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A theoretical framework for scaling ecological niches from individuals to species

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The niche is a key concept that unifies ecology and evolutionary biology. However, empirical and theoretical treatments of the niche are mostly performed at the species level, neglecting individuals as important units of ecological and evolutionary processes. So far, a formal mathematical link between individual-level niches and higher organismal-level niches has been lacking, hampering the unification of ecological theories and more accurate forecasts of biodiversity change. To fill in this gap, we propose a bottom–up approach to derive population and higher organismal-level niches from individual niches. We demonstrate the power of our framework by showing that 1) the statistical properties of higher organismal-level niches (e.g., niche breadth, skewness, etc.) can be partitioned into individual contributions and 2) the species-level niche shifts can be estimated by tracing the responses of individuals. By using individual-level GPS (Global Positioning System) tracking data from three different species, we show that climate change could have contrasting consequences on population-level niche shift depending on individual niche compositions. Our method paves the way for a unifying niche theory and enables mechanistic assessments of organism–environment relationships across organismal scales.

climate change vulnerability | thermal performance curve | individual specialization | mixture distribution

The niche is one of the few unifying concepts in ecology and evolutionary biology across spatial, temporal, and organismal scales (1–3). The idea that every individual, population, and species should have a favorable set of environments (abiotic or biotic) allowing its persistence has been deeply ingrained in ecologists' minds since Grinnell and Hutchinson (4–6). The niche concept underlies almost every explanation of and forecast for biodiversity change: from the accumulation of species richness over geologic time scales (7–9), the maintenance of diversity through coexistence mechanisms and ecological drift (10–13), to the predicted sudden collapse of ecosystems under global change (14, 15).

However, despite the nominal conceptual unification of the niche (16, 17), its empirical estimation with environmental data is almost exclusively focused on the species level (18–20). Such a species-centric view omits a simple but fundamental fact: the species niche, as well as the niches of higher taxonomic levels (e.g., genus and family), is an emergent property of the constituent individuals (21–24). The conventional species-centric view overlooks the role of individuals as the fundamental units of ecological and evolutionary processes (25). Species-level niche-based studies have assumed that individual variation is either small or negligible compared with between-species variation (21). However, due to the strong spatial, temporal, and ontogenetic heterogeneity within populations, considerable individual niche variation is the norm rather than the exception (24, 26–28). Recent empirical evidence has repeatedly demonstrated the importance of individual variation in driving species' coexistence (29, 30), ecosystem functioning (31, 32), and adaptive capacity (33).

Ignoring individual variation also reduces our capacity to make accurate predictions about the impacts of climate change on ecosystems (34–36). For example, if individuals and the populations they form are highly specialized to their local environments and differentiated across a species' geographic range (37–39), a small change in mean environmental conditions can negatively impact all populations but may be judged unharmful by a species-level vulnerability analysis (40). If individual niches are highly nested within one another (28), small environmental changes might have little impact on a species' geographic range size but could extirpate specialized individuals that provide vital ecosystem functions (31, 41). Moreover, individual variation provides the fuel for evolutionary adaptation (42). Neglecting individual variation inevitably leads to biased

Significance

The ecological niche—the environmental conditions that an organism requires to persist—is fundamental to many inquiries in ecology and evolutionary biology, from understanding the maintenance of biodiversity to predicting the impact of climate change on ecosystems. However, despite the central relevance of the niche concept, ecologists have struggled to mathematically link niche variations across organismal scales—from individuals to populations and species—due to a variety of conceptual confusions and operational difficulties. Here, we propose a mathematical framework that characterizes higher organismal-level niches iteratively from individual niches. Our approach enables a more synthetic understanding and accurate forecast of biodiversity change across organismal levels and facilitates the integration of the rapidly growing individual-level data in addressing macroecological questions.

The authors declare no competing interest.

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estimation of niche dynamics and species distributions under climate change (43).

There are two main reasons for historically ignoring individual variation in niche-based studies. The first is operational: Due to the scarcity of individual data, niche estimation has only been feasible at the species level for many studies that use opportunistic observational data (20). However, the tide has turned in recent years with the rapid accumulation of individual data such as those provided by animal GPS tracking (44, 45) camera trapping (46, 47). By far, the amount of individual animal movement data had exceeded the amount of all other biodiversity data combined (48–50). The rapid growth of individual data now provides a valuable opportunity to examine niche variation below the species level (26, 28) and better integrate biogeography with behavioral ecology (51). Broadly, it offers the potential for a more mechanism-driven prediction of large-scale biodiversity changes using a bottom–up approach (34, 52–54).

The second reason is conceptual. Ecologists have struggled to mathematically relate species niches to individual niches (22, 24, 55). The problem largely stems from the failure to reconcile different niche concepts over the years (17). The widely accepted Hutchinsonian niche concept, defined as the environmental conditions where a species has positive population growth rate, is usually infeasible to quantify empirically (2) [e.g., being too costly for large-scale analysis and, until recently, undefined at the individual level; (56)]. As a result, ecologists are forced to use surrogate niche measures that bring inconsistency and confusion to the niche concept, such as habitat suitability (57) estimated from occurrence data (most commonly performed using species distribution models), putative functional differentiation calculated from species-level trait data (58), and thermal performance in physiological studies (59, 60).

Characterizing ecological niches from individuals requires a niche measure that is scalable for empirical studies across organismal levels and mathematically tractable for the development of theory. Despite the lack of consensus on what exactly is the meaning of the niche (16, 61, 62), an operational niche measure has emerged independently from several empirical applications and become commonly used and well-accepted—the niche as measured by the probabilistic distribution of a taxonomic unit in the environmental or trait space (63–65): In macroecology, the niche of a species is quantified by its relative occurrence rate in climate space (57); in community ecology, a species' niche is often quantified by the distribution of individuals or biomass in the functional space (58, 66); in nutritional ecology, an animal's dietary preference is measured by the relative frequency of food consumption in isotopic space (67, 68); in movement ecology, the niche of an individual is quantified by the utilization distribution or resource selection function in environmental space (69). This probabilistic niche measure not only benefits from a suite of increasingly mature multidimensional computational tools to describe their geometric features such as the volume and overlap (70, 71), but has also been used to develop ecological theories such as the theory of limiting similarity (72) and the trait-driver theory (66).

