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Non-random latitudinal gradients in range size and niche breadth predicted by spatial patterns of climate

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Abstract

Aim: Tropical species are thought to experience and be adapted to narrow ranges of abiotic conditions. This idea has been invoked to explain a broad array of biological phenomena, including the latitudinal diversity gradient and differential rates of speciation and extinction. However, debate continues regarding the broad-scale applicability of this pattern and potential processes responsible. Here, we use a simulation approach to test two propositions: (a) strong geographical patterns in realized niche breadth variation can arise in the absence of variance in fundamental niche breadth size, and (b) realized niche breadths can show latitudinal patterns as a consequence of spatio-temporal climate change, even when fundamental niche breadths are unrelated to latitude and dispersal abilities are held constant.

Location: Global.

Time period: Simulations were conducted using climate models from over the last 120 ka, with trait dynamics captured at 95 ka and in the Modern.

Major taxa studied: We used virtual species with traits based loosely on plants.

Methods: We simulated latitudinal trends of niche breadth and range size for virtual species using a cellular automaton algorithm that linked a gridded geographical domain with a three-dimensional environmental landscape.

Results: In all simulations, strong spatial patterns in realized niches were obtained in the absence of niche evolution, and realized niches showed geographical patterns deriving only from realistic, spatio-temporal variation in climate. We noted contrasting patterns of niche breadth in different environmental dimensions, with temperature breadth increasing with latitude, but precipitation breadth decreasing with latitude. Overall, simulation outcomes mimicked the real-world pattern of latitudinal range extent co-varying with amount of land area.

Main conclusions: Tropical species can have narrower niche breadths for maximum and minimum temperature ranges compared with temperate species solely as the result of the spatial arrangement of environments. We therefore suggest that the complex spatio-temporal distribution of global abiotic environments has strong potential for structuring observed latitudinal gradients of niche breadths.

KEYWORDS

cellular automaton algorithm, diversity patterns, fundamental niche, latitudinal trends, niche breadth, Rapoport's rule, realized niche

1 | INTRODUCTION

Few species can occur in all environments on Earth, from the tropics to the poles and from the tops of mountains to the deepest caverns. Instead, most species are adapted to a certain range of environmental conditions, referred to as the ecological niche (Peterson et al., 2011). The concept of the niche is essential to describing micro- and macroevolutionary patterns quantitatively and testing hypotheses of evolutionary process. Niche concepts underlie, for example, most of our current understanding of ecology (Petitpierre et al., 2012; Saupe et al., 2015; Vázquez & Stevens, 2004), evolutionary biology (Bonetti & Wiens, 2014; Buckley et al., 2010; Rangel, Diniz-Filho, & Colwell, 2007; Saupe et al., 2014), and biogeography (Brown, 2014; Pyron & Wiens, 2013; Stephens & Wiens, 2009).

Niche breadths are generally thought to vary positively with latitude (Deutsch et al., 2008; Ghalambor, Huey, Martin, Tewksbury, & Wang, 2006; Janzen, 1967; MacArthur, 1972; Pagel, May, & Collie, 1991; Papacostas & Freestone, 2016; Salisbury, Seddon, Cooney, & Tobias, 2012; Sexton, Montiel, Shay, Stephens, & Slatyer, 2017; Sunday, Bates, & Dulvy, 2012). Tropical species, for example, are considered to experience and be adapted to only a narrow and constant range of abiotic conditions in comparison to temperate species (Gaston & Chown, 1999; Janzen, 1967; Terborgh, 1973). These ideas have been invoked to explain diverse biological phenomena, from the latitudinal diversity gradient (Buckley et al., 2010; Pyron & Wiens, 2013; Rangel et al., 2007; Salisbury et al., 2012; Stevens, 1989) to debates regarding the tropics as a cradle versus museum of biodiversity (Jablonski et al., 2013).

Klopfer (1959) and Janzen (1967) envisioned finer specialization and adaptation at low latitudes as resulting from more stable tropical climates. They and many others argued that more variable conditions select for tolerance to a broader range of conditions, whereas stable climates allow for specialization in a narrower range of conditions (Bozinovic, Calosi, & Spicer, 2011; Colwell & Hurtt, 1994; Janzen, 1967; Levins, 1968; Lin & Wiens, 2017; Lynch & Gabriel, 1987; Pianka, 1966; Pintor, Schwarzkopf, & Krockenberger, 2015). Others have explained narrower niches at low latitudes on the basis of more intense competition (Dobzhansky, 1950) or from trade-offs between dispersal ability and ecological specialization (Jocque, Field, Brendonck, & Meester, 2010).

The hypothesis that tropical species are more specialized than temperate species is commonly assumed. However, the broad-scale applicability of this pattern and specific processes that produce it are still debated (e.g., narrowing of overall tolerance limits versus limited occupation of fundamental niches; Sexton et al., 2017). Climate and geography are two factors that may limit occupation of fundamental niches to generate macroecological patterns. This idea has its roots

in the work of Janzen (1967) and the “spatial heterogeneity” hypothesis (Kassen, 2002; Pianka, 1966; Simpson, 1964), which rely, in part, on environmental barriers restricting species' occupation of space. Janzen (1967), for example, hypothesized that tropical mountain passes would be more effective barriers to species dispersal than temperate mountain passes of similar elevation because of the lower annual temperature variation in the tropics compared with temperate regions (but see Currie, 2017; Zuloaga & Kerr, 2017). Climatically, this contrast implies less thermal overlap between low and high elevations in the tropics versus in the temperate zones. Thus, if reduced tropical temperature variation leads to selection for more narrowly adapted species, tropical mountain passes will pose much larger climate barriers than those in temperate regions, resulting in smaller distributions and narrower realized niches for species.

Following ideas proposed by Quintero and Wiens (2013), we use a simulation model to assess possible influences of spatial climatic heterogeneity (change across space) on macroecological patterns. The model is run on a landscape with realistic geography and climate, and is simple in that evolutionary adaptation (i.e., fundamental niche evolution) and biotic interactions are deliberately not permitted. This design allowed us to focus on the role that spatio-temporal climate patterns and land shape have in structuring latitudinal trends of species' realized niche breadths.

We test two major propositions: (a) strong geographical patterns in realized niche breadth variation can arise in the absence of variance in fundamental niche breadth size, and (b) macroecological patterns in realized niche breadth can derive from non-evolving “species” responding to climate fluctuations across complex geography. Our simulation approach reduces the multifaceted set of species-environment interactions to a simple few, to isolate effects of climate and geography on patterns of realized niche breadth and geographical range size across latitudes. With the observation that precipitation is more spatially heterogeneous at low latitudes, and temperature is more spatially heterogeneous at high latitudes (Figure 1; Supporting Information Figure S1; Held & Soden, 2006; New, Lister, Hulme, & Makin, 2002; Quintero & Wiens, 2013; Vázquez & Stevens, 2004), we anticipate an inverse relationship between latitude and realized niche breadth for precipitation, but a positive relationship for realized temperature niche breadth. Therefore, given the same range of niche breadths and dispersal abilities, species at high latitudes should be able to occupy more diverse temperature regimes, but less diverse precipitation regimes; this pattern could occur even when species are characterized by geographical ranges of similar size across latitudes, or when species have larger geographical ranges at low latitudes.

