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Review

Scale-sensitivity in the measurement and interpretation of environmental niches

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Species environmental niches are central to ecology, evolution, and global change research, but their characterization and interpretation depend on the spatial scale (specifically, the spatial grain) of their measurement. We find that the spatial grain of niche measurement is usually uninformed by ecological processes and varies by orders of magnitude. We illustrate the consequences of this variation for the volume, position, and shape of niche estimates, and discuss how it interacts with geographic range size, habitat specialization, and environmental heterogeneity. Spatial grain significantly affects the study of niche breadth, environmental suitability, niche evolution, niche tracking, and climate change effects. These and other fields will benefit from a more mechanism-informed choice of spatial grain and cross-grain evaluations that integrate different data sources.

Highlights

Organisms experience environmental conditions over contiguous geographic space. However, empirical studies tend to characterize this environment in a way that is discrete and often subjective.

Owing to practical limitations, the spatial grain (resolution) at which we record environmental conditions often fails to capture the true environmental variation experienced by a species, therefore hindering estimation of the ecological niches of species.

Despite the general awareness of the importance of spatial scale in niche studies, the impact of variable spatial grains in biodiversity and environmental data on ecological and evolutionary inference remains insufficiently appreciated.

We illustrate the key drivers and consequences of the grain size-dependence of environmental niche estimates and provide general recommendations on how to address the issue of grain size-dependence in empirical studies.

Environmental niches and mismatches with spatial grain

The concept of the **niche** (see Glossary) is one of the cornerstones of ecology [1]. The environmental niche in particular has taken on a special relevance because organisms are increasingly facing the threat of climate change [2]. Although well conceptualized by Hutchinson as an ***N*-dimensional hypervolume** in the environmental space within which a species can survive and reproduce [1], the measurement of niches (particularly the **fundamental niche**) is challenging and has been heatedly debated [3,4]. With the rapid growth of spatial biodiversity and environmental data [5,6] and the development of new computational methods [7–9], much of ecology (particularly macroecology and global change ecology) has embraced a practical approach toward the measurement of environmental niches based on presence data [10,11]. With a focus on **realized niches** [2], scientists broadly rely on spatial data to measure environmental or climatic niches, such as **incidental records** from museum specimen or citizen science projects, atlas data, and **range maps** [12]. Essential in all niche work relying on spatial data is the choice of the size of the units analyzed – the spatial grain [13]. We review here the fundamental relevance this spatial grain has for any inference or comparisons of environmental niches.

Spatial scale, in both its grain and extent aspects, is a prominent issue in ecology [14] owing to the non-uniform geographic distribution of environmental conditions and scale-specific biological processes [15]. Given different body sizes, mobilities, behaviors, etc., species vary in the spatial grain at which they respond to such environmental variation [16]. For example, larger animals require a higher daily energy intake and will need to cover a larger geographic area to find resources than smaller animals [17]; highly mobile animals such as birds can explore a much larger area than less-mobile animals such as rodents [18]; given the same traveling distance, animals using a 'target-search' foraging strategy will have a larger home range size than those using a 'systematic-search' strategy [19]. We illustrate the different spatial scaling of the environmental niches for two species in Box 1. Full knowledge of the predominant spatial grain at which a suite of biological processes operate, namely the biological **response grain** [20], would in principle enable

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correct niche measurement and inference. However, such information is often unavailable [18], and a process-informed choice of spatial grain is only rarely executed [20–22].

The resulting grain size-mismatch between the underlying processes and measurement is a pervasive but unresolved issue in empirical niche studies. We identified the five major themes that rely on spatially measured environmental niches, and then evaluated the most cited papers within each theme (varying from 22 to 55 per theme) published in 2007–2022 (Figure 1). We found that the spatial grains these reports used for environmental niche analysis ranged from 1 m to 300 km (Table S1 in the supplemental information online), and within each theme exhibited strong heterogeneity and an imbalanced distribution with a positive skew (average skewness across themes: 2.47, P <0.001 for each theme). Spatial grain did not differ significantly among themes (Kruskal–Wallis test: $P = 0.57$; Figure 1), but varied significantly among taxonomic groups (Kruskal–Wallis test: $P = 0.001$). Consistent with the expectation that highly mobile animals have a larger response grain than less mobile organisms [18], environmental niche studies on plants and invertebrates were conducted at a smaller spatial grain than those for birds (pairwise Wilcoxon test with Holm correction: P <0.05; Figure S2 in the supplemental information online). Except for studies focused on the issue of grain size-dependence, only 12 of 221 empirical niche papers used multiple spatial grains. Closer examination indicated that the authors cited prior knowledge about the response grain (such as the home range size) in only 18 cases. We further found that the choice of analysis grain differed significantly among studies using different biodiversity data types (Kruskal–Wallis test: P <0.001) and roughly matched the sampling resolution of the readily available biodiversity and environmental data (Figure S2 and Table S1 in the supplemental information online). For example, studies based on expert maps tend to use a ~100 km resolution, reflecting the reliable spatial grain of this data type which has a high false presence rate at finer spatial grains [23]; studies based on atlas data tend to follow the spatial grain of their design, usually 50–10 km; finally, studies based on occurrence data often used 1 km resolution (Figure S1 in the supplemental information online), the typical resolution of frequently used global environmental datasets such as WorldClim [24] and CHELSA (climatologies at high resolution for the Earth's land surface areas) [5]. The covariation between data type and spatial grain imposes another constraint on the comprehensiveness of niche studies [12]: occurrence data have the advantage of capturing the fine-grain variation of temporal and spatial dynamics of species, but suffer from low and biased taxonomic or environmental coverage [12,25]; coarser-resolution data tend to have greater taxonomic or environmental coverage for large-extent comparisons but lack the detailed information required for narrow-ranged and specialist species [26].

Box 1. The spatial scaling of environmental niches in practice

We illustrate the spatial scaling of the environmental niches for two species (Figure IA,B). The 32 km and 128 km buffers around the occurrence points (corresponding to two different grain sizes) are shown as blue and green circles. Black polygons show the range maps for each species (Figure IA,B). The estimated niches at different grain sizes are visualized by the contour line of the 50% quantile of the Gaussian kernel density estimate. The niche breadths (calculated as the generalized variance estimated from 50 occurrence points) of the two species show strong but different patterns of grain size-dependence: that of the narrow-ranged Berylline hummingbird (*Saucerottia beryllina*) consistently decreases, whereas that of the wide-ranged Orange-winged amazon (*Amazona amazonica*) first increases then decreases with spatial grain (Figure IE). The niche shape (measured by the correlation between temperature and precipitation) of the Berylline hummingbird is more sensitive to the change of grain size than that of the Orange-winged amazon (Figure IF). The former species appears to be more environmentally specialized than the latter at a finer spatial grain, but this relationship is reversed at a coarser spatial grain (Figure IE). To better appreciate the effect of spatial averaging on local conditions, we demonstrate the environmental changes in one example occurrence location for each species (Figure IA–D). With increasing spatial grain, the example location of the Berylline hummingbird moves toward higher precipitation and temperature space (Figure IC) as a result of including more low-elevational areas (Figure IA). By contrast, the example location of the Orange-winged amazon first decreases then increases in temperature (Figure ID) with increasing spatial grain because of the more complex thermal landscape in the region (Figure IB).

Glossary

Fundamental niche: the set of environmental conditions where a species has a positive intrinsic population growth rate in the absence of other factors such as biotic interactions or dispersal limitation.

Incidental records: spatial coordinates where a species is reported to be present at a given time. These are typically collected in a non-systematic way (e.g., a citizen science project).

Niche: the set of abiotic and biotic environmental conditions that are required by a species to maintain a positive intrinsic growth rate. The abiotic environmental niche is also called the Grinnellian niche; the biotic environmental niche is also called the Eltonian niche.

