RESEARCH PAPER

Geological and climatic histories likely shaped the origins of terrestrial vertebrates endemic to the Tibetan Plateau

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Abstract

Aim: The Tibetan Plateau (TP) hosts many endemic species, but questions regarding when and from where these species originated have not been comprehensively answered. Here, we provide a synthesis of the biogeographical history of terrestrial vertebrates endemic to the TP and investigate the potential drivers of their spatio-temporal origins.

Location: Tibetan Plateau and its surrounding regions.

Time period: Cenozoic.

Major taxa studied: Terrestrial vertebrates.

Methods: We used dispersal–extinction–cladogenesis models based on time-calibrated phylogenies to reconstruct the ancestral ranges of 174 endemic TP species and compiled the ancestral ranges and age estimates of their dispersal events. We generated a possibility map of source areas for endemic TP species by counting the incidence of non-TP sister clades in 110 km × 110 km grid cells. We used generalized linear mixed models to assess the relative importance of historical processes and environmental factors in explaining the geographical variations in the source areas. We created subsets based on four vertebrate classes to test whether the dispersal events varied spatially and temporally among taxonomic groups.

Results: We found that the endemic species colonized the TP as early as 55 Ma, and that the main colonization phase started to increase around 15 Ma and peaked after 6 Ma. The major source areas of endemic TP species include the Hengduan Mountains, the Himalayas, and Central Asia. Elevation difference had the strongest effect on the source areas, followed by geographical distance. The spatio-temporal origins of species endemic to the TP and the potential drivers showed significant differences among vertebrate classes.

Main conclusions: Our study supports the hypothesis that endemic TP species originated from various zoogeographical regions at different times and highlights the important roles of the TP uplift and past climatic changes for determining the spatio-temporal origins of endemic TP species.

KEYWORDS
biogeography, colonization, dispersal–extinction–cladogenesis model, endemic species, origin, Tibetan Plateau

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1 | INTRODUCTION

The Tibetan Plateau (TP) is a unique and fascinating region of the world and has long attracted the attention of evolutionary biologists and biogeographers (Deng et al., 2020; Favre et al., 2015; Mosbrugger et al., 2018). The TP extends across a vast area (*c.* 2.5 million km^2) with an average elevation exceeding 4,500 m and features extreme coldness, severe aridity and oxygen deficiency (Wang et al., 2015). As a harsh highland region surrounded by warm and humid lowlands, the TP has been recognized as an island-like system with highly endemic biodiversity, wherein many adaptive radiations have occurred over geological time (Favre et al., 2015; Wen et al., 2014). Geologically, the TP was part of the Tethys Ocean by the Palaeocene and did not emerge above sea level until *c.* 55–50 million years ago (Ma) due to the Indo–Asian collision (Hu, Garzanti, et al., 2016; Royden et al., 2008). As such, species endemic to the TP are expected to have colonized from surrounding regions followed by vicariant speciation and diversification (Päckert et al., 2020; Wen et al., 2014). However, given that strong reconfiguration of the geographical setting and atmospheric circulation have profoundly altered the biota on the TP over the past 50 Myr (He et al., 2020; Mosbrugger et al., 2018), the origins of these species and their time of arrival on the TP remain unclear.

There are varying opinions on the temporal origins of TP species (Deng et al., 2019; Yang et al., 2009), in part due to the controversy over the plateau's uplift history (Botsyun et al., 2019; Renner, 2016; Spicer et al., 2020). Based upon summaries of divergence time estimates, previous phylogenetic studies suggested that species endemic to the TP colonized the plateau no earlier than *c.* 9–7 Ma (Päckert et al., 2015; Yang et al., 2009). More recently, however, studies have increasingly reported much earlier divergence times between endemic TP species and their sister clades, suggesting that colonization may have occurred as early as *c.* 50–40 Ma (Agarwal et al., 2014; Pisano et al., 2015; Wu et al., 2019). Evidence from tectonics (Clark et al., 2004), geology (Wang et al., 2008), palaeoaltimetry (Rowley & Currie, 2006), sedimentology (Guo et al., 2002) and palaeontology (Su et al., 2018) has supported an earlier uplift of the TP, and combined with phylogenetic estimates, this evidence challenged the relationship between the young node ages of clades and the assertion of recent TP uplift (Renner, 2016).

Geographically, four potential colonization routes for species into the TP have been hypothesized based on fossil deposits and phylogeographical inference. The proposed northern route from Central Asia (Guo & Wang, 2007; Li & Wang, 2015; Li et al., 2018; Pisano et al., 2015) would suggest a similar environment and biome (i.e. desert and open steppe) to those on the TP. The southern route was proposed to have resulted from the Indo–Asian collision and emergence of lowland habitats along the southern margin of the TP during the Eocene, facilitating the dispersal of Indian and Southeast Asian organisms to the TP (Liu et al., 2019; Wu et al., 2019, 2020). In addition, several species were considered to have colonized the TP via a western route from West Asia (Hauenschild et al., 2017; Solovyeva et al., 2018) or an eastern route from South China

(Lu et al., 2012). Notably, the four hypothesized routes were observed to vary across taxa. For example, most reptiles and amphibians were considered to have colonized the TP via the southern route (Agarwal et al., 2014; Che et al., 2010; Wu et al., 2020), whereas mammals were more likely to have favoured the northern route (Li & Wang, 2015; Pisano et al., 2015). Since past biogeographical studies were typically analysed on a case-by-case basis, furthering our understanding of the spatio-temporal origins of the TP species and the variation among vertebrate classes has been hampered by the limited taxonomic coverage in previous studies.