Understanding macroevolutionary patterns in niche breadth and the processes that generate them is crucial to a synthetic

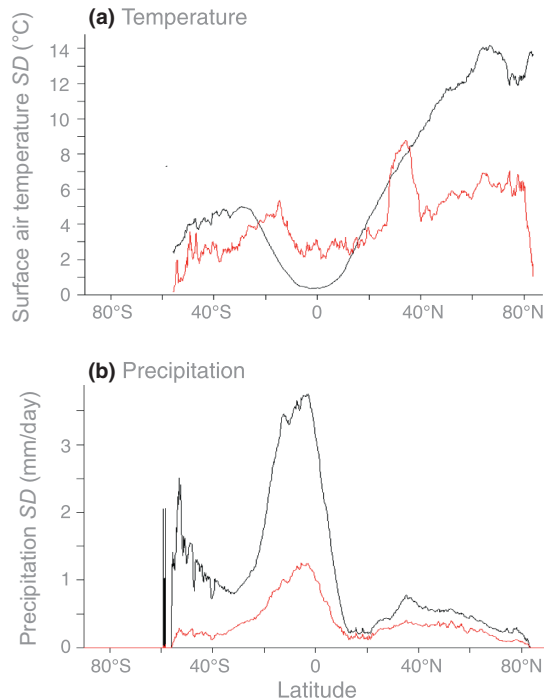


FIGURE 1 Changes in modern observed climate variability by latitude. (a) Standard deviation of annual means of surface air temperature for each latitudinal band (red), and standard deviation over the seasonal cycle (intra-annual) using monthly mean temperature (in degrees Celsius) for each latitudinal band (black). (b) Same as in (a), but for precipitation (in millimetres per day). Observational monthly means were sourced from New et al. (2002) and averaged over 1960–1990 on 0.16° spatial resolution for terrestrial areas globally. Similar patterns of climate variability were inherent in the general circulation model data used in our simulations, shown in the Supporting Information (Figure S1) [Colour figure can be viewed at wileyonlinelibrary.com]

understanding of ecology and evolution, particularly given the importance of niche concepts to diverse biological disciplines.

2 | MATERIALS AND METHODS

2.1 | Niche concepts

Diverse definitions exist for ecological niches (Chase & Leibold, 2003). Most definitions, however, fall into one of two main perspectives: (a) the Grinnellian niche, which is defined by the abiotic, environmental conditions required for survival and reproduction; and (b) the Eltonian niche, which is defined by ecological responses to biotic interactions and the environment, such as feeding strategies or other life-history traits (Soberón, 2007). Of course, these two niche types may also interact, such as the coupling of seasonal productivity with resource specialization (Valentine & Jablonski, 2010). Here, we develop a suite of simulations within the Grinnellian niche perspective.

Following Grinnell's (1917) basic ideas, Hutchinson (1957) proposed that the full suite of abiotic conditions allowing survival and

reproduction be termed the fundamental niche. Occupation of the fundamental niche by populations of a species can be limited by a number of factors. First, not all combinations of environments in the fundamental niche may exist on landscapes at a given time. Consequently, the fundamental niche is reduced to a potential (or existing fundamental) niche, which is a function of both time and geographical region (Jackson & Overpeck, 2000). Second, occupation of existing environments may be reduced further by biotic interactions or dispersal constraints. The set of temperature and precipitation combinations that is occupied by a species is referred to as the realized niche, which is also a function of both time and geographical region, because it describes the outcome of species' interactions with specific existing climates, landscapes, and communities.

Given that our goal was to assess whether the structure and dynamics of the abiotic environment can produce latitudinal patterns in niche breadth, we chose to explore a simplified virtual world in which biotic interactions were absent. Fundamental niche breadths in our simulations were set a priori and then reduced by the interplay between available environments and dispersal ability. Our analyses therefore focused on how realized niche breadths respond to latitudinal and temporal variation in climate conditions (Peterson et al., 2011; Soberón & Peterson, 2005).

2.2 | Simulation overview

Distributional patterns and associated niche variation across space and through time were simulated using a cellular automaton algorithm (Grimm et al., 2005; Hooten & Wickle, 2010) that linked a gridded geographical domain with a three-dimensional environmental landscape (Qiao, Saupe, Soberón, Peterson, & Myers, 2016; Rangel et al., 2007, 2018) to examine latitudinal trends of niche breadths. The gridded geographical domain consisted of terrestrial areas globally, whereas the environmental landscape was characterized by realistic climate patterns derived from global climate models. Species originated randomly across global terrestrial areas; the range size and location of each species changed across this dynamic landscape in response to estimated climate changes over the last 120 ka, given limitations from assigned dispersal and niche traits (Figure 2). In environmental space, species' fundamental niches were characterized by three-dimensional boxes representing precipitation and temperature (maximum and minimum) dimensions, within which all conditions were considered suitable. Representation of a species' fundamental niche on the landscape in our simulation (i.e., its realized niche) was limited by environmental combinations existing at a given time step within the area accessible to the species via dispersal.

We analysed resulting latitudinal trends in species' niches under multiple combinations of dispersal ability (poor and good) and fundamental niche breadth (narrow and broad), using 1,000 replicate simulations per combination, for a total of 4,000 simulations. The framework builds on the model introduced by Qiao et al. (2016) and is similar in concept to simulations explored by Rangel et al. (2007), Nakazawa (2013), Tomašových, Jablonski, Berke, Krug, and Valentine (2015) and Rangel et al. (2018). Our model differs from other models,