***N*-dimensional hypervolume:** a geometric characterization of niche in a high-dimensional space such as the trait space or the environmental space, and that is typically used to quantify the range of conditions where a species is present or has a positive population growth rate.

Range maps: coarse-resolution maps (e.g., a polygon) of where a species is likely to occur. These are usually drawn by experts who have sufficient empirical knowledge about the species.

Realized niche: the set of environmental conditions where a species can persist when all other processes such as biotic interactions and dispersal are considered.

Response grain: the grain at which a species perceives environmental variation; it is usually correlated with the dispersal ability or the body size of a species. It is also called the 'characteristic scale' or 'intrinsic scale' in the literature.

Spatial scale: the extent and the grain of data used in geographic analysis. Extent is the overall area (scope) of the geographic domain, whereas grain (resolution) represents the size of individual units.

Species distribution model (SDM): a statistical model that is used to predict the geographic distribution of a species, which typically involves estimating the environmental suitability of a site for a species.

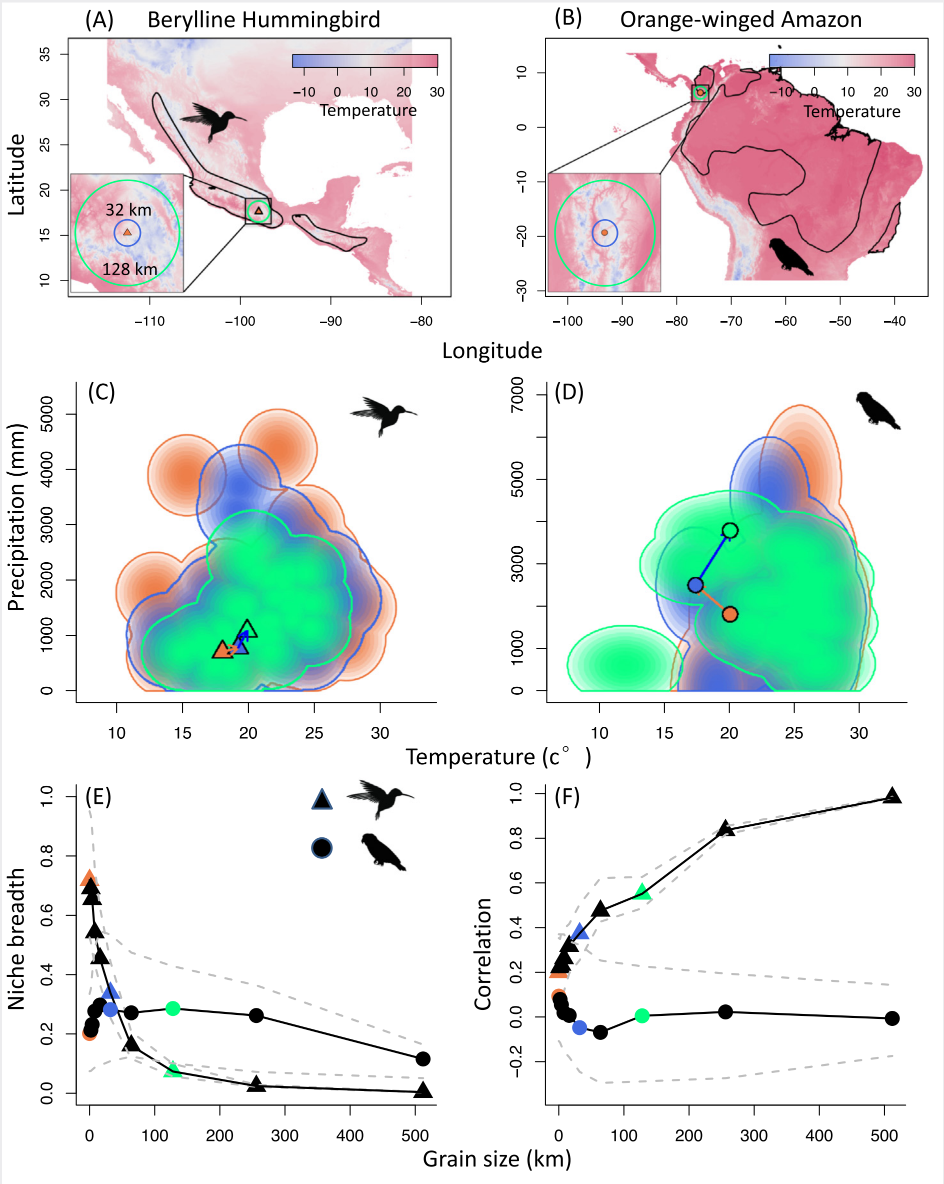

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Figure I. Niche scaling of Berylline hummingbird (*Saucerottia beryllina*) and Orange-winged amazon (*Amazona amazonica*). (A,B) Example occurrence points of the two species. (C,D) Triangles show the example occurrence points of the Berylline hummingbird at different scales; circles show the example points of the Orange-winged amazon. (E) Spatial scaling of niche breadth. Broken gray lines show the 95% quantile of 100 random draws, unbroken lines show the median. (F) Spatial scaling of niche shape. Berylline hummingbird and Orange-winged amazon are shown respectively by triangles and circles. Further information on the data and methods is given in Box S1 in the supplemental information online.

The six orders of magnitude we found in the variation of spatial grains reveals a highly heterogeneous and potentially precarious foundation for environmental niche inference and comparison among species. The specific impact of potential mismatch between analysis and response grain will depend on the grain size-sensitivity of niche measurement and its covariation with the biological and geographical drivers.