The advantages of the probabilistic niche measure have been demonstrated in the study of individual niche specialization, where the total niche breadth can be partitioned into the between-individual and within-individual components using ANOVA (21, 26). Such an approach has led to valuable insights into the drivers of ecological niche breadth, such as niche expansion induced by ecological release from competitors is mainly achieved by the increase of between-individual niche component (73). Recent studies have further shown that keystone niche individuals can disproportionally expand the population niche breadth (74, 75), highlighting the necessity of considering the full spectrum of individual niche variation in a population. To date, a general approach to study how important niche properties beyond niche breadth are shaped by individual variation is strongly desired to better appreciate how species respond to climate change. One prominent example is the skewness of the thermal niche, as exemplified by the left-skewed thermal performance curve (76). The rapid decrease of thermal performance once past the optimal condition implies that individuals and species might respond strongly to warming once a certain threshold is crossed and result in sudden population declines (40, 77). To date, we have little knowledge about how individual variation drives the asymmetry of the species-level thermal niche.

In this paper, we propose a framework to relate estimated niches across organismal scales. Our primary goals are 1) to show that the population- and species-level niches can be analytically derived from individual niches, which provides a convenient way to partition population-level niche properties (including but not limited to niche breadth and skewness) into individual contributions regardless of the underlying distributions, and 2) to show that our framework is widely applicable to many ecological and evolutionary questions that require predicting species-level niche change from individuals, such as niche shifts under climate change. We demonstrate the utility of our framework using animal tracking data for three example species, the Galápagos giant tortoise (*Chelonoidis donfaustoi*) from the eastern side of Santa Cruz Island, the Gadwall (*Mareca strepera*), and the African bush elephant (*Loxodonta africana*), but our method is generalizable to any mobile organisms and other types of individual data.

Methods

Probabilistic Niche Measures. We briefly recapitulate our definition of probabilistic measures of individual niches and population niches before elucidating their mathematical relationship.

The individual niche here is measured as the relative occurrence rate of an individual in environmental space. In a one-dimensional example where the environmental variable is denoted by x, the niche of the ith individual is measured by the probabilistic density function $f(x)_i$, describing the individual's relative occurrence rate in the environmental space. This measure follows the convention of how individual niche is quantified in movement ecology (26, 28).

The population niche is measured as the relative occurrence rate of individuals from the population in the environment. In the one-dimensional example, the population niche is measured by the probabilistic density function, $F(x)$. This measure follows the logic of how population-level or species-level niches are quantified in species distribution modeling if individuals are randomly sampled from the landscape (57).

We have not explicitly distinguished from the fundamental niche and the realized niche in our treatment. Our framework is kept as general as possible to be applicable to both the realized niche and the fundamental niche as long as they are measured by probability density functions (78). Although in practice, we acknowledge that because the fundamental niche is difficult to estimate from observational data, the probability measure of the niche is most often applied to the realized niche.

The key to link population-level niches to individual niches is to realize that the probability of any individual from the population occurring in a certain environment can be calculated by a two-stage sampling process: first choosing an individual from the population, then choosing the environment for the individual to occur in. Let us use a heuristic example to demonstrate this calculation.

A Heuristic Example of the Mixture Distribution. For a heuristic example, let us consider a population of a chameleon species consisting of three individuals that have distinctive temperature niches (Fig. 1*A*). The population niche can be derived using conditional probabilities: The relative occurrence rate of individuals from the population in environment x is calculated by the probability of choosing

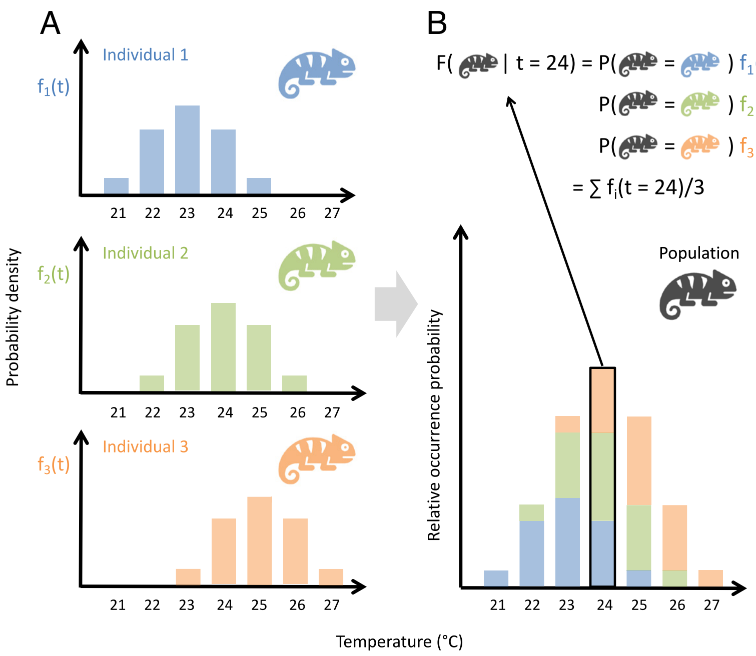

Fig. 1. Conceptual figure of scaling from (*A*) individual niches to the (*B*) population niche. The population niche (*B*) is described by a mixture distribution of individual niches from three animals (*A*). $f_1(t)$, $f_2(t)$, and $f_3(t)$ represent the temperature niche of the three individuals.

the *i*th individual in the population w_i, multiplied by the relative occurrence rate of the *i*th individual in the environment $f(x)_i$, then summed across all individuals in the population (Fig. 1*B*).