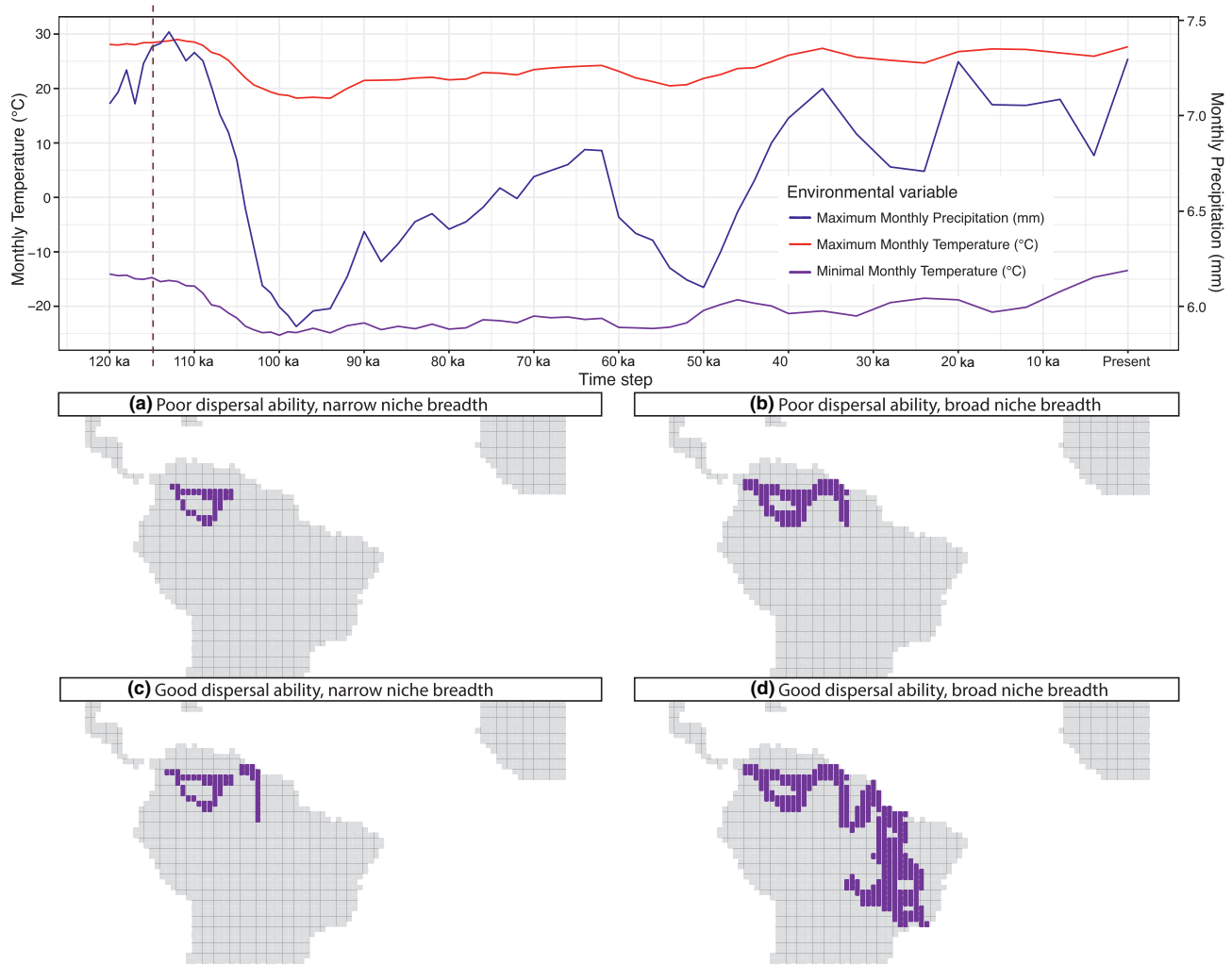


FIGURE 2 Distributional dynamics for four virtual species that derive from the same seed point during warm conditions 115 ka (maroon dashed line). Top panel depicts the global mean monthly maximum temperature (in degrees Celsius; red line), global mean monthly minimum temperature (in degrees Celsius; purple line), and global mean monthly maximum precipitation (in millimetres; blue line) for the last 120 ka. The four exemplar virtual species are shown in South America with poor dispersal abilities and either a narrow (a) or a broad niche breadth (b), and with good dispersal abilities and either a narrow (c) or a broad niche breadth (d) [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

such as those of Hubbell (2001) and Worm and Tittensor (2018), in using realistic geography and climate, and in its focus on the positions, sizes, and shapes of geographical distributions and associated niches.

2.3 | Geographical extent

The geographical component of the model consisted of a global $1^\circ \times 1^\circ$ grid of continental regions. Each grid cell corresponded to environmental values representing temperature and precipitation parameters (see Section 2.4 below). The model simulated state changes of each grid cell (i.e., occupied versus empty); cell occupation at any point in time was determined by the overlap between species' fundamental niche dimensions, the environmental conditions of that cell, and the ability of the species to disperse to that cell from cells already occupied. The environmental conditions of each cell changed through time, following a 120,000-year record of past

climate conditions (see Section 2.4). Therefore, a given cell could be favourable or unfavourable for a species at different times during the simulation depending on whether the environmental conditions fell within its fundamental niche.

2.4 | Climate model data

General circulation model (GCM) simulations for the last 120 ka were performed with the Hadley Centre coupled atmosphere–ocean–vegetation model, HadCM3, originally used in Intergovernmental Panel on Climate Change (IPCC) future climate projections. The version of the climate model used here includes interactive vegetation and is described by Singarayer, Valdes, and Roberts (2017) and Davies-Barnard, Ridgwell, Singarayer, and Valdes (2017). For use in the present study, climate outputs were downscaled from $2.5^\circ \times 3.75^\circ$ to $1^\circ \times 1^\circ$ horizontal resolution using bicubic interpolation via the climate anomaly method. These modelled data were then interpolated linearly to 100-year time

steps, resulting in 1,201 time slices for each of three modelled climate layers used in the simulation: mean monthly maximum temperature, mean monthly minimum temperature, and mean monthly maximum precipitation. Minimum monthly precipitation is zero for nearly all localities on Earth and therefore was not included. Climate model details, including evaluation using modern data and palaeoclimate records, are presented in section one of the Supporting Information.

2.5 | Virtual species

Each species began the simulation as a single point on the gridded geographical domain during interglacial climate conditions (120 ka). We generated 1,000 such seed points at random from within continental areas globally. The temperature and precipitation values of the seed point cell defined the optimal environmental conditions for that virtual species (i.e., the centre of the species' fundamental ecological niche). We applied symmetrical deviations from this point (Qiao et al., 2016; Rangel et al., 2007) based on two niche breadths (narrow and broad), corresponding to temperature and precipitation tolerances of 21 and 31°C, and 4 and 7 mm/day, respectively. Niche breadths were derived from empirical temperature and precipitation tolerances of agriculturally important plant species (Food and Agriculture Organization of the United Nations; see Hijmans, Guarino, Cruz, and Rojas (2001)). The dimensions for the narrow and broad niche breadths were chosen from among species in the lower and upper quartiles, respectively, of the distribution of niche breadths from this database.

We defined minimum temperature as one limiting variable and maximum temperature as another, to control for niche breadth within each environmental parameter and across latitudes. This choice was necessary to permit us to examine null expectations of the influence of spatial environmental heterogeneity on niche occupation, and has some theoretical backing from evidence that these two niche dimensions often vary independently (Addo-Bediako, Chown, & Gaston, 2000; Araújo et al., 2013; Hoffmann, Chown, & Clusella-Trullas, 2013). Seasonality was considered tangentially in the model, because maximum and minimum temperatures will differ more markedly at more seasonal, higher latitudes (Supporting Information Figures S2 and S3). Our focus, however, was on the breadth of tolerances for each temperature extreme independently, so we examined latitudinal trends in niche occupation within each of these environmental layers (i.e., minimum and maximum temperature). Importantly, however, if temperature tolerances were defined as a continuum, the patterns discussed below remained qualitatively similar. In this alternative method of defining thermal tolerance, no lower limit was imposed for the maximum temperature layer, and no upper limit for the minimum temperature layer. Instead, symmetrical deviations of 10.5° (narrow niche) and 15.5° (broad niche) were applied to the maximum and minimum temperature values of the seed point, such that if a seed point landed on a cell with a minimum temperature of 10°C and a maximum temperature of 20°C, the narrow niche would be [10–10.5°C, 20 + 10.5°C] and the broad niche [10–15.5°C, 20 + 15.5°C].