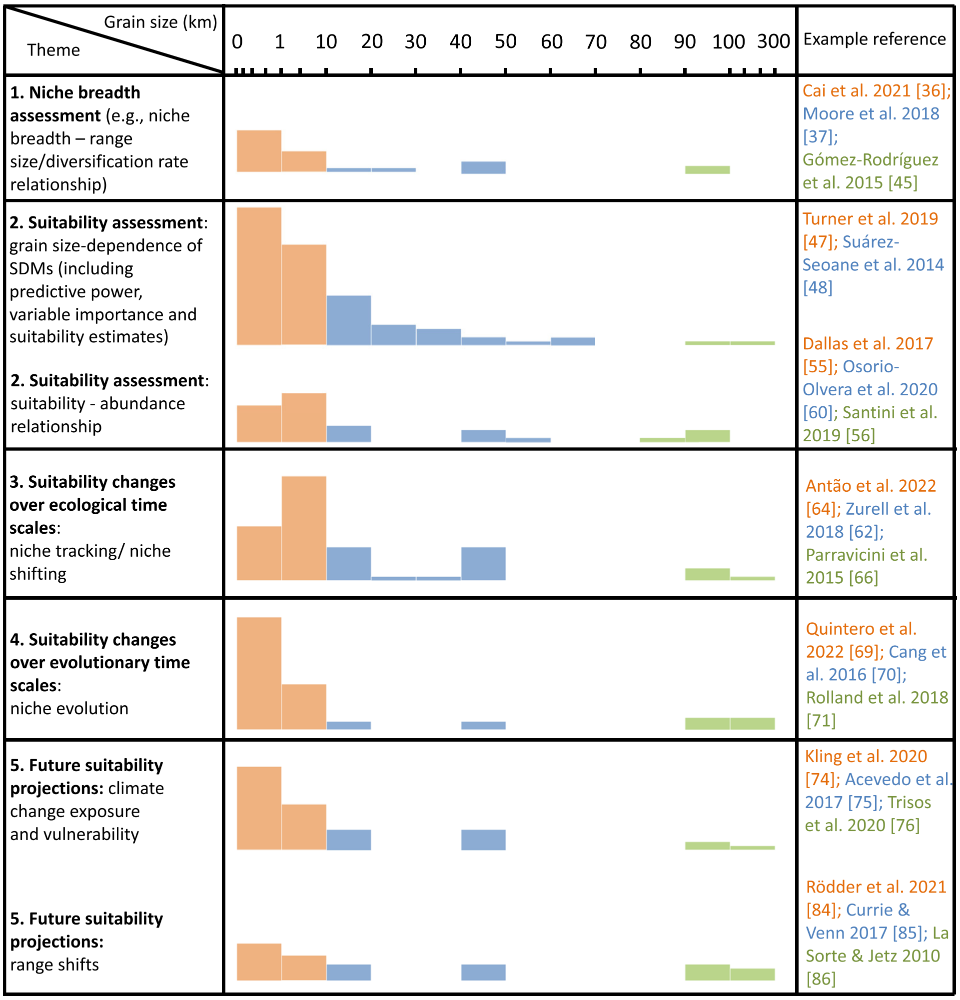

Figure 1. Frequency of grain sizes used in niche studies. We performed a literature search of the Web of Science (https://www.webofknowledge.com/) using the keywords environmental niche* or Grinnellian niche* or climatic niche*, and with the aid of cross-references for each topic chose the top 262 most cited papers (22–55 per topic, see Table S1 in the supplemental information online for a full list). We identified five main themes in niche studies: (i) niche breadth assessment, which studies the relationship between environmental niche breadth and other biological variables such as range size, diversification rate, and abundance; (ii) suitability assessment, which includes studies that investigate how environmental suitability estimates depend on spatial scale, and the relationship between suitability and abundance; (iii) suitability changes over ecological timescales, which includes studies on niche shifting and niche tracking for a short period of time (e.g., months, years, decades); (iv) suitability changes over evolutionary timescales which mainly focus on niche dynamics at a geological timescale, typically using phylogenetic analysis; (v) future suitability projections, including studies that assess the future climate change vulnerability and elevational or latitudinal range shifts of species. We randomly chose two to three example papers matched to the respective spatial grain size represented by different colors (orange, fine; blue, intermediate; green, coarse). The assessment does not include studies that attempt to summarize environmental variables over a range of distances around focal points ('focal analyses') (Figures S1 and S2 and Table S1 in the supplemental information online). The 0–1 bin includes grain sizes equal to or less than 1 km. The 1–10 bin includes grain sizes larger than 1 km, and equal to or less than 10 km. Abbreviation: SDM, species distribution model.

The grain size-dependence of environmental niches

The spatial grain size-dependence of environmental niche measurement (as represented by the volume, position, and shape of the *N*-dimensional hypervolume) emerges from fine-grain variability in the environmental conditions occupied by a species that is incompletely captured at coarser spatial grains. Local environmental conditions are grain size-invariant only when measured environmental variables are homogeneous or exhibit linear trends; in all other cases, a grain size-dependence arises. When the landscape is fully occupied by a species, spatial averaging should lead to a reduction in variation when spatial grain coarsens and causes a decrease in niche volume. We illustrate the grain size-dependence of environmental niches and its consequences in the simplified case of a 1D landscape (Figure 2).

Direct drivers of grain size-dependent environmental niches

Because the grain size-dependence of niche measurement arises from the abovementioned spatial averaging process which is only affected by the fine-grain occupancy pattern of a species at the landscape, we argue that it has three direct drivers: (i) the environmental variation across the landscape, as measured by the geographic environmental heterogeneity; (ii) the extent of the landscape that is occupied by a species, as measured by the range size of a species; and (iii) how selective a species is in occupying areas within its geographic range, as measured, for example, by its habitat specialization.

First, we focus on niche volume in relation to the three direct drivers. Lower levels of environmental heterogeneity should lead to a smaller change of niche volume with increasing spatial grain as a result of smaller variation at finer grain (Figure 2A). In wide-ranged species, niche volume should be less affected by grain size because it is mainly driven by the environmental distance between locations that are geographically far apart (Figure 2B). Thus, toward coarser grains, we would expect a smaller change in niche volume for wide-ranged species than for narrow-ranged species. Similarly, at coarser grains we might expect a smaller change in niche volume for habitat generalists than for specialist species because environmental variation between different habitat types is less sensitive to grain size.

However, the above notion of a decrease in niche volume with increasing grain size in a fully occupied landscape does not necessarily apply to habitat specialist species: when a species is highly specialized and only occupies a small area within a coarse grain, its niche volume could increase with coarser spatial grains if much of the unsuitable area is included in its niche measurement (Figure 2C).

We next examine the effects of grain size on the position and shape of environmental niches, which – assuming a normal distribution – are represented by the center (Figure 2) and the correlation among niche axes in the multidimensional space (Figure 3). Given its nature as an 'average' statistic, the niche center is generally less sensitive to spatial grain [27,28]. However, a grain size-dependence of niche position can arise, for example, for narrow-ranged or specialist species or in the presence of strong environmental gradients, because coarsening the grain can cause a directional shift of the niche space (Figure 2). For niche shape, narrow-ranged or specialist species are expected to be particularly sensitive to spatial grain (Figure 3) because for them a coarser grain is more likely to include novel combinations of environmental conditions which can alter the correlations among niche axes.

Indirect drivers of the grain size-dependent environmental niches

Biotic interactions and spatial/temporal disequilibrium with environmental conditions (such as source–sink dynamics [29] and response lag to the temporal environmental changes [30]) can indirectly influence the grain size-dependence of niche measurement through their effects on realized range size and habitat specialization.

We expect the implications of biotic interactions to depend on the fine-grain segregation between species. If coarse-grain species compete for the fine-grain environmental conditions more or less