Mathematically, the resulting population niche can be expressed as a mixture distribution of the individual niches, with w_i representing individual weights (in this case, each individual has the same weight because they contribute equally to the population):

$$F(x) = \sum_{i=1}^{n} w_i f(x)_i. \qquad \textbf{[1]}$$

Alternatively, we can arrive at the same mixture distribution by converting an individual-level occurrence dataset to a species-level occurrence dataset by removing individual identity information (79, 80). For our heuristic chameleon example (Fig. 1), this procedure is equivalent to stacking the three individual niches together (Fig. 1*A*) and renormalizing it to get the probability density distribution that measures the population niche (Fig. 1*B*).

Partitioning the Population Niche into Its Individual Contributions. As well-established in the statistical literature, the moments of the mixture distribution can be derived from the moments of the component distributions (81). For a trivial example, the first moment of the population distribution (the population mean, μ) is just the weighted sum of the individual mean, μ_i, where *i* denotes the *i* th individual and w_i denotes the weight:

$$\mu = \sum_{i=1}^{n} w_i \mu_i. \qquad \textbf{[2]}$$

Nontrivial cases are shown by the individual partitioning of the higher moments:

Niche breadth is often represented by the second moment (the variance). In this case, the population niche breadth can be written as:

$$\sigma^2 = E[X^2] - \mu^2 = \sum_{i=1}^{n} w_i({\sigma_i}^2 + {\mu_i}^2 - \mu^2), \qquad \textbf{[3]}$$

where ${\sigma_i}^2$ denotes the individual niche breadth. Eq. **3** provides a natural partitioning of the population niche breadth into contribution through individual niche breadth, ${\sigma_i}^2$, and the contribution through niche position, ${\mu_i}^2 - \mu^2$. ${\sigma_i}^2$ and ${\mu_i}^2 - \mu^2$ can also be interpreted as the within-individual variation and between-individual variation in light of the ANOVA. Note that to compare the relative contribution of the two components, ${\mu_i}^2 - \mu^2$ must be non-negative to be interpretable. To achieve this, individual niche centers should be rescaled so that the population niche center $\mu = 0$.

The third moment of the population niche (the skewness, γ) can be written as:

$$\gamma = E[(\frac{X-\mu}{\sigma})^3] = \frac{1}{\sigma^3}\left[\sum_{i=1}^{n} w_i(\gamma_i{\sigma_i}^3 + 3\mu_i{\sigma_i}^2 - 3\mu\sigma^2 + {\mu_i}^3 - \mu^3)\right], \textbf{[4]}$$

where the population skewness is partitioned into a within-individual component $\gamma_i{\sigma_i}^3$ and a between-individual component $3\mu_i{\sigma_i}^2 - 3\mu\sigma^2 + {\mu_i}^3 - \mu^3$. The between-individual component is determined by the means and variances of individual niches, while the within-individual component is determined by the skewness and variances of individual niches. Alternatively, $\gamma_i{\sigma_i}^3 + 3\mu_i{\sigma_i}^2 - 3\mu\sigma^2$ roughly correspond to the contribution through niche breadth, and ${\mu_i}^3 - \mu^3$ represent the contribution through niche position alone as in the case of variance partitioning.

Multivariate Niches. Eq. **1** is equally applicable to the multidimensional niche space, although in this case an additive partitioning of all the moments is not applicable. Instead, we show that the ratio between the multivariate population niche breadth (as defined by the generalized variance) and the individual niche breadth can be partitioned into univariate components and a dimensionality component (*SI Appendix*), and this ratio is closely related to Wilk's Lambda in the multivariate ANOVA (82).

Beyond Population Niches. The implication of our framework goes beyond population niche estimates. In many ecological and evolutionary studies, the weights in Eq. **4** can be chosen to reflect the relative abundance in each group. Such a procedure can be used iteratively to build species-level niches from subpopulations (20), and to build clade-level niches such as genus-level niche and family-level niche (83) using species-level niche as the units with weights reflecting the number of species in each clade.

Predicting Future Population Niches. Our framework can also be used to make predictions about the change in population-level niches by linking the values of w_i to the propensity fitness concept in evolutionary biology (84). For example, predation may disproportionately affect individuals with particular niche preferences (85, 86). Another example is climate change can change the fitness of individuals with different niches (87), and cause a population-level niche shift. In such cases, we can modify the values of w_i such that they reflect the relative contributions of different individuals to the population in the future. Such individual fitness data, for example, can be independently estimated from individual-level life history traits (84), or approximated by correlational SDM approaches.

Empirical Example: Niche Shifts under Climate Change. For a simple empirical demonstration of our framework, we projected the niche shifts of a Galápagos giant tortoise (*C. donfaustoi*) population (88) (11 individuals, 121,601 observations), a Gadwall (*M. strepera*) population (89) (14 individuals, 1,849 observations) and an African bush elephant (*L. africana*) population (90) (15 individuals, 59,790 observations; *SI Appendix*, Fig. S1) under an *ad hoc* climate change scenario and a naive dispersal assumption (that individuals are only allowed to move within the modeling domain). We further assume that future fitness of individuals (w_i in Eq. **1**) corresponds to the ratio of their future environmental suitability and current environmental suitability estimated from individual-level SDMs. Note that this assumption makes the future projection entirely dependent on observational data and the estimated realized niches. As a result, the SDM-based projection only provides approximations to the true niche shift. However, more mechanistic predictions can be made if individual fitness is estimated from independent data such as individual-level life history traits (84).

Here, we do not attempt to provide a rigorous climate change projection but to simply illustrate the predictive capacity of the presented framework. Our analysis involves 4 steps (for more details, see in *SI Appendix*, Fig. S1):

1) Estimate individual niches (i.e., temperature selection functions) using the observed occurrence using GPS data and remotely sensed temperature data, with an inhomogeneous Poisson point process model (91).
2) For each individual, calculate the current and future climatic suitability for each 1 km pixel over the landscape. The pixel level suitability is estimated from individual temperature selection functions.
3) For each individual, calculate the average suitability across the landscape (all 1 km pixels) respectively for current and future climatic conditions. Then calculate the weights in Eq. **1** as the ratio between the average future suitability and the average current suitability. The higher an individual's weight is, the more likely it will contribute to the future population niche.
4) Estimate the future population niche using Eq. **1** with the calculated weights, and compare it with the current population niche.