From its point of origin, each species spread by “searching” for suitable sites (i.e., grid cells with environmental conditions included within their fundamental niches) that are accessible given their dispersal ability. Dispersal was considered as a consequence of two exponential decay functions that reflected the ability of a species to search outside its present range for habitable cells; the steeper the decay curve, the less likely the species was to disperse long distances. From a given occupied cell, a species was allowed to search, at maximum, four (good dispersers) or two (poor dispersers) cells in a single simulation step, corresponding to distances of c. 400 and c. 200 km, respectively. Species searched for suitable cells simultaneously from all cells currently occupied, and each cell was assigned a different probability of dispersal, drawn at random from the dispersal function. Dispersal values are provided in the Supporting Information (Table S1) and are based loosely on known dispersal abilities of empirically-derived seed dispersal capacities in plants (Cain, Milligan, & Strand, 2000; Svenning & Sandel, 2013). Both poor and good dispersers could jump over unsuitable patches to encounter more spatially remote but suitable cells elsewhere. Dispersal in this formulation is stochastic and represents a process of exploration, with possible colonization and range expansion, and thus differs from other definitions of dispersal at local scales, such as movements of individuals.

2.6 | Simulations

Simulations were initiated in 120 ka climate conditions and run forwards in time to the present. Each of the 1,000 initial seed points was tested under all combinations of niche breadth and dispersal ability. This replication resulted in 4,000 total unique simulations.

Throughout all simulations, species occupied any suitable cell encountered in the dispersal process, as long as that cell remained suitable (Gotelli et al., 2009; Rangel et al., 2007). This process imitated natural range dynamics of species, which are thought often to begin small and expand subsequently (Liow & Stenseth, 2007; Webb & Gaston, 2000). Environmental changes modified distributions of suitable cells uniquely for each species (i.e., dependent on niche dimensions); species tracked suitable cells through these changes as a function of their dispersal ability. One consequence of environmental change may be fragmentation of suitable areas, resulting in newly-isolated populations, or elimination of occupied suitable areas. The former can result in speciation, whereas the latter can result in extinction. In this way, we integrated the dynamics of speciation and extinction into each simulation.

Speciation was defined allopatrically (Barracough & Vogler, 2000; Edwards, Keogh, & Knowles, 2012; Fitzpatrick, Fordyce, & Gavrillets, 2009; Mayr, 1942; Turelli, Barton, & Coyne, 2001; Wiley & Lieberman, 2011). Environmental changes can fragment species' ranges, resulting in isolation of “populations”, defined as a contiguous set of occupied cells. Populations that experienced isolation for 10,000 years were treated as new, independent species. In nature, speciation may take longer (Avice, 1998) or shorter (Hendry, Nosil, & Rieseberg, 2007; Lamichhaney et al., 2018) than 10,000 years,

but this duration is not unreasonable based on palaeontological and neontological data (Johnson & Cicero, 2004; Knowles & Alvarado-Serrano, 2010; Lande, 1980; Valentine, 1985). Importantly, we needed to choose a time-to-speciation that was proportional to the time steps available in the climate model; if we had chosen a longer time-to-speciation, we could not have retrieved speciation events at the scale of climate-change steps. The climate model we used represents a full, transitory global climate trajectory from the last interglacial period to the present; no other general circulation model outputs of this nature are available to our knowledge, nor is the HadCM3 model available at this temporal resolution for earlier periods.

Following Qiao et al. (2016), daughter species in our simulations had the same niches and dispersal abilities as their parent species, which invoked the fewest assumptions regarding demographic processes, genetic/phenotypic plasticity, and evolvability during speciation. As described above, niche evolution was not included purposely, in order to isolate effects of the spatial distribution of environments on the latitudinal structure of niche breadths. In natural systems, niche breadth and dispersal ability will vary among species; how this variation might affect macroecological patterns is not treated in this generation of our simulations. Populations that separated and re-merged in <10,000 time steps were not regarded as distinct species. Once produced, daughter species immediately began searching and occupying all suitable cells within their dispersal reach and were not prohibited from cell occupation by the presence of another species. In this sense, biotic interactions did not exclude species from suitable areas or impact extinction dynamics.

In each simulation, extinction occurred when all occupied suitable habitat (i.e., all occupied cells) for a species disappeared. We followed Qiao et al. (2016) in applying no specific demographic model or inferred minimum population survivorship threshold. Rather, a strict extinction criterion was used because it invoked the fewest assumptions and because our simulations had a relatively coarse spatial resolution (i.e., $1^\circ \times 1^\circ$).

To evaluate the role of temporal versus spatial variation in climate conditions, simulations were repeated for a situation of constant climate. That is, species could occupy suitable cells based on their niches and dispersal abilities, but climate remained static over the course of the 120,000-year simulation. We performed two separate simulations without climate change; one using 120 ka climate conditions, and the other using present-day climate conditions.

2.7 | Analyses of latitudinal trends

2.7.1 | Traits

We assessed latitudinal trends in seven traits from our models (Table 1) that characterize species distributions in geographical and environmental spaces: latitudinal range extent, geographical range size, realized niche breadth of minimum and maximum temperature, realized niche breadth of maximum precipitation, overall realized niche breadth, and realized seasonal temperature range. Variables

TABLE 1 Seven biogeographical traits tested under a null model of species distributional and niche change by latitude

Trait	Metric
Latitudinal range	Difference between maximum and minimum latitudinal extent
Geographical range	Number of pixels occupied
Minimum temperature	Breadth of minimum temperatures occupied geographically
Maximum temperature	Breadth of maximum temperatures occupied geographically
Maximum precipitation	Breadth of maximum precipitation values occupied geographically
Niche breadth area	Two-dimensional environmental area of maximum temperature and maximum precipitation conditions occupied geographically
Seasonal temperature range	The difference between the maximum temperature of the mean monthly maximum temperature layer occupied geographically and the minimum temperature of the mean monthly minimum temperature layer occupied geographically

were defined as follows: (a) latitudinal extent is the difference (in degrees of latitude) between the northernmost and southernmost pixels occupied by a species (Stevens, 1989); (b) geographical range size is the total number of pixels occupied by a species worldwide; (c–e) realized niche breadths are the range of environmental values occupied by a species for each environmental parameter (maximum temperature, minimum temperature, and maximum precipitation); (f) overall realized niche area is the area of the rectangular envelope of the range of maximum temperature and maximum precipitation conditions occupied by species, using centred and standardized variables (we did not include minimum temperature to avoid biasing volume estimates towards the temperature dimension); and (g) realized seasonal temperature range is the difference between the maximum value of the maximum monthly temperature layer and the minimum value from the minimum monthly temperature layer (Table 1). Trait conditions for all seven variables were captured 25 kyr after the simulation began (i.e., at 95 ka during cooler and drier times; Marine Isotope Stage 5.3) and in present-day climate conditions when the simulations completed.