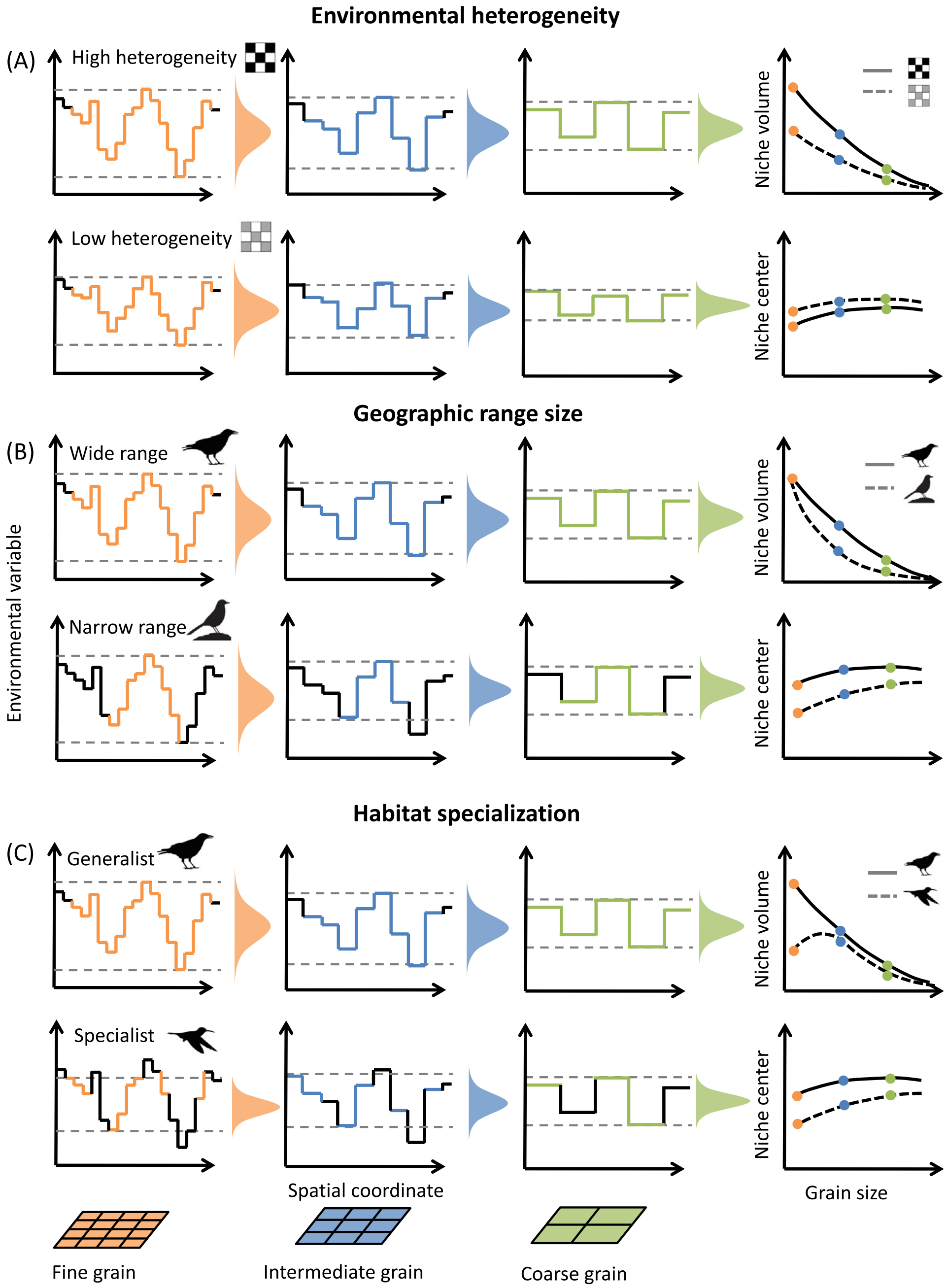

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Figure 2. Drivers of grain size-sensitivity of environmental niches. (A) Environmental heterogeneity, (B) geographic range size, and (C) habitat specialization. Panels show the effects of changing spatial grain on niche volume and center along a hypothetical 1D spatial transect. The *y* axis denotes the environmental values, and the *x* axis denotes the spatial coordinates. Grain size is represented by the interval length of the coordinates in the 1D transect. Areas occupied by the species are shown in color, and unoccupied areas are shown in black. Orange represents fine grain, blue represents intermediate grain, and green represents coarse grain.

stochastically (as in the Eltonian noise hypothesis [14], where biotic interactions lose importance toward coarse grains), the measured niche volume and shape should be insensitive to the change of grain size. By contrast, if biotic interactions facilitate the segregation of species along

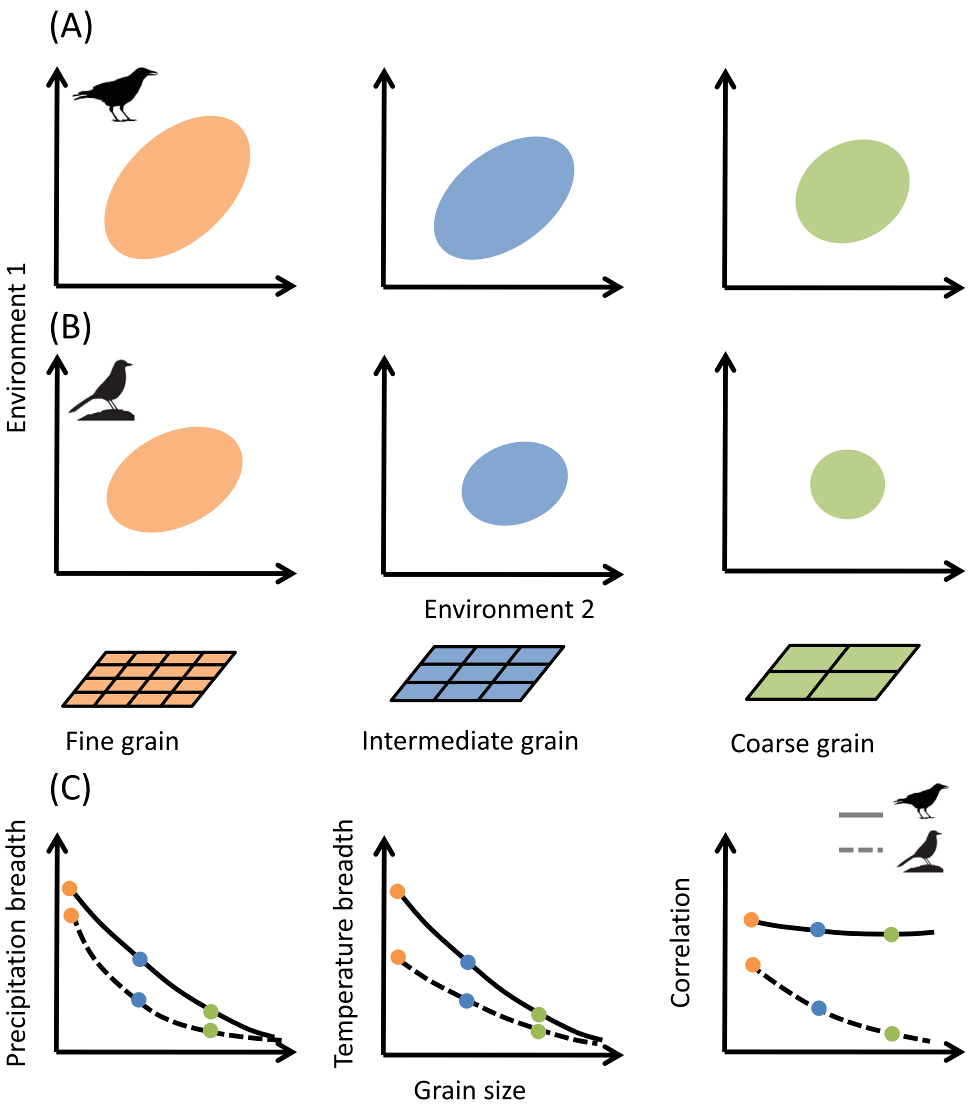

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Figure 3. Grain size-sensitivity of 2D niches for two species. (A) A wide-range/generalist species, and (B) a narrow-range/specialist species. Both niche breadth (characterized as the area of the ellipsoid niche) and shape (measured by the correlation between the niche axes) change with spatial grain. (C) The spatial scaling of niche breadth and shape for the two species.

environmental gradients [31], they are likely to increase the grain size-dependence of niche measurement among interacting species. Moreover, if biotic interactions also affect coarse-grain range limits [32,33], they can strengthen the grain size-dependence of niche measurement by reducing the range size of a species.

Both spatial and temporal disequilibrium with environmental conditions such as the source–sink dynamics [29] and temporal lag in response to climate change [30] enable a species to appear more often in an unsuitable environment and are therefore poised to reduce the grain size-dependence of environmental niche measurement.

The consequences of spatial grain size-mismatch

We illustrate the impact of spatial grain on the interpretation of niche-based research for key topics among five major themes.

Niche breadth assessments

The niche breadth–range size relationship

Niche breadth is hypothesized to drive the variation in geographic range size among species: generalist species tend to have a larger geographic range than specialist species owing to wider environmental tolerance [34]. However, measured niche breadth varies idiosyncratically with spatial grain among species, and how well it captures actual tolerances will depend on the biological mechanisms and attributes of the study organisms (Figure 4A). This suggests that the niche breadth–range size relationship is not necessarily stronger at coarser grains, as shown by a recent study on European plants [35]. The grain at which niche breadth–range size relationships can be detected also depends on environmental heterogeneity [36]. This was demonstrated in recent studies showing that spatial autocorrelation of environmental variables can inflate the slope of the niche breadth–range size relationship [37–39]. Therefore, identifying the relevant spatial grain becomes crucial for testing the niche breadth–range size relationship, especially when the spatial scaling of niche breadth covaries with range size (Figure 2B).