Results

Partitioning the Population Niche: Hypothetical Scenarios. To conceptually demonstrate the utility of the partitioning framework, we consider three hypothetical scenarios made up of six individuals along a one-dimensional temperature niche space (Fig. 2). Each individual is assumed to have a normally distributed temperature niche. The "evenly distributed" scenario assumes that individuals have the same niche breadth, and their niche position is uniformly distributed in the environmental space (Fig. 2*A*). The "clustered" scenario assumes that individuals centered at the same niche positions have different niche breadth (Fig. 2*B*). The "nested" scenario assumes that the individual niche position is correlated with the individual niche breadth (Fig. 2*C*). This requires the niches of the specialized individuals to be a subset of the niches of the generalized individuals.

Under an even distribution of individual niches along an environmental gradient (Fig. 2*A*), the major variation in the individual contribution to the population niche breadth is through variation in individual niche positions, wherein individuals adapted to more extreme environments have a larger contribution to the population niche breadth than those adapted to intermediate environments. In contrast, if individual niches are highly clustered (Fig. 2*B*), then the major variation in the individual contribution to the population niche breadth is through variation in individual niche breadths, to which generalized individuals have a larger contribution to the population niche breadth. When the individual niches are nested, the bivariate plot of individual contribution through niche breadth and niche position shows a clear hump-shaped pattern (Fig. 2*C*). Furthermore, the nested scenario also shows that a skewed population-level niche can arise from the clustering of specialized individuals in extreme environments even when individual niches are symmetric and have no skews.

Empirical Examples: Niche Shifts under Climate Change. The giant tortoise population (Fig. 3, first row) has substantial individual niche variations, with individual niche breadth contributing to only 58.4% of the population niche breadth (2.98). Some individuals are characterized by a bimodal temperature preference which partially contribute to the population-level bimodal temperature preference (Fig. 3 *A* and *B*). The current population niche is slightly negative-skewed (−0.09), while the individual niche skewness contribution is to the opposite direction (0.09). Overall, the interaction between individual niche breadth, position, and skewness (Eq. **4**; corresponding to the contribution through niche breadth in skewness partitioning) contributes to 63.9% of the population skewness. Under a hypothetical scenario of 2.4 degrees of warming (~RCP 3.4 climate scenario), the future population niche (Fig. 3*B*) is estimated to be 0.7 °C higher on average (from 26.72 to 27.39 °C), with slightly narrower niche breadth (from 2.98 to 2.62), and much more negatively skewed (from −0.09 to −0.65). The selection for warm-adapted specialist individuals is projected to drive the changes of both the niche position and skewness (Fig. 3*A*).

The Gadwall population (Fig. 3, second row) is also characterized by substantial individual niche variations (Fig. 3*A*). Overall, 69.5% of the population niche breadth (3.64) is contributed by individual niche breadth rather than variation in individual niche position. The interaction between individual niche breadth, position, and skewness contributes strongly (60.0%) to a positively skewed population niche (0.60), while the effect of individual skewness alone is negligible (0.0099). Under a hypothetical scenario of 2.4 degrees of warming (~RCP 3.4 climate scenario), the future population niche (Fig. 3*B*) is estimated to shift toward a higher mean (from 25.37 to 25.97 °C), a wider niche breadth (from 3.70 to 5.15), and to be less skewed (from 0.61 to 0.16). A closer examination of the individual partitioning of the population niche breadth and skewness shows that the shift toward wider niche breadth is predominantly driven by a strong selection for warm-adapted or generalist individuals (Fig. 3*C*), while the change of skewness is driven by the loss of thermal specialists that clustered at the relatively cold end of the population niche (Fig. 3*D*).

The case of the African bush elephants provides an interesting contrast to both the Giant tortoise and the Gadwall examples (Fig. 3, third row). The individual niche breadth of the African bush elephants contributes even more to the population niche breadth (79%). In terms of the skewness, the individual niche skewness contributes to 44% of the strongly negatively skewed population niche (−0.47).

Because of the predominant role of the within-individual niche contribution in driving the population niche (Fig. 3*A*). The 2.4 degrees of warming causes a much lower magnitude of niche shift at the population level (Fig. 3*B*), with only a 0.1 °C shift of the niche center (37.5 to 37.6 °C), a slight decrease of niche breadth (2.33 to 2.24), and increase of the magnitude of skewness (−0.46 to −0.54). The individual partitioning of the population niche shows that although the selection for generalists (Fig. 3*C*) and for highly negatively skewed individuals (Fig. 3*D*) exists, it is unlikely to cause a drastic change in population niche due to the lack of between-individual variation.

In terms of spatial prediction, the range of the giant tortoise is estimated to shrink toward the southwest part of the Santa Cruz

