separated or overlapped in the environmental space, respectively. If two niches occupy more similar positions (i.e., similar niches), $Sim > 0.5$, whereas if two niches occupy more dissimilar positions (i.e., dissimilar niches), $Sim < 0.5$. Note that the similarity between native and introduced niches is different to the niche similarity test based on the COUE scheme. To visually examine the dynamics between native and introduced niches, we developed eight simplified scenarios by combining four scenarios of changes in niche breadth, that is, native niche was containing ($E = 0$), larger than ($B_N > B_I$), smaller than ($B_N < B_I$), or belonging to ($U = 0$) introduced niche, with two scenarios of changes in niche position, that is, niches were similar ($Sim > 0.5$) or dissimilar ($Sim < 0.5$).

Bayesian Inference Techniques. We applied Bayesian inference techniques to estimate the distribution of values for five niche metrics (i.e., breadth ratio, similarity, expansion, stability, and unfilling) for all species and for each group of organisms. For the estimation of each metric, we used weakly informative priors with 0 as the mean and 2 as the SD following a Gaussian distribution. A total of 12,000 posterior values of model parameters were generated from four chains of 5,000 iterations with the first 2,000 steps as the burn-in. To account for the heterogeneity of species and data among studies (i.e., publications) included in the analysis, study was set as the random factor for each model. Good chain convergence was confirmed by values of Rhat (the potential scale-reduction factor) less than 1.01 (49).

The association of each of the five metrics with seven factors related to the species analyzed and the data used (i.e., the group of organisms, intentionality of introduction, the year of introduction, resolution, number of predictors, and number of native and introduced occurrences) were modeled using Bayesian hierarchical models, with study as the random factor. Hierarchical models have demonstrated great flexibility to accommodate for the complex relationships of multiple factors at different levels (49). Values of five metrics were proportionally transformed between 0 and 1, so that effects of different factors were comparable in one framework. Values of each continuous factor were standardized with the mean of 0 and the SD of 1. Weakly informative priors were adopted on all variables (mean = 0; SD = 2) and the global intercept (mean = 0; SD = 10). Parameters of each factor were estimated based on 24,000 posterior values calculated from four chains of 10,000 iterations with the first 4,000 steps as the burn-in. The Rhat values of all covariates were below 1.01 in all models, suggesting the good convergence of chains. All Bayesian inference techniques were performed using the brm function in the brms package (49), and all analyses were conducted in R (50).

Data Availability. The data used in all analyses are provided as Dataset S1. All data and R code are available from Figshare repository: [10.6084/m9.figshare.12782366](https://doi.org/10.6084/m9.figshare.12782366).

ACKNOWLEDGMENTS. C.L. was sponsored by the International IGB Fellowship Program in Freshwater Science, the Second Tibetan Plateau Scientific Expedition and Research Program (STEP) (no. 2019QZKK0501), and the National Natural Science Foundation of China (no. 31472016). J.M.J. was supported by a Heisenberg grant from the Deutsche Forschungsgemeinschaft (JE 288/9-2). W.X. was supported by the National Natural Science Foundation of China (no. 31872568) and the Natural Science Foundation of China-Shandong Joint Fund for Marine Ecology and Environmental Sciences (no. U1606404). We are grateful to Achyut Banerjee, Cristiana Barbosa, Wouter Beukema, Regan Early, Mirko Febbraro, Ileana Herrera, Wanwan Liang, Maxwell Obiakara, Blaise Petitpierre, Luiz Ribas, and Diederik Strubbe for providing data on niche dynamics. Comments by the editor and two anonymous reviewers greatly improved the manuscript.

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