The niche breadth–diversification relationship

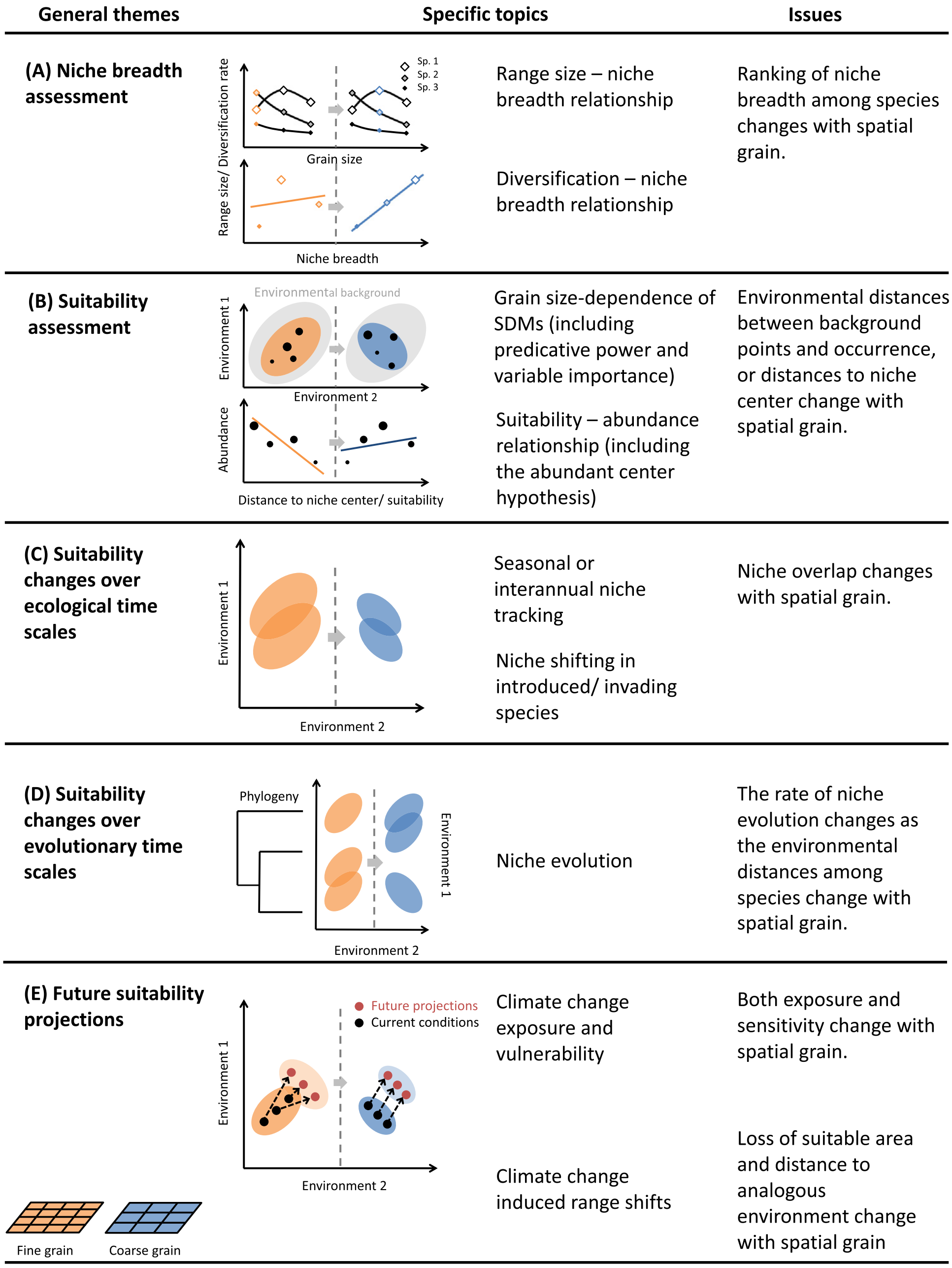
Narrower niche breadth is hypothesized to increase the diversification rate by increasing the chance of allopatric speciation because of greater susceptibility to habitat fragmentation, competition, and climate change [40]. Although some studies have found that more specialized species have higher diversification rates [41–43], a recent study using coarse-grain data shows that there is no consistent relationship between niche breadth and diversification rates [44]. Here again we suggest that grain size issues need to be confronted to support robust tests of the hypothesis. Family-level and genus-level niche breadth–diversification relationships [45] will also be complicated by variable grain size-sensitivity of species within the clade, for instance, owing to highly disjunct geographic distributions [46].

Environmental suitability assessments

The grain size-dependence of niche measurement also broadly affects all estimates of environmental suitability and their association with the observed occurrence or abundance pattern. We illustrate the issue for two classic ecological topics: **species distribution models (SDMs)** and the environmental suitability–abundance relationship.

The grain size-dependence of SDMs

Numerous studies have examined how spatial grain impacts the performance of SDMs, but often with mixed findings depending on the geographic region and study organism [47,48]. The issue can be recast in a hypervolume view for further clarity. SDM-derived suitability measures the relative occurrence probability of a species with respect to the environmental background, which is affected by the similarity between the probabilistic distributions of the realized niche and the environmental background [11]. The change of grain size therefore affects the estimated suitability through overlap between the hypervolume of the realized niche and the hypervolume of the environmental background (a measure of similarity between two distributions) (Figure 4B). For narrow-ranged and specialist species, we expect the performance and the estimated suitability of SDMs to be particularly prone to differences in spatial grain because – compared to wide-ranged and generalist species – their realized niches overlap less with the environmental background [49,50], and the hypervolumes of the realized niche and the environmental background are likely to respond differently to spatial grain (Figure 2). Suitability estimates



General themes	Specific topics	Issues
(A) Niche breadth assessment	Range size – niche breadth relationship Diversification – niche breadth relationship	Ranking of niche breadth among species changes with spatial grain.
(B) Suitability assessment	Grain size-dependence of SDMs (including predicative power and variable importance) Suitability – abundance relationship (including the abundant center hypothesis)	Environmental distances between background points and occurrence, or distances to niche center change with spatial grain.
(C) Suitability changes over ecological time scales	Seasonal or interannual niche tracking Niche shifting in introduced/ invading species	Niche overlap changes with spatial grain.
(D) Suitability changes over evolutionary time scales	Niche evolution	The rate of niche evolution changes as the environmental distances among species change with spatial grain.
(E) Future suitability projections	Climate change exposure and vulnerability Climate change induced range shifts	Both exposure and sensitivity change with spatial grain. Loss of suitable area and distance to analogous environment change with spatial grain

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Figure 4. The implications of grain size-dependent niche measures for ecological and evolutionary inference. (A) A change of niche breadth results in a change in the rankings of niche breadth among species, hence altering the range size–niche breadth relationship and the diversification rate–niche breadth relationship. The size of the diamonds is proportional to the range size or diversification rate. (B) Suitability estimate is both impacted by the change of niche shape and volume with grain size. The size of the solid points is proportional to population density. (C) Assessing suitability changes over time, such as niche shifting and niche tracking, involves comparing niche overlap, which is impacted by the change of niche position, volume, and shape with grain size. (D) The rate of niche evolution is also impacted by niche overlap among species. (E) Climate change vulnerability assessment is influenced by both the change of exposure and sensitivity. For spatial analysis, spatial grain also influences the distance to an analogous environment and the loss of suitable areas. Red points represent future climates and black points represent current climates.

are additionally affected by the spatial autocorrelation of the landscape [20,51], also through the similarity between the occupied environment and the available background. Low autocorrelation should lead to less overlap between the realized niche and the environmental background, and therefore to greater grain size-dependence. More generally, any factor that influences the performance and estimates of SDMs (e.g., the modeling extent) can be translated into comparing the overlap between the hypervolumes of the realized niche and the environmental background.