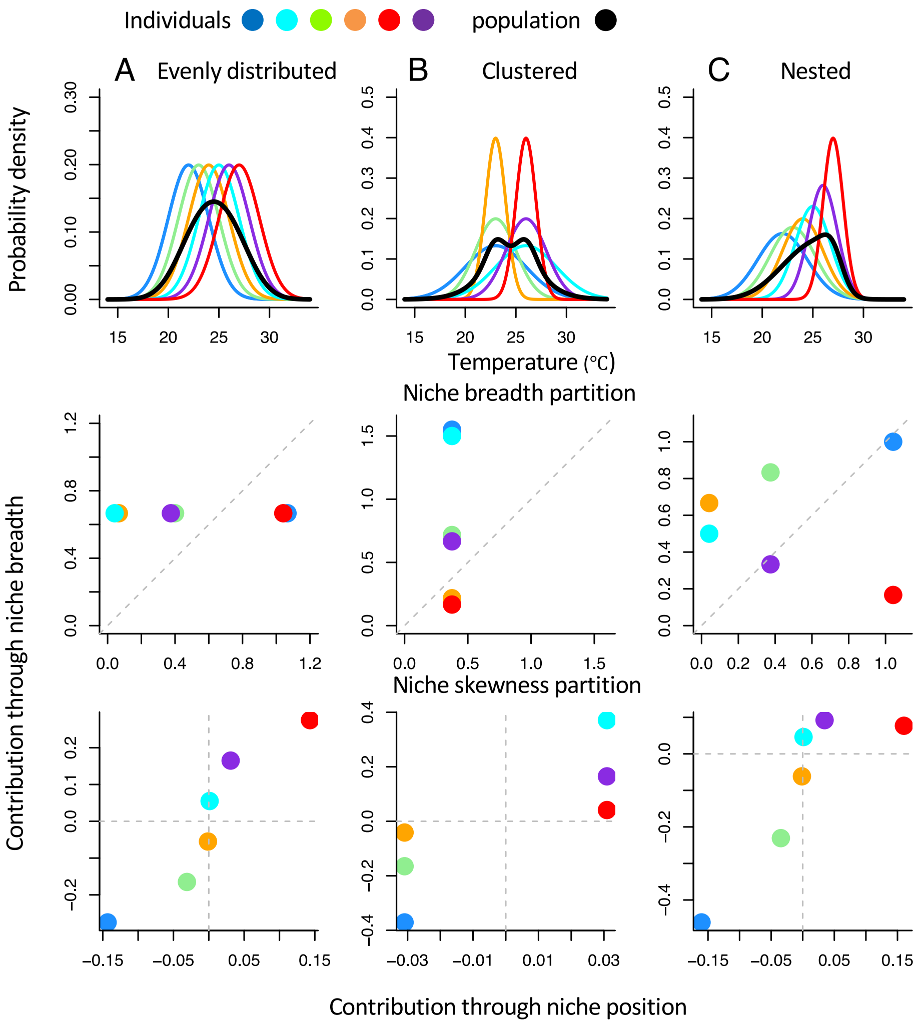

Fig. 2. The conceptual figure for different scenarios of individual niche variations. Individuals are assumed to have a normally distributed environmental niche. Black lines represent the population niche, colored lines represent individual niches. (*A*) The evenly distributed scenario assumes that individuals have the same niche breadth and evenly spaced niche center along a one-dimensional environmental axis. (*B*) The clustered scenario assumes that individuals have different niche breadths and highly clustered niche positions. (*C*) The nested scenario assumes that the niches of the more specialized individuals are a subset of the niches of the more generalized individuals. The second and third rows show the partitioning of the population-level variance and skewness into individual contributions. The gray dashed lines in the niche breadth partition plot and the skewness partition plot respectively show the 1:1 line and 0 lines, respectively. For the niche breadth partitioning, the contribution through niche breadth is the individual niche breadth multiplied by its weight, $w_i{\sigma_i}^2$, and the contribution through niche position is the squared distance between individual niche mean and the population niche mean multiplied by its weight, $w_i({\mu_i}^2 - \mu^2)$. The weights are equal for all individuals ($w_i = 1/n$). The mean values are scaled so that $\mu = 0$ to make sure the contributions are positive and interpretable. For the niche skewness partitioning, the contribution through niche breadth is $w_i(\gamma_i{\sigma_i}^3 + 3\mu_i{\sigma_i}^2 - 3\mu\sigma^2)/\sigma^3$, where γ_i is the skewness of the individual niche, and the contribution through niche position is $w_i(\mu_i^3 - \mu^3)/\sigma^3$. Positive values mean that the individual contributes to the longer right tail of the niche (mean larger than the median), while negative values mean that the individual contributes to the longer left tail of the niche (mean smaller than median). Note that positive and negative individual contributions to population skewness can cancel out to give rise to a symmetric population niche (the Evenly distributed and the Clustered scenarios).

Island (*SI Appendix*, Fig. S1*A*). While the individual-based model predicts low suitability at the central high-elevation area of the island (Fig. 4*A*), the species-based model wrongly concludes that the central part of the island will be highly favored (Fig. 4 *B* and *C*). As a result, such difference is reflected by the highest Root Mean Squared Error (0.06) between the predictions of the individual-based model and the species-based model among three species (Fig. 4*D*). The Gadwalls are estimated to shift toward higher elevations in face of warming (*SI Appendix*, Fig. S1*B*). Our individual-based model predicts a less concentrated preference in the geographic space (Fig. 4*A*) compared to the conventional species-level model (Fig. 4*B*), and higher suitability at low elevation areas (Fig. 4*C*) largely due to an increase in future niche breadth (Fig. 3*B*). The two models provide discrepant spatial predictions (R^2 = 0.85, RMSE = 0.04), especially toward the more suitable pixels (Fig. 4*D*). The African bush elephants are predicted to shift toward inland areas under warming (*SI Appendix*, Fig. S1*C*). Because little niche shift is incurred by warming (Fig. 3*B*), the individual-based model and the conventional species-level model yield almost identical spatial predictions of habitat suitability (R^2 = 0.98, RMSE = 0.01; Fig. 4*D*).

Sensitivity-analysis confirms that the above results are robust to the individual sampling efforts such as sampling duration time and number of observations (*SI Appendix*, Figs. S2–S5). The individual niche accumulation curves suggest that the population-level niche statistics generally stabilize when less than 10 individuals are included in the analysis (*SI Appendix*, Fig. S6).

Discussion

In this study, we introduce a bottom–up approach to characterizing population-level and species-level niches from individual niches. We demonstrate the utility of this framework for partitioning individual niche contributions and predicting species-level