2.7.2 | Tests for latitudinal patterns

Latitudinal trends in these seven traits were analysed using three approaches: Steven's method (Stevens, 1989), the midpoint method (Graves, 1985; Rohde, Heap, & Heap, 1993), and the most-distal point method (Pagel et al., 1991). The Steven's method calculates the mean (or median) value of a trait from a collection of species with ranges that fall within each of a series of 1° latitudinal bands. This method suffers from lack of statistical independence, because the average (or median) trait values for different latitudinal bands

are influenced by the same species in adjacent bands. That is, bands that are closer together share a higher proportion of species, and thus have more similar trait values (Gaston, Blackburn, & Spicer, 1998; Rohde et al., 1993). The midpoint method avoids this issue by treating individual species as data points and evaluating the interspecific relationship between a trait and the latitudinal midpoint of the species' range; notably, however, both of these methods can suffer from edge effects (Colwell & Hurlt, 1994; Connolly, 2009). The most-distal point method categorizes a species by the latitude within its range that is farthest from the Equator and evaluates the interspecific relationship between these most-distal points and the trait of interest. We examined all three methods to test for congruence among the approaches.

To apply Steven's method, we took the central tendency (mean and median) of 10 species selected randomly from each 1° latitudinal band for a series of 100 bootstrap replicates. One hundred and thirty bands were considered, removing the highest latitudes because minimal land areas there may bias the analysis. For the midpoint and most-distal point methods, 130 unique species were randomly selected for each of 1,000 bootstrap replicates. In this way, the same number of species (130,000) was considered for both Steven's and the midpoint/most-distal point methods. Spearman correlation coefficients were generated for each replicate and statistical significance was assessed using the "rcorr" function in the "Hmisc" package v.3.17-4 for R (Harrell, 2016).

In addition to analysing distributions of these species as a result of the combined effects of niche and dispersal, we quantified the same seven traits as a function of species' potential (or existing) fundamental niches by removing dispersal from the simulation. The potential fundamental niche can be defined most broadly as the environments within a species' fundamental niche that exist at a particular time and place, which we define here as all terrestrial areas on Earth. Thus, this set of analyses allowed us to explore the same questions as above, but without dispersal constraints (i.e., species in this scenario were not limited by dispersal and occupied all suitable area at any given time slice). An identical simulation and data collection procedure were applied as described above, with the same methodological frameworks we used to analyse relationships between species' niche traits and latitude.

Geographical range size and latitudinal extent may co-vary as a function of land area. The dominance of Northern Hemisphere studies noting this pattern has, in part, led to general acceptance of Rapoport's rule (Gaston et al., 1998). As a result, we analysed patterns separately for the Southern and Northern Hemispheres. We used the absolute value of latitude within each hemisphere; that is, an inverse correlation of a trait with latitude means that the trait value is larger at low latitudes. The same bootstrap routine was used as outlined for the global analyses.

2.8 | Analyses of trends by climate region

In addition to examining how the seven traits vary with latitude, we assessed how they vary environmentally by climate regime. We

defined warm and cold (i.e. tropical and temperate) regimes as having mean annual temperatures >18 and <18°C, respectively (Lamb, 1972; Prentice, 1990). Some virtual species, however, could live in both climate regimes (i.e., they occupied temperatures characteristic of both regimes); these species defined a third, "mixed" category. Fifty species were bootstrapped in each regime 1,000 times to analyse trends for the seven traits (Table 1). As previously, data were collected at 95 ka and in present-day climate conditions.

2.9 | Climate variability trends

Our aim was to examine whether the spatio-temporal geometry of climate and continents can produce latitudinal trends in niche breadth and range size, all else held constant. To quantify spatial and temporal climate trends, we performed three sets of analyses, as follows. (a) To examine how climate varies spatially by latitude, we calculated the standard deviation of maximum and minimum temperature and precipitation in each 1° latitudinal band using only present-day climate, and using the climate model data averaged across all 1,201 time steps (Figure 1; Supporting Information Figure S1). (b) To assess whether maximum and minimum temperature exhibit similar patterns of spatial variability across latitudes, we examined Spearman's rank correlations of the standard deviation of maximum temperature and minimum temperature across all 1° latitudinal bands and 1,201 time steps (note that the relationship between minimum and maximum temperature was monotonic). (c) To examine how climate varies seasonally by latitude, we calculated mean differences between minimum and maximum temperatures across cells in each 1° latitudinal band, averaged across all 1,201 time steps (Supporting Information Figure S2).

To examine the influence of spatial climate variability on realized niche breadth across latitudes, we correlated spatial variability (maximum precipitation, maximum temperature, and minimum temperature) in each 1° latitudinal band (calculated above) with mean realized niche breadths (maximum precipitation, maximum temperature, and minimum temperature) in each of those latitudinal bands (Figure 3). Mean realized niche breadth values were derived from Steven's method (see Section 2.7.2), and Spearman's rank correlations then calculated.

3 | RESULTS

3.1 | Realized niche trends

We assessed model predictions for how the seven species traits (Table 1) varied with latitude using Spearman correlations for patterns at 95 ka (cold conditions) and the present day (warm conditions). All traits varied positively with latitude except maximum precipitation and latitudinal extent, which tended to be negatively correlated with latitude (Figure 4; Supporting Information Figures S4–S17). That is, although species were accorded the same fundamental niche breadths for temperature and precipitation, their realized niche breadths varied by latitude (Figure 4). Correlations with