Environmental suitability–abundance relationship

One simple but prominent suitability–abundance relationship is that of the 'abundant center' hypothesis which states that a species is most abundant in the center of its geographic range or environmental niche [52,53]. This hypothesis has been used as a basic assumption in many theoretical and statistical models [54], but its validity has recently been challenged [55,56]. A more general version of the 'abundant center' hypothesis assumes that environmental suitability derived from SDMs should be positively correlated with abundance, because more favorable habitats should have a higher population growth rate or carrying capacity. The empirical support for the suitability–abundance relationship is mixed [57,58], and most testing has been conducted at a single spatial grain for all species. We note that single-grain analyses become insufficient when species have a different response grain for environmental variables as a result of trait and behavior variations [17,59]. An ideal test of the 'abundant center' hypothesis would examine the relationship at the spatial grain relevant to each species and disentangle the contributions of different niche factors to the observed patterns [20]. We suggest that multi-grain approaches would provide stronger test of the 'abundant center' hypothesis and have the potential to provide deeper insights into how species traits modulate the abundance–distribution relationship [60,61].

Suitability change over ecological timescales: niche tracking and niche shifting

Assessments of environmental niche tracking under changing climate [62–64] or niche shifts in newly introduced geographical space [65,66] necessitate a comparison of environmental niches in different time or space. Because the volume and shape of the compared niches change with spatial grain in idiosyncratic ways (Figure 4C), the spatial scaling of niche overlap becomes contingent on the heterogeneity of the environmental layers of different times or in different biogeographic regions. This has major implications if a species originates from the tropics and was introduced into a temperate area, or when climate change not only raises the mean temperature but also makes the landscape more heterogeneous [67]. More importantly, the position of the non-overlapping niche space determines whether the encountered novel environments are at the upper or lower limit of a niche axis, and will have different effects on the fitness of a species [68].

Suitability changes over evolutionary timescales: niche evolution

In niche evolution research, spatial grain affects assessments of evolutionary rates [44,69–71] and of phylogenetic niche divergence [72]. Rates of climatic niche evolution should be lower at coarse spatial grains because spatial averaging reduces the overall climatic distance among species. Coarse spatial grains will also favor the detection of phylogenetic niche conservatism [73] because of reduced among-species environmental niche variation (Figure 4D).

Suitability change projections

A primary goal of studying environmental niches is to better evaluate the responses of species to climate change. Understanding and accounting for grain size-dependence is thus of pivotal interest for conservation.

Exposure and sensitivity to climate change

Assessing the vulnerability of species to climate change is crucial for conservation management [74–76]. A simple measure of community-level vulnerability to climate change is the gap between local niche preference and future climate [77]. For species-level or population-level vulnerability, a common framework separates exposure from sensitivity [78], where exposure is the magnitude of climate change and sensitivity corresponds to the environmental tolerance of a species (often measured by niche breadth). Climatic novelty for a site is measured in a similar way, where the niche breadth of a species is replaced by historical climatic variation [79]. The grain size-dependence in vulnerability assessments comes from two sources: (i) the grain size-dependence of exposure, for example, because changes in microclimates driven by forest cover significantly lag behind landscape-level climate changes [80]; and (ii) the grain size-dependence in sensitivity, because grain size affects estimates of niche volume. Given the same amount of climate change, a smaller niche volume leads to higher climate change vulnerability; even when niche volume is unaffected by spatial grain, vulnerability can still be impacted by the change of correlations between niche axes (Figure 4E) [81]. The grain size-dependence in sensitivity can significantly impact on the vulnerability assessment, as supported by a recent study showing that coarsening the spatial grain will increase the estimated amount of novel and disappearing climates as a result of the decrease in environmental variability [82]. The grain size-dependence in vulnerability is especially an issue for narrow-ranged and habitat specialist species [83], and needs careful attention in global change research (Figure 2).

Range shifts

Studies addressing range shifts have raised concerns about the ability of species to move or adapt in response to changing local environments [84–86]. Grain size-mismatch affects estimates of the distance to an analogous environment and the loss of suitable areas [67,82]. The potential for elevational range shifts in particular has received much attention because mountains harbor many evolutionarily distinct species that have narrow elevational distributions and high extinction risk [87,88]. The problem of grain size-mismatch in quantifying environmental niches is likely to be more severe for mountainous species [89] because (i) complex topographies in mountainous areas lead to more idiosyncratic changes of local environments with spatial grain; and (ii) mountains, from top to bottom, often span a large temperature or precipitation gradient, which, combined with the narrow elevational range of a species, is likely to cause directional shift of niche space when spatial grain coarsens. This has major implications for predicting the directions of elevational range shifts because evidence for some bird species shows that temperature change predicts upslope shifts whereas precipitation change predicts downslope shifts [88].

Practical recommendations for the choice of spatial grain size

Identifying an optimal grain of analysis for a particular system is one of the greatest challenges in spatial ecology [21]. Given that processes operating at different spatial grains might combine to affect the distribution of organisms [22], the search for a single 'best' grain size might be fraught with difficulty [90]. Our general recommendation is to conduct analyses across multiple spatial grains when possible and to include an assessment of the grain size choices and sensitivity in the interpretation of results.

Although a perfect *a priori* choice of grain size might not exist, an ecologically or statistically guided identification of at least relevant spatial grain sizes is, however, still possible. For many questions a natural choice of the most suitable grain may come from matching with prior knowledge about the body size or home-range size of a species [91], or the area of a population [18]. For example, for predicting individual-level habitat selection over a small geographic extent, the grain size might be chosen to be as fine as possible to match the body size of the organism;

however, for predicting species-level occurrence at the regional level and over long periods, the most appropriate grain size might be the one that matches the home-range size or dispersal neighborhood of a species. Although an empirically exact determination here might be out of reach, it can still help to delimit the range of grain sizes considered. In large-extent studies that rely on expert range maps which are necessarily of coarse resolution [23], a refinement with data about elevational ranges [69] or about habitat preferences and habitat-suitable areas [92] can support more accurate niche estimates. If multiple processes operating at different spatial grains (e.g., population-level and individual-level) are expected, environmental covariates characterized at multiple process-specific grains can also be included in a model to improve predictions [20,93,94]. When no *a priori* information on response grain is available, machine learning or statistical approaches could be used to select among a range of possible grains per variable – an approach that is increasingly facilitated by versatile cloud-based environmental annotation tools that enable fast multiple-grain characterization [94]. To further improve model predictions, one could use a focal analysis that summarizes environmental data from neighborhood windows of various sizes around each occurrence [95] instead of assuming equal values for occurrences within the same coarse grain [96]. We also advocate cross-validations [97] over model selection based on fitting statistics [e.g., Akaike information criterion (AIC)] to avoid 'overfitting' of the optimal grain, as well as generally cautious interpretation of such 'automatically' selected combinations.

Concluding remarks

The grain size-mismatch between observations and ecological processes poses a significant challenge for testing niche-based hypotheses in ecology and evolution, as well as for the assessment of climate change effects on biodiversity. A fruitful and crucial step is to assess the sensitivity of measured environmental niches to spatial grain (see Outstanding questions). Recent technological advances provide many new opportunities to do so, such as microclimatic data derived from remote sensing products [98], geophysical downscaling models [99], and fine-grain biodiversity data from global positioning system (GPS) tracking and camera traps [26,100].

By reviewing the major drivers of the grain size-dependence of environmental niches, we have aimed to illustrate the pervasive nature of the issue across a broad range of research areas and to provide guidance on its consideration. Environmental niche estimates in ecology, evolution, and conservation will benefit from a more mechanism-informed choice of spatial grain and cross-grain evaluations that integrate different data sources.

Outstanding questions

How sensitive is the characterization of environmental niches to spatial grain?

To what degree can the grain size-dependence of an environmental niche be predicted by species traits such as range size, body mass, and dietary preferences?

How does the grain size-dependence of environmental niche vary across different niche factors?

What are the spatial patterns of the grain size-dependence of environmental niche characterization?

How does the grain size-dependence of environmental niches impact our understanding of the abundance and distribution of species, such as the range size–niche breadth relationship and the abundant-center hypothesis?

How does the grain size-dependence of an environmental niche affect climate change assessments?

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Declaration of interests

No interests are declared.