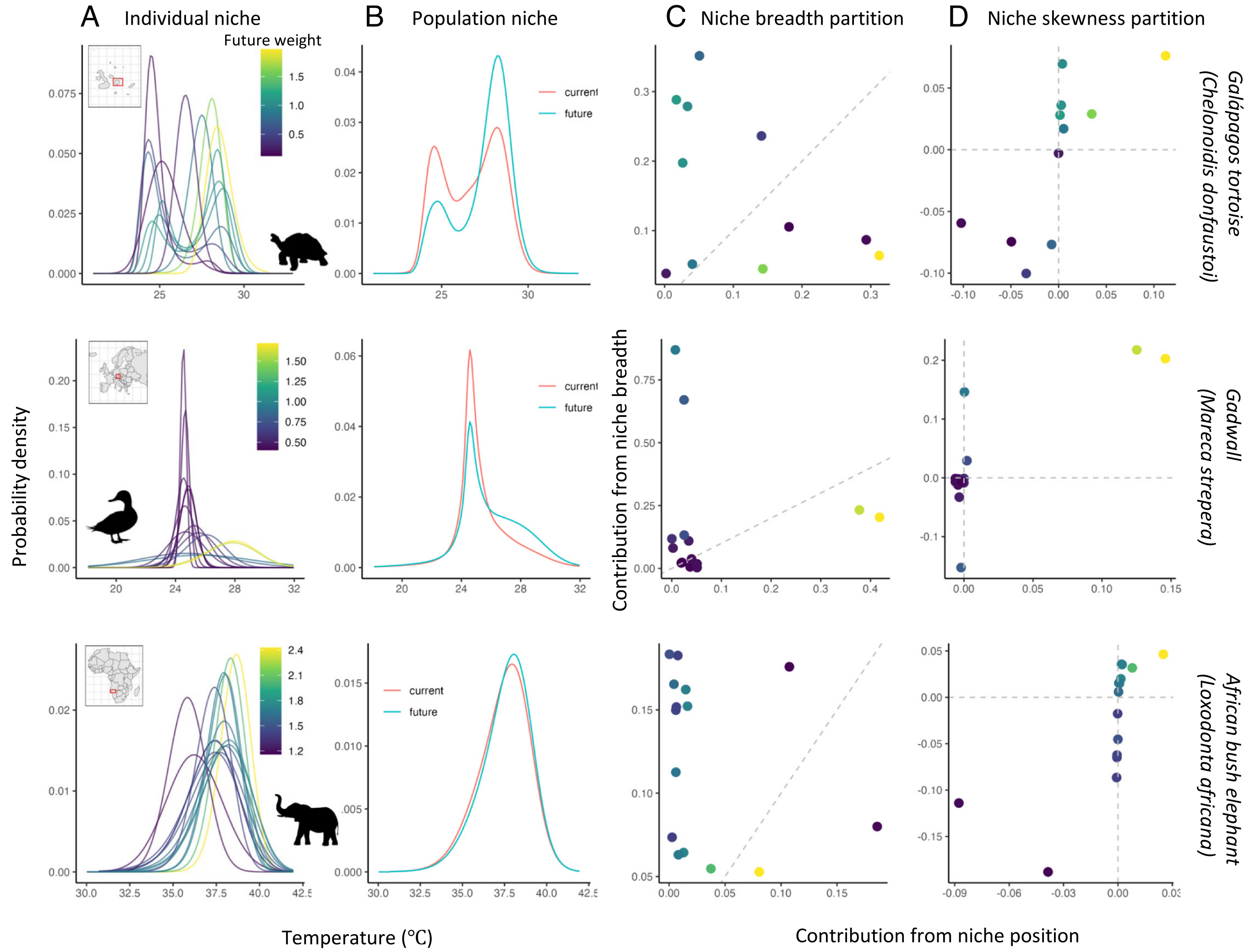

Fig. 3. Individual niches (*A*) and population niches under future warming of 2.4 °C (*B*) in 11 Galápagos giant tortoises in the Eastern Santa Cruz Island (first row), 14 Gadwall from southern Germany (second row), and 15 African bush elephants from the Etosha National Park (third row). (*C*) and (*D*) respectively show the partitioning of population niche variance and skewness into individual contributions. Colors in (*A*), (*C*), and (*D*) refer to future weights of individual niches in the warming scenario. The weight of each individual is calculated by the ratio between future habitat suitability and current habitat suitability. The gray dashed lines in (*C*) show the 1:1 lines. The horizontal and vertical gray dashed lines in (*D*) mark the 0 lines. For the niche breadth partitioning, the contribution through niche breadth is the individual niche breadth multiplied by its weight, $w_i\sigma_i^2$, and the contribution through niche position is the squared distance between individual niche mean and the population niche mean multiplied by its weight, $w_i(\mu_i^2 - \mu^2)$. The weights are equal for all individuals ($w_i = 1/n$). The mean values are scaled so that $\mu = 0$ to make sure the contributions are positive and interpretable. For the niche skewness partitioning, the contribution through niche breadth is $w_i(\gamma_i\sigma_i^3 + 3\mu_i\sigma_i^2 - 3\mu\sigma^2)/\sigma^3$, where γ_i is the skewness of the individual niche, and the contribution through niche position is $w_i(\mu_i^3 - \mu^3)/\sigma^3$. Positive values mean that the individual contributes to the longer right tail of the niche (mean larger than the median), while negative values mean that the individual contributes to the longer left tail of the niche (mean smaller than median).

niche shifts. We do not characterize the species-level niche from individual-level process in the sensu stricto Hutchinsonian definition, as attempted by recent studies (55, 56). Rather, we adopt a more operational measure of niche, the probabilistic occurrence niche, that stems from the use of species distribution modeling in macroecology (65) and resource utilization function (69) in movement ecology. By following the logic of how niches are characterized in these disciplines, we show that there is an elegant mathematical link between individual-level niche and higher organizational-level niches that opens many possibilities for future theoretical and empirical studies to investigate ecological and evolutionary processes across scales.

Implications for Intraspecific Niche Variation. The individual niche partitioning enabled by our framework recovers the traditional top–down variance partitioning approach for studying within-individual and between-individual niche variation (21, 92), but further ties the contribution to species-level niche formation to specific individuals. Moreover, our method goes beyond investigating the niche breadth (as measured by the variance) and extends to all moments of the niche such as skewness, regardless of the underlying distributions.