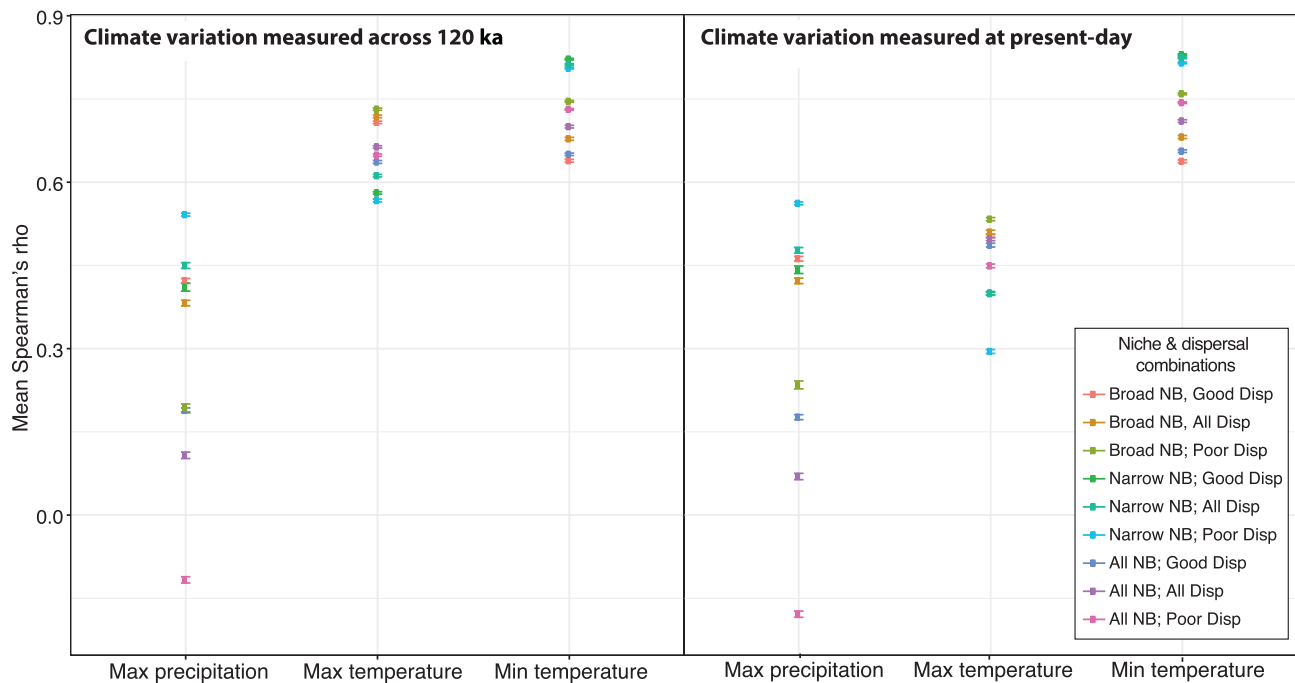


FIGURE 3 Spearman's rank correlation of spatial climate variability and mean realized niche breadth. Spatial climate variability was calculated for each 1° latitudinal band for all time steps (left), and for present-day conditions only (right). Mean realized niche breadth values were derived from Steven's method (see Section 2.7.2 for a description of this method). The variability of maximum precipitation in each 1° latitudinal band was correlated with the mean realized niche breadth for maximum precipitation in each 1° latitudinal band. Error bars show 95% confidence intervals across bootstrap replicates. All = both niche (broad and narrow) and/or dispersal (poor and good) combinations; Disp = dispersal; max = maximum; min = minimum; NB = niche breadth [Colour figure can be viewed at wileyonlinelibrary.com]

latitude were statistically significant for all traits in most (>75%) bootstrap replicates, except for latitudinal extent, for which only Steven's method was significant (Supporting Information Figure S9). Results were consistent across all dispersal and niche breadth scenarios and did not seem to be method dependent, although the midpoint and most-distal point methods produced fewer significant patterns. Results were also largely consistent when patterns were examined under cool (95 ka) and warm (present-day) climate conditions, except that in the former, trends were less clear for maximum precipitation (Supporting Information Figure S6), and latitudinal extent was positively (rather than negatively) correlated with latitude in species with broad niche breadths and good dispersal abilities (Supporting Information Figure S9).

The constant-climate simulations yielded results that were largely congruent with results from simulations run under Pleistocene-to-Recent climate change (Supporting Information Figure S18), indicating that the spatial configuration of climate at any point in time is likely to be sufficient to produce the spatial structure in climatic niches. We focus here only on the more realistic analyses incorporating climate change.

3.2 | Realized niche trends by hemisphere

We assessed model predictions for how the seven traits (Table 1) varied with latitude within each hemisphere. These patterns were

similar to the global analyses obtained for all variables, except latitudinal extent and geographical range size (Supporting Information Figures S19–S25). Latitudinal extent and geographical range size were positively and negatively correlated with latitude in the Northern and Southern Hemispheres, respectively, although trends were often weak or not significant for latitudinal extent in the Northern Hemisphere (Supporting Information Figures S23 and S24). This reversal in the direction of correlation between latitude and range size within each hemisphere is congruent with previous studies that have found that range size will co-vary positively with land area (Gaston et al., 1998), because land area is greater at lower latitudes in the Southern Hemisphere and at higher latitudes in the Northern Hemisphere.

Realized niche patterns by hemisphere were consistent across dispersal and niche scenarios, and under cool (95 ka) and warm (present-day) climate conditions, except for minimum temperature, which showed a weak negative, rather than positive, correlation with latitude for Southern Hemisphere virtual species (Supporting Information Figure S20).

3.3 | Potential niche trends

We assessed model predictions for how the seven traits varied with latitude when the influence of dispersal was removed (i.e., considering predictions for latitudinal trends in the potential niche). In this