Supplemental information

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References

1. Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Harb. Symp. Quant. Biol.* 22, 415–427
2. Pearman, P.B. *et al.* (2008) Niche dynamics in space and time. *Trends Ecol. Evol.* 23, 149–158
3. McInerny, G.J. and Etienne, R.S. (2012) Ditch the niche – is the niche a useful concept in ecology or species distribution modelling? *J. Biogeogr.* 39, 2096–2102

4. Angilletta, M.J. *et al.* (2019) Fundamental flaws with the fundamental niche. *Integr. Comp. Biol.* 59, 1038–1048
5. Karger, D.N. *et al.* (2017) Climatologies at high resolution for the Earth's land surface areas. *Sci. Data* 4, 170122
6. Anderson, R.P. (2012) Harnessing the world's biodiversity data: promise and peril in ecological niche modeling of species distributions. *Ann. N. Y. Acad. Sci.* 1260, 66–80
7. Blonder, B. *et al.* (2014) The n-dimensional hypervolume. *Glob. Ecol. Biogeogr.* 23, 595–609
8. Mammola, S. and Cardoso, P. (2020) Functional diversity metrics using kernel density n-dimensional hypervolumes. *Methods Ecol. Evol.* 11, 986–995
9. Lu, M. *et al.* (2021) A unifying framework for quantifying and comparing n-dimensional hypervolumes. *Methods Ecol. Evol.* 12, 1953–1968
10. Blonder, B. (2018) Hypervolume concepts in niche- and trait-based ecology. *Ecography* 41, 1441–1455
11. Merow, C. *et al.* (2013) A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* 36, 1058–1069
12. Jetz, W. *et al.* (2012) Integrating biodiversity distribution knowledge: toward a global map of life. *Trends Ecol. Evol.* 27, 151–159
13. Soberón, J. (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecol. Lett.* 10, 1115–1123
14. Soberón, J. and Nakamura, M. (2009) Niches and distributional areas: concepts, methods, and assumptions. *Proc. Natl. Acad. Sci. U. S. A.* 106, 19644–19650
15. Tuanmu, M.N. and Jetz, W. (2015) A global, remote sensing-based characterization of terrestrial habitat heterogeneity for biodiversity and ecosystem modelling. *Glob. Ecol. Biogeogr.* 24, 1329–1339
16. Wiens, J.A. (1989) Spatial scaling in ecology. *Funct. Ecol.* 3, 385–397
17. Thornton, D.H. and Fletcher, R.J. (2013) Body size and spatial scales in avian response to landscapes: a meta-analysis. *Ecography* 37, 454–463
18. Nadeau, C.P. *et al.* (2017) Coarse climate change projections for species living in a fine-scaled world. *Glob. Chang. Biol.* 23, 12–24
19. Stephens, P.A. *et al.* (2019) The limits to population density in birds and mammals. *Ecol. Lett.* 22, 654–663
20. Mertes, K. and Jetz, W. (2018) Disentangling scale dependencies in species environmental niches and distributions. *Ecography* 41, 1604–1615
21. Jackson, H.B. and Fahrig, L. (2015) Are ecologists conducting research at the optimal scale? *Glob. Ecol. Biogeogr.* 24, 52–63
22. Mertes, K. *et al.* (2020) Hierarchical multi-grain models improve descriptions of species' environmental associations, distribution, and abundance. *Ecol. Appl.* 30, e02117
23. Hurlbert, A.H. and Jetz, W. (2007) Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proc. Natl. Acad. Sci. U. S. A.* 104, 13384–13389
24. Fick, S.E. and Hijmans, R.J. (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* 37, 4302–4315
25. Oliver, R.Y. *et al.* (2021) Global and national trends, gaps, and opportunities in documenting and monitoring species distributions. *PLoS Biol.* 19, e3001336
26. Jetz, W. *et al.* (2019) Essential biodiversity variables for mapping and monitoring species populations. *Nat. Ecol. Evol.* 3, 539–551
27. Alhajeri, B.H. and Fourcade, Y. (2019) High correlation between species-level environmental data estimates extracted from IUCN expert range maps and from GBIF occurrence data. *J. Biogeogr.* 46, 1329–1341
28. Rotenberry, J.T. and Balasubramaniam, P. (2020) Connecting species' geographical distributions to environmental variables: range maps versus observed points of occurrence. *Ecography.* 43, 897–913
29. Pulliam, H.R. (2000) On the relationship between niche and distribution. *Ecol. Lett.* 3, 349–361
30. Gaüzère, P. and Devictor, V. (2021) Mismatches between birds' spatial and temporal dynamics reflect their delayed response to global changes. *Oikos* 130, 1284–1296
31. Godsoe, W. *et al.* (2015) The effect of competition on species' distributions depends on coexistence, rather than scale alone. *Ecography* 38, 1071–1079
32. Armitage, D.W. and Jones, S.E. (2020) Coexistence barriers confine the poleward range of a globally distributed plant. *Ecol. Lett.* 23, 1838–1848
33. Afkhami, M.E. *et al.* (2014) Mutualist-mediated effects on species' range limits across large geographic scales. *Ecol. Lett.* 17, 1265–1273
34. Slatyer, R.A. *et al.* (2013) Niche breadth predicts geographical range size: a general ecological pattern. *Ecol. Lett.* 16, 1104–1114
35. Kambach, S. *et al.* (2019) Of niches and distributions: range size increases with niche breadth both globally and regionally but regional estimates poorly relate to global estimates. *Ecography* 42, 467–477
36. Cai, Q. *et al.* (2021) The relationship between niche breadth and range size of beech (*Fagus*) species worldwide. *J. Biogeogr.* 48, 1240–1253
37. Moore, T.E. *et al.* (2018) Spatial autocorrelation inflates niche breadth–range size relationships. *Glob. Ecol. Biogeogr.* 27, 1426–1436
38. Cardillo, M. *et al.* (2019) The relationship between environmental niche breadth and geographic range size across plant species. *J. Biogeogr.* 46, 97–109
39. Ficetola, G.F. *et al.* (2020) Microhabitat analyses support relationships between niche breadth and range size when spatial autocorrelation is strong. *Ecography* 43, 724–734
40. Sexton, J.P. *et al.* (2017) Evolution of ecological niche breadth. *Annu. Rev. Ecol. Evol. Syst.* 48, 183–206
41. Rolland, J. and Salamin, N. (2016) Niche width impacts vertebrate diversification. *Glob. Ecol. Biogeogr.* 25, 1252–1263
42. Velasco, J.A. *et al.* (2016) Climatic niche attributes and diversification in *Anolis* lizards. *J. Biogeogr.* 43, 134–144
43. Qiao, H. *et al.* (2016) Impacts of niche breadth and dispersal ability on macroevolutionary patterns. *Am. Nat.* 188, 149–162
44. Pie, M.R. *et al.* (2021) The evolution of climatic niche breadth in terrestrial vertebrates. *J. Zool. Syst. Evol. Res.* 59, 1155–1166
45. Gómez-Rodríguez, C. *et al.* (2015) Is diversification rate related to climatic niche width? *Glob. Ecol. Biogeogr.* 24, 383–395
46. Yin, X. *et al.* (2021) Niche overlap and divergence times support niche conservatism in eastern Asia–eastern North America disjunct plants. *Glob. Ecol. Biogeogr.* 30, 1990–2003
47. Turner, J.A. *et al.* (2019) How does spatial resolution affect model performance? A case for ensemble approaches for marine benthic mesophotic communities. *J. Biogeogr.* 46, 1249–1259
48. Suárez-Seoane, S. *et al.* (2014) Scaling of species distribution models across spatial resolutions and extents along a biogeographic gradient. The case of the Iberian mole *Talpa occidentalis*. *Ecography* 37, 279–292
49. Connor, T. *et al.* (2018) Effects of grain size and niche breadth on species distribution modeling. *Ecography* 41, 1270–1282
50. Gábor, L. *et al.* (2020) The effect of positional error on fine scale species distribution models increases for specialist species. *Ecography* 43, 256–269
51. Sandel, B. (2015) Towards a taxonomy of spatial scale-dependence. *Ecography* 38, 358–369
52. Sagarin, R.D. *et al.* (2006) Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends Ecol. Evol.* 21, 524–530
53. Sagarin, R.D. and Gaines, S.D. (2002) The 'abundant centre' distribution: to what extent is it a biogeographical rule? *Ecol. Lett.* 5, 137–147
54. Merow, C. *et al.* (2017) Integrating occurrence data and expert maps for improved species range predictions. *Glob. Ecol. Biogeogr.* 26, 243–258
55. Dallas, T. *et al.* (2017) Species are not most abundant in the centre of their geographic range or climatic niche. *Ecol. Lett.* 20, 1526–1533
56. Santini, L. *et al.* (2019) Addressing common pitfalls does not provide more support to geographical and ecological abundant-centre hypotheses. *Ecography* 42, 696–705
57. de la Fuente, A. *et al.* (2021) Predicting species abundance by implementing the ecological niche theory. *Ecography* 44, 1723–1730