One prominent example of the importance of considering skewness in species niche is the use of thermal performance curves (TPC) in assessing the risk of climate change (76). Thermal performance curves are usually derived from individual-based physiological experiments (93, 94). The generally highly left-skewed individual-level TPC predicts that organisms will respond to warming more abruptly than cooling (77). One key question of applying experimentally derived thermal performance curves to predict species' distribution at the macroecological scale is how well individual-level TPCs represent species-level thermal response (76). Our study shows that the species-level skewness of a climatic niche is determined not only by individual-level skewness but also by the interaction between individual-level niche position and niche breadth. As clearly demonstrated in our empirical examples,

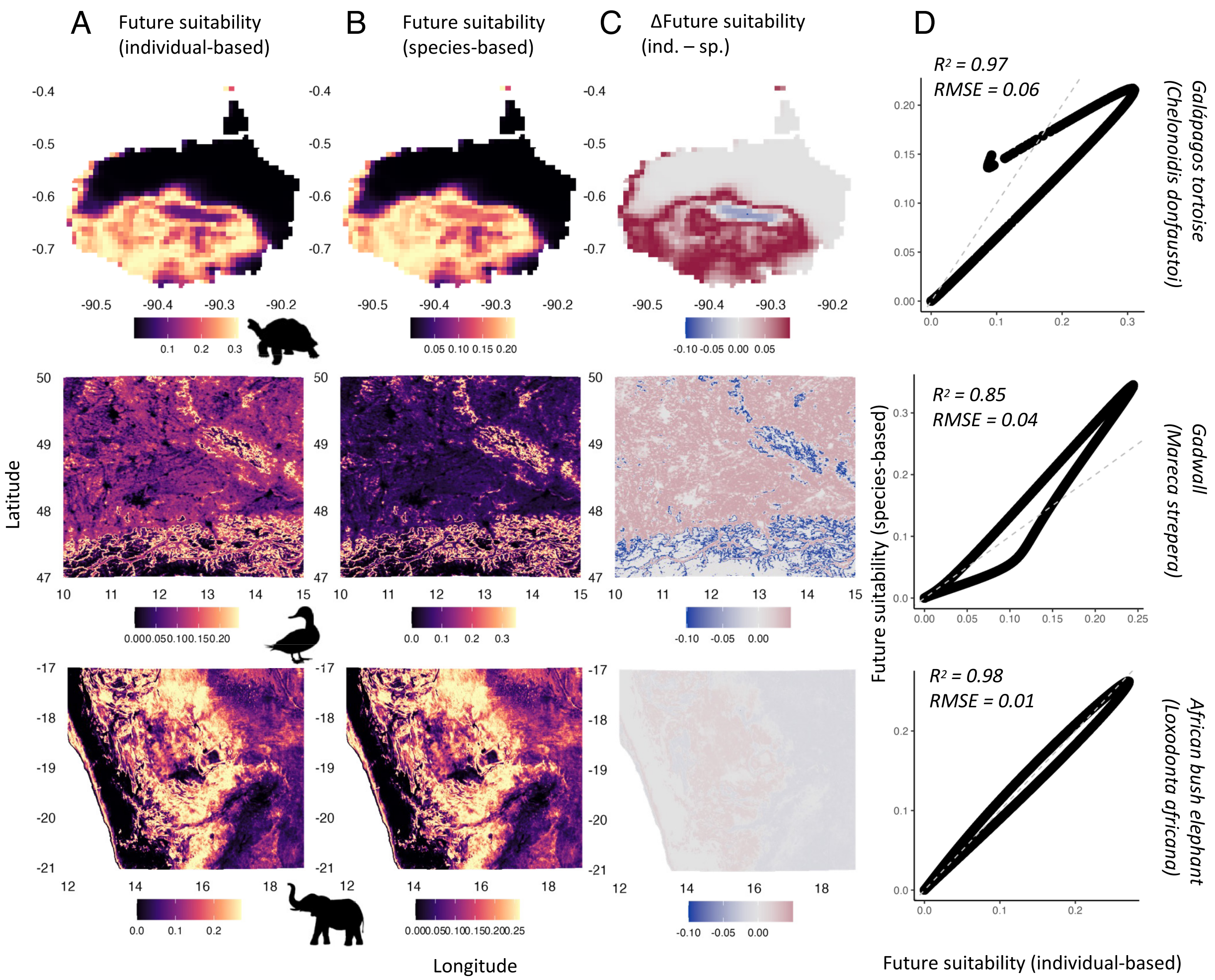

Fig. 4. (*A*) The future suitability estimated from individual-based niche models (accounting for future niche shift). (*B*) The future suitability estimated from species-based niche models (not accounting for future niche shift). (*C*) Difference between future suitability estimated from individual-based model and species-based model. (*D*) Scatter plot of future suitability of pixels estimated from species-based model against future suitability estimated from individual-based model. The gray dashed lines show the 1:1 line. RMSE shows the rooted mean squared error between the two predictions.

while the population skewness of the African bush elephants is largely determined by individual-level skewness, the giant tortoise population and the gadwall population show the opposite pattern. To what extent individual-level niche skewness dictates species-level skewness in general presents an interesting arena for future empirical research.

The ability to disentangle and characterize higher-level niches at the individual level enables us to account for life-history specific, spatial and temporal variation of species. For example, some bat species have highly segregated sex-specific habitat requirements (95), which can be incorporated under our framework to improve species-level niche estimates. In addition, accounting for population demographic structure will allow a better understanding about how species-level niche changes over time. Larval frogs (tadpoles) typically have different habitat, dietary, and thermal requirements than adults (96). During certain parts of the year, tadpoles can greatly outnumber adults, and in other parts of the year they are completely absent, which can heavily sway population-level niche estimates if such temporal variation of demographic structure is not accounted for. Our framework can also be used to combine different temporal niches to obtain a species' annual niche response. For example, our findings suggest that migrating bird species that have different niche tracking strategies over seasons (97) could have drastically different mean annual niche responses: Species that have more variable seasonal niche breadths but fixed niche centers are more likely to have a highly skewed mean annual niche. In summary, our framework helps better understand the source of intraspecific niche variation and allows us to make more effective conservation decisions for different species depending on their biological characteristics.