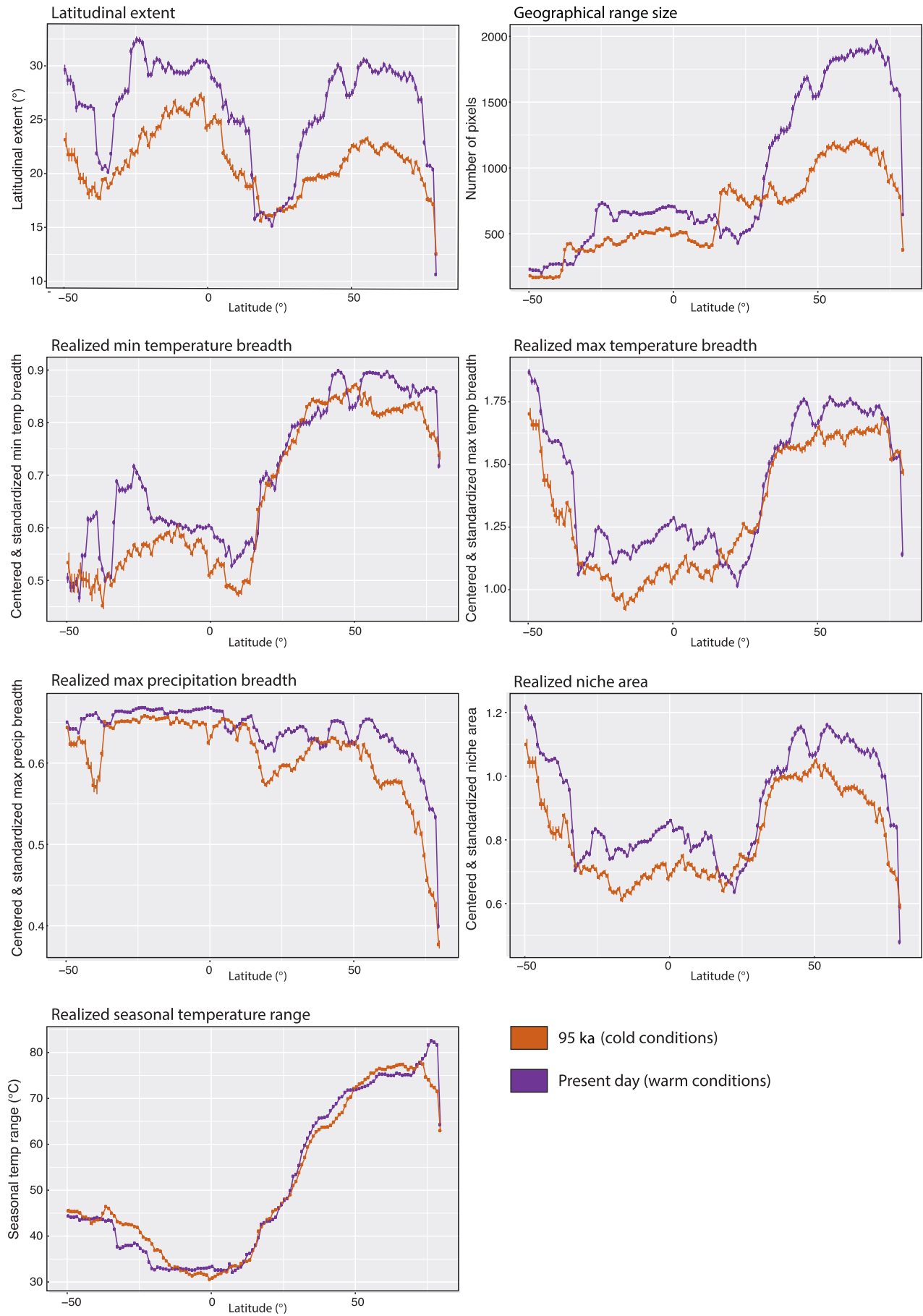


FIGURE 4 Mean realized trait values for each latitudinal band for species with poor dispersal abilities and narrow niches, calculated by taking 50 species per latitudinal band for a series of 100 bootstrap replicates. Error bars represent 95% confidence intervals across bootstrap replicates. Trait dynamics are shown under cold conditions (maroon line; 95 ka) and under warm conditions (purple line; present-day). Breadth and area measurements were centred and standardized. All other niche and dispersal combinations are shown in the Supporting Information (Figures S11–S17) [Colour figure can be viewed at wileyonlinelibrary.com]

scenario, all traits were positively correlated with latitude except for latitudinal extent and maximum precipitation, closely mirroring the simulation results when dispersal was included (Supporting Information Figures S26–S32). Although niche area was positively correlated with latitude, this relationship was not significant for >25% of bootstrap replicates using the midpoint and most-distal point methods (Supporting Information Figure S29). Results were consistent across niche breadths, and in both cool (95 ka) and warm (present-day) climate conditions.

3.4 | Climate region trends

We assessed how the seven traits might differ between species living in tropical environments and those species living in temperate environments. All traits had significantly smaller realized niche breadths for species inhabiting tropical regions compared with those restricted to temperate regions (Figure 5; Supporting Information Figure S33–S39). The only exception to this pattern was maximum precipitation, in which tropical species had broader niches (Figure 5; Supporting Information Figure S35), again consistent with our expectations based on the spatial variability of climate by latitude. “Mixed” species found in both climate regions had trait values intermediate to species in tropical and temperate regions, with the exception of latitudinal extent and maximum precipitation; values of these two traits were typically highest for “mixed” species (Supporting Information Figures S35 and S38).

3.5 | Climate variability trends

The standard deviation of climate variables by latitudinal band reveals that spatial heterogeneity (variability) is larger at high latitudes for temperature and at low latitudes for precipitation (Figure 1; Supporting Information Figure S1). Therefore, realized niche breadths for each climate parameter were positively correlated with the spatial variability of that parameter, both when climate variability was measured over the entire 120 ka, and when measured only in present-day conditions (Figure 3). Spatial variability in minimum temperature and maximum temperature were similar across latitudes, measured as the correlation of the standard deviation of these two climate variables in each latitudinal band ($r = 0.56$). As is well known, higher latitudes were characterized by greater seasonal variation in temperature conditions (Supporting Information Figure S2).

4 | DISCUSSION

We used simulated species interacting with dynamic global environments to explore the question of whether species' abiotic niche

traits might be structured latitudinally by the geographical distribution of abiotic environments. This hypothesis reflects decades of ecological research on modern and fossil species to explain patterns of narrow geographical range and niche characteristics in the tropics compared with higher latitudes (Deutsch et al., 2008; Eeley & Foley, 1999; Ghalambor et al., 2006; Krasnov, Shenbrot, Khokhlova, Mouillot, & Poulin, 2008; MacArthur, 1972; Pagel et al., 1991; Papacostas & Freestone, 2016; Tomašových et al., 2015; Vázquez & Stevens, 2004). Our simple “null model” controlled for fundamental niche breadth and dispersal ability to create simulated species that dispersed and colonized, speciated, and went extinct over a changing global environmental landscape over 120,000 years.

Broadly, our simulations show: (a) that the fundamental and realized niche and their geographical patterns can contrast markedly, and (b) that latitudinal patterns in realized niche breadth can derive only from realistic, spatio-temporal variation in climate. Fundamental niche breadths were held constant across latitudes in our simulations, yet we obtained significant variation in breadth (Figure 4) from the conjunction of dispersal constraints and the spatial arrangement of climates and continents on Earth. We also noted that realized niche breadths for temperature (both maximum and minimum) vary positively with latitude, whereas realized niche breadths for minimum precipitation vary negatively with latitude, in the absence of other processes. That is, given identical and conserved fundamental niches, low-latitude species exist within narrower ranges of temperature, but broader ranges of precipitation; this relationship holds across all combinations of fundamental niche breadth and dispersal ability examined. Such patterns arose from the degree of spatial environmental variation in these parameters by latitude; the tropics have more homogeneous and heterogeneous temperature and precipitation conditions, respectively (Figure 1; Supporting Information Figure S1; Bonetti & Wiens, 2014; Quintero & Wiens, 2013; Vázquez & Stevens, 2004). The spatial arrangement and availability of climate, then, seem to provide a mechanism for generating latitudinal gradients in empirical niche breadth, which appear qualitatively similar to simulated patterns. Spatially-homogeneous temperature conditions at low latitudes have the potential to prevent low-latitude species from “seeing” the full suite of conditions across which they could persist (Figure 1; Supporting Information Figure S1). The result of restricting species' occupation of tolerance ranges may then work together with seasonal variability to explain latitudinal trends in range size and niche breadth (Bozinovic et al., 2011; Janzen, 1967; Quintero & Wiens, 2013), because spatial and temporal gradients are not mutually exclusive (Tomašových et al., 2015).