58. Lee-Yaw, J.A. *et al.* (2022) Species distribution models rarely predict the biology of real populations. *Ecography* 2022, e05877
59. Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology* 73, 1943–1967
60. Osorio-Olvera, L. *et al.* (2020) Relationships between population densities and niche-centroid distances in North American birds. *Ecol. Lett.* 23, 555–564
61. Williams, J.J. and Newbold, T. (2021) Vertebrate responses to human land use are influenced by their proximity to climatic tolerance limits. *Divers. Distrib.* 27, 1308–1323
62. Zurell, D. *et al.* (2018) Do long-distance migratory birds track their niche through seasons? *J. Biogeogr.* 45, 1459–1468
63. Di Marco, M. *et al.* (2021) Drivers of change in the realised climatic niche of terrestrial mammals. *Ecography* 44, 1180–1190
64. Antão, L.H. *et al.* (2022) Climate change reshuffles northern species within their niches. *Nat. Clim. Chang.* 12, 587–592
65. Broennimann, O. *et al.* (2021) Distance to native climatic niche margins explains establishment success of alien mammals. *Nat. Commun.* 12, 2353
66. Parravicini, V. *et al.* (2015) Niche shift can impair the ability to predict invasion risk in the marine realm: an illustration using Mediterranean fish invaders. *Ecol. Lett.* 18, 246–253
67. Garcia, R.A. *et al.* (2014) Multiple dimensions of climate change and their implications for biodiversity. *Science* 344, 1247579
68. Riddell, E.A. *et al.* (2021) Exposure to climate change drives stability or collapse of desert mammal and bird communities. *Science* 371, 633–636
69. Quintero, I. *et al.* (2022) Macroevolutionary dynamics of climatic niche space. *Proc. R. Soc. B Biol. Sci.* 289, 20220091
70. Cang, F.A. *et al.* (2016) Climate change is projected to outpace rates of niche change in grasses. *Biol. Lett.* 12, 20160368
71. Rolland, J. *et al.* (2018) The impact of endothermy on the climatic niche evolution and the distribution of vertebrate diversity. *Nat. Ecol. Evol.* 2, 459–464
72. Nunes, L.A. and Pearson, R.G. (2017) A null biogeographical test for assessing ecological niche evolution. *J. Biogeogr.* 44, 1331–1343
73. Esparza-Estrada, C.E. *et al.* (2022) Evolutionary dynamics of climatic niche influenced the current geographical distribution of Viperidae (Reptilia: Squamata) worldwide. *Biol. J. Linn. Soc.* 135, 665–678
74. Kling, M.M. *et al.* (2020) Multiple axes of ecological vulnerability to climate change. *Glob. Chang. Biol.* 26, 2798–2813
75. Acevedo, P. *et al.* (2017) Predictor weighting and geographical background delimitation: two synergetic sources of uncertainty when assessing species sensitivity to climate change. *Clim. Chang.* 145, 131–143
76. Trisos, C.H. *et al.* (2020) The projected timing of abrupt ecological disruption from climate change. *Nature* 580, 496–501
77. Blonder, B. *et al.* (2015) Linking environmental filtering and disequilibrium to biogeography with a community climate framework. *Ecology* 96, 972–985
78. Dickinson, M.G. *et al.* (2015) Separating sensitivity from exposure in assessing extinction risk from climate change. *Sci. Rep.* 4, 6898
79. Mahony, C.R. *et al.* (2017) A closer look at novel climates: new methods and insights at continental to landscape scales. *Glob. Chang. Biol.* 23, 3934–3955
80. Zellweger, F. *et al.* (2020) Forest microclimate dynamics drive plant responses to warming. *Science* 368, 772–775
81. Mahony, C.R. and Cannon, A.J. (2018) Wetter summers can intensify departures from natural variability in a warming climate. *Nat. Commun.* 9, 783
82. Morrison, B.D. *et al.* (2019) Spatial scale affects novel and disappeared climate change projections in Alaska. *Ecol. Evol.* 9, 12026–12044
83. Colwell, R.K. (2021) Spatial scale and the synchrony of ecological disruption. *Nature* 599, E8–E10
84. Rödder, D. *et al.* (2021) Climate change drives mountain butterflies towards the summits. *Sci. Rep.* 11, 14382
85. Currie, D.J. and Venne, S. (2017) Climate change is not a major driver of shifts in the geographical distributions of North American birds. *Glob. Ecol. Biogeogr.* 26, 333–346
86. La Sorte, F.A. and Jetz, W. (2010) Avian distributions under climate change: towards improved projections. *J. Exp. Biol.* 213, 862–869
87. Elsen, P.R. and Tingley, M.W. (2015) Global mountain topography and the fate of montane species under climate change. *Nat. Clim. Chang.* 5, 772–776
88. Tingley, M.W. *et al.* (2012) The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. *Glob. Chang. Biol.* 18, 3279–3290
89. Lembrechts, J.J. *et al.* (2019) Incorporating microclimate into species distribution models. *Ecography* 42, 1267–1279
90. Stuber, E.F. and Fontaine, J.J. (2019) How characteristic is the species characteristic selection scale? *Glob. Ecol. Biogeogr.* 28, 1839–1854
91. Northrup, J.M. *et al.* (2022) Conceptual and methodological advances in habitat-selection modeling: guidelines for ecology and evolution. *Ecol. Appl.* 32, e02470
92. Powers, R.P. and Jetz, W. (2019) Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. *Nat. Clim. Chang.* 9, 323–329
93. Šímová, P. *et al.* (2019) Fine scale waterbody data improve prediction of waterbird occurrence despite coarse species data. *Ecography* 42, 511–520
94. Li, R. *et al.* (2021) A cloud-based toolbox for the versatile environmental annotation of biodiversity data. *PLoS Biol.* 19, e3001460
95. Miguet, P. *et al.* (2017) How to quantify a distance-dependent landscape effect on a biological response. *Methods Ecol. Evol.* 8, 1717–1724
96. Cheng, Y. *et al.* (2021) Using centroids of spatial units in ecological niche modelling: effects on model performance in the context of environmental data grain size. *Glob. Ecol. Biogeogr.* 30, 611–621
97. Tredennick, A.T. *et al.* (2021) A practical guide to selecting models for exploration, inference, and prediction in ecology. *Ecology* 102, e03336
98. Zellweger, F. *et al.* (2019) Advances in microclimate ecology arising from remote sensing. *Trends Ecol. Evol.* 34, 327–341
99. Maclean, I.M.D. (2020) Predicting future climate at high spatial and temporal resolution. *Glob. Chang. Biol.* 26, 1003–1011
100. Jetz, W. *et al.* (2022) Biological Earth observation with animal sensors. *Trends Ecol. Evol.* 37, 293–298