Implications for Species Distribution Models. Our method also provides a natural way to build species distribution models (SDM) from individual resource selection functions (52, 79). The conventional way of accounting for individual-level variation in SDMs typically treats individual variation as a random effect in a generalized mixed effect model (52), and uses the mean regression coefficients to represent the population-level response. In our empirical examples, we show that to characterize species-level SDMs from individual data that is comparable to the occurrence-derived SDMs (79), the population response should be calculated as a mixture distribution of individual resource selection functions (53) rather than using their mean regression coefficients. The difference between the two approaches of modeling population-level or species-level response is due to Jensen's inequality [the mean response is not equivalent to the response of the mean; (98)]. An important limitation of our method is that it depends strongly on the random sampling of individuals across space and time. This means that in ecological systems with high temporal variability or strong stochasticity (99), it requires longer tracking time and more intense sampling to capture the full range of environmental conditions experienced by different individuals. It further implies that the reliability of among-individual comparison of their contributions to the population niche is likely to be limited by the individual with the least sampling effort. When estimating population-level niches, individual weights might need to be adjusted to account for sampling bias associated with certain individual traits (e.g., smaller body size). Moreover, the standard practice of removing duplicate records in a grid cell (using grid cell rather than individual as the sampling unit) before fitting a SDM (57) might also hinder the integration of our approach with traditional methods. However, we expect that the gap will be increasingly bridged by the rapid growth of individual data (45, 49). To fully tap the potential of our framework for SDM, further investigation on the optimal sampling of individuals that yield the highest gain of information regarding habitat requirement (100, 101) is also needed.

Given the reliance on sufficient tracking data, the applicability of the demonstrated approach in the empirical example is undoubtably biased toward well-studied vertebrates (44). For data-limited groups such as invertebrates, estimates from mechanistic niche modeling or experimental evidence could potentially be combined to derive the species-level niche. For example, thermal response curves of different populations or individuals with different traits can be independently obtained from experiments, then the species-level niche can be derived by accounting for relative abundance of populations or trait distributions with weights in Eq. **1**.

Implications for Climate Change Vulnerability Assessment. A framework that can utilize individual-level information is especially important for climate change research. First, individual-based niche models using movement data may reshape estimates of animal redistributions and more accurately account for the effect of dispersal under climate change (102–104). Second, animals may evolve their thermal preferences to adapt to local conditions (105), which may occur at different rates based on body size and other individual-level factors (106, 107). Third, given that extreme weather events are expected to increase in severity and frequency under climate change (108), incorporating shorter term climatic anomalies in niche models could determine whether the exposure of individuals to extreme climatic conditions goes beyond their niche limits. Importantly, the thermal limits of individuals are expectedly narrower than those of the species, suggesting that individual-level climate change vulnerability may be masked by species-level models. Moreover, our findings suggest that different individual-level niche configurations are likely to produce different species-level responses to climate change. For example, in the clustered scenario (Fig. 2), populations are more likely to undergo an abrupt collapse of half of their individuals under climate change; in the nested scenario, the niche structure might have the potential to alleviate the threat of climate change not only by favoring warm-adapted individuals but also generalists in the future (Fig. 3), as illustrated in the Gadwall example. Without a thorough understanding of individual niche variation within species, it is impossible to accurately forecast species' extinction risk to climate change. From a conservation perspective, our findings suggest that highly diverse populations will have intense variation in individual vulnerability to climate change with possible population impacts. As a result, identified vulnerable subgroups and life stages may merit increased prioritization for conservation in the face of climate change for population maintenance (109). Moreover, the "leading edge" or "trailing edge" of a species should be identified in the context of intraspecific niche variation, as a species-level vulnerability assessment could mask the true adaptive capacity of specialized local populations (40).

Implications for Ecological Theory. The utility of the framework goes beyond empirically partitioning the niche or predicting niche shift and lies in its potential for developing individual-based ecological theories.

Previous theoretical studies have examined how the evolution of niche breadth is influenced by both intra- and interspecific competition, abundance of resources, and the strength of natural selection (23, 110). Our framework enables the investigation of the general shape of the ecological niche (111) which includes important attributes such as skewness.

Another important field that can clearly benefit from our findings is the investigation of functional traits. Traits are often used as proxies for niches, in which cases, the $f(x)_i$ in Eq. **2** can be used to describe the distribution of biomass or abundance of species in the functional trait space. The partitioning of trait attributes such as skewness and kurtosis into within-species and between-species components fits nicely into the regime of the trait driver theory, which links the distribution of traits to ecosystem functioning, productivity, stability, and climate change (66, 112).

Connection to the Hutchinsonian Niche. The link of our approach to the sensu stricto Hutchinsonian niche can be further explored through the weight function in Eq. **1**. In our demonstration of the niche shifts examples (Fig. 3), we have implicitly assumed that the future environmental suitability of an individual represents its relative fitness under climate change. To further accommodate the Hutchinsonian niche concept, we can use absolute fitness rather than relative fitness to calculate weight in Eq. **1**. If fitness information on individuals can be obtained independently from occurrence data, then we can select or weight the contributions of individuals to population-level Hutchinsonian niche based on their contributions to the long-term persistence of the species (56). For example, consider the case that inferior competitors of an animal population leaving high-quality natal habitats for inferior habitats, and many of these animals will likely die or may not reproduce given poor habitat quality. If we were to estimate the species niche for all individuals, we may estimate a wider species niche than the actual Hutchinsonian niche, as the peripheries of this estimated distribution do not contribute to species' persistence. This problem of overestimating the Hutchinsonian niche with observed occurrence is particularly insidious in the case of ecological traps: Individuals may be attracted to habitats that actually harm individual fitness (113), leading to overestimation of the species-level reliance on poor habitats.

Conclusion

The unification of niche estimates across organismal levels provides a valuable opportunity to further advance ecological theories, refine climate change predictions, and inform biodiversity conservation efforts. The increasing integration of individual-level studies into global biodiversity research will greatly enrich our understanding of biodiversity changes across spatial, temporal, and organismal scales.

Data, Materials, and Software Availability. Previously published data were used for this work (88–90). The datasets and codes to reproduce the study are stored in Zenodo (https://doi.org/10.5281/zenodo.16007926) (114).

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