The virtual species qualitatively retrieved the close correlation between geographical range size and available land area found in nature (Cardillo, 2002; Gaston et al., 1998). Latitudinal extents

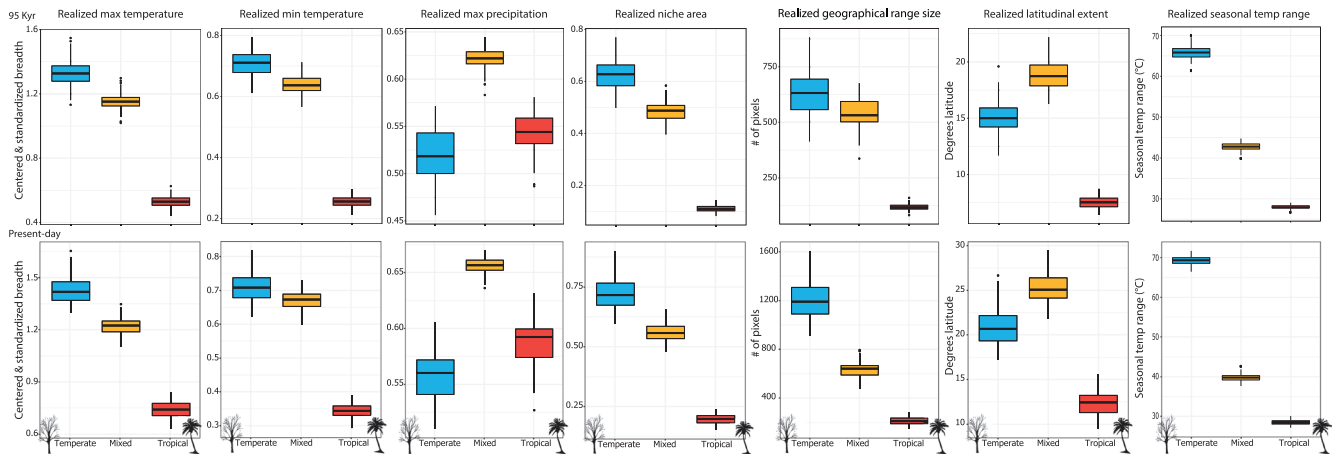


FIGURE 5 Trait values for virtual species with narrow niche breadths and poor dispersal abilities when the analysis is segregated into three climate regimes: temperate (blue), tropical (red), and mixed temperate and tropical (yellow). Box plots represent the mean trait values for 50 species in a series of 100 bootstrap replicates. Patterns were analysed in cold (95 ka) and warm (present-day) climate conditions. All other niche and dispersal combinations are shown in the Supporting Information (Figures S33–S39) [Colour figure can be viewed at wileyonlinelibrary.com]

and geographical range sizes were larger at high latitudes in the Northern Hemisphere, but smaller at low latitudes in the Southern Hemisphere when breadth of tolerance and dispersal ability were held constant in our simulations. Rapoport's rule, the tendency for the geographical range sizes of species to increase with latitude (Gaston et al., 1998; Lyons & Willig, 1997; Orme et al., 2006; Pinter et al., 2015; Rohde, 1999; Šizling, Storch, & Keil, 2009; Stevens, 1989; Tomašových et al., 2016), can therefore be manifested in the Northern Hemisphere solely as a null response to land area positively co-varying with latitude (Gaston et al., 1998). Although land area controls latitudinal patterns in range size, it does not seem to affect latitudinal trends in realized niche breadths, because the same niche patterns are recovered in both hemispheres, even when range size trends are reversed.

Our simulations indicate that the spatial configuration of continents and climates on Earth can reproduce empirically-derived gradients of macroecological traits with latitude, which are sometimes interpreted as evidence for adaptive processes (Bonetti & Wiens, 2014; Quintero & Wiens, 2013; Vázquez & Stevens, 2004). These results coincide with those of previous work (Quintero & Wiens, 2013) that found that latitudinal trends in niche breadth can be driven by differences not only in climate variation within localities (seasonal), but also by climate variation among localities (spatial). Although the spatial arrangement of climate may exert a first-order control on latitudinal gradients in niche breadth, selective processes could further amplify these macroecological patterns. For example, selection on temporal climate variation is usually invoked to explain why high-latitude species have broader temperature tolerances than low-latitude species (Bozinovic et al., 2011; Janzen, 1967; Quintero & Wiens, 2013); similar selective processes could operate on spatial climate variability, particularly if a fitness cost is associated with maintaining a broad niche in the absence of extreme environmental conditions (Kassen, 2002).

It is important to note that these simulations are relevant for the set of parameters considered here, and simulations cast in the context of other environmental variables might show different patterns. Moreover, macroecological trait estimates for virtual species were often fairly large, because even virtual species with "narrow" niche breadths could tolerate ranges of 21°C for both maximum and minimum temperature. Although simulated patterns were not dependent on niche breadth, whether they hold for narrower (and potentially more realistic) breadth estimates remains to be tested.

Our results may also be dependent on the relatively coarse spatial grain of the simulations ($1^\circ \times 1^\circ$), which is known to have an effect on observed patterns of species richness (Kaspari, Yuan, & Alonso, 2003; Lira-Noriega, Soberón, Navarro-Sigüenza, Nakazawa, & Peterson, 2007; Lyons & Willig, 2002; Rahbek & Graves, 2001). The resolution of our simulations was constrained by the spatial resolution of the climate model, but is likely to be appropriate for approaching and assessing broad-scale macroecological patterns (Blackburn & Gaston, 2002). Analyses at finer scales might produce different results; for example, we did not test how local-scale climate fluctuations might affect realized niche breadth patterns (Nakazawa, 2013). Notably, however, spatial resolution was not found to affect results in a meta-analysis of range size and latitude (Ruggiero & Werenkraut, 2007).

Finally, our simulations rely on the accuracy and fidelity of the global climate models themselves. Although HadCM3 has been shown to be robust and to reproduce well both modern (Valdes et al., 2017) and past changes (Harrison et al., 2014; Hoogakker et al., 2017), different patterns may result under different GCMs. However, no equivalent set of simulations currently exists for any alternative climate model. Although GCMs generally reproduce patterns of temperature change better than they do precipitation change, HadCM3 has been shown to reproduce some key hydrological indicators (DiNezio & Tierney, 2013; Singarayer et al., 2017), providing additional confidence in the conclusions drawn here.

To summarize, we explore a “null model” for biogeography, in which abiotic environments and their variation in time and space are examined as a contributor to niche breadth structure. Species do not interact in this model, and the only evolutionary mechanism is “cladogenetic”, with newly generated species showing complete niche conservatism. Under these assumptions, we conclude that the complex, spatio-temporal distribution of global abiotic environments has strong potential for structuring observed latitudinal gradients of niche breadths, without the need for biotic interactions or evolution in niche parameters. Thus, we provide both a unique method and perspective on the long-standing debate of the spatial structure of biodiversity on Earth.

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AUTHOR CONTRIBUTIONS

E.E.S. designed the study. E.E.S. and H.Q. performed the analyses. J.S. and P.V. provided climate data and analysis. E.E.S., H.Q., C.E.M., A.T.P. and J.S. analysed the results. E.E.S. wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

DATA ACCESSIBILITY

Data and code associated with this manuscript are available via Dryad: <https://doi.org/10.5061/dryad.vd80g8n>

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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