Understanding the factors influencing the source regions of endemic TP species is challenging owing to the complex interactions between historical and ecological drivers (Mosbrugger et al., 2018; Päckert et al., 2020). In general, the colonization success of the disperser strongly decreases with geographical distance based on the island biogeography theory (MacArthur & Wilson, 1967); briefly, more opportunities exist for species to colonize the TP from shorter distances. Similarly, areas with higher regional species richness are more likely to be source regions of TP species. In addition, TP species may have colonized from regions with similar environmental conditions as those found on the TP, based on niche conservatism (Wiens et al., 2010), or they may exhibit the opposite pattern based on ecological speciation (Rundle & Nosil, 2005). However, few studies have examined the generality of each of these factors among taxa or simultaneously evaluated the relative strength of relationships between the geographical origin and these factors.

Here, we aimed to investigate the geographical and temporal origins of species endemic to the TP and explore the drivers underlying these patterns. Although it is possible to reconstruct the origins of species using palaeontological data, the extreme scarcity and uneven distribution of fossil deposits on the TP limits our capacity to constrain biogeographical scenarios within a spatio-temporal framework. Thus, we compiled a comprehensive dataset consisting of nearly all terrestrial vertebrates endemic to the TP to estimate their biogeographical origins. First, we assessed the ancestral range and age estimate of each independent species dispersal event based on ancestral range estimate models. We identified the source areas from where endemic TP species originated and tested whether these source areas varied among taxa or through different periods. Finally, we assessed the relative importance of historical processes and environmental factors in explaining these source areas.

2 | METHODS

2.1 | Species data

We compiled a checklist of terrestrial vertebrates endemic to the TP according to the species distribution data against the TP's geographical range (see Supporting Information Appendix S1: Figure S1.1). The species geographical ranges were obtained from the International Union for Conservation of Nature (IUCN) Red List database (http://www.iucnredlist.org) for mammals and amphibians,

BirdLife International and NatureServe (http://www.birdlife.org) for birds, and Roll et al. (2017) for reptiles. We combined the geographical range data with data from the Global Biodiversity Information Facility (GBIF; http://www.gbif.org) and Fauna of China (see Supporting Information Appendix S2) to validate the checklist of endemic TP species. Finally, we identified 178 terrestrial vertebrates endemic to the TP, including 68 mammals, 57 birds, 23 reptiles and 30 amphibians (see Supporting Information Appendix S3).

We obtained dated phylogenies from Upham et al. (2019) for mammals, Jetz et al. (2014) for birds, Tonini et al. (2016) for reptiles, and Jetz and Pyron (2018) for amphibians. These phylogenies are available online (http://vertlife.org/phylosubsets) as the posterior distribution of trees ($n = 1,000$), and we built maximum clade credibility phylogenies using the 'phangorn' package (Schliep, 2011) in R version 3.6.0 (R Development Core Team, 2019). The number of endemic TP species that could be matched to the tips in the phylogenies was 174 (out of the 178 species). To conduct biogeographical analyses, we extracted clades from the maximum clade credibility phylogenies based on the presence of endemic TP species. This means a clade subset should have contained at least one species endemic to the TP and comprised all species belonging to the genus. For genera containing only a few species, we further extracted tips from their closest sister clades to ensure each phylogeny subset had a minimum of seven species (Antonelli et al., 2018). Finally, our dataset resulted in 64 phylogeny subsets comprising a total of 2,156 species (including 174 endemic TP species) to estimate ancestral area (Supporting Information Table S1.1).

2.2 | Ancestral range estimation

To explore the geographical and temporal origins of species endemic to the TP, we applied a dispersal–extinction–cladogenesis (DEC) model (Ree & Smith, 2008) in the R package 'BioGeoBEARS' (Matzke, 2014). This model can reconstruct temporal changes in the geographical range of a species within a likelihood framework (Ree et al., 2005), and thus, it can infer the ancestral ranges and biogeographical scenarios of certain species (Ree & Smith, 2008). We coded the geographical distributions of species as presence/absence in 11 zoogeographical regions, namely, Tibetan Plateau, South Asia, Southeast Asia, South China, North China & Korea, Central Asia, Euro-Siberia, West Asia, Africa, Australia and the Americas (Supporting Information Figure S1.2). To account for the changes in geographical setting among these regions over geological time, we incorporated time-stratified dispersal multiplier matrices (Supporting Information Figure S1.3) and adjacency matrices (Supporting Information Table S1.2) in the model fitting. The dispersal probability was assigned to one of three categories: $p = .1$ (non-neighbouring areas), $p = .5$ (partly connected areas), and $p = 1.0$ (neighbouring areas) for four-time-slice matrices (120–60, 60–40, 40–20 and 20–0 Ma). We constrained the maximum range size to between two and seven areas according to the geographical distributions of species within specific phylogeny subsets. Notably, as some species in the phylogenies

were interpolated without molecular data (Supporting Information Table S1.1), the placements and divergence times in a phylogeny might be biased to some degree. To verify our results, we repeated our analysis based on 47 relatively well-sampled phylogeny subsets in which > 60% of species had molecular data.

2.3 | Spatio-temporal analysis

To estimate the spatio-temporal origins of species endemic to the TP, we compiled the ancestral ranges and age estimates of dispersal events of TP species based on the DEC models. Although the dispersal events might have involved both 'into TP' dispersals and 'out of TP' dispersals (Deng et al., 2020; Päckert et al., 2020), we only considered the 'into TP' dispersal events that represented the first establishment of a specific clade on the TP. Given that all of the terrestrial organisms here should have originated outside the TP, the 'into TP' dispersal events could be expected to have occurred earlier than the 'out of TP' dispersal events. We quantified the number of dispersal events within each 1-Myr time bin and constructed a cumulative frequency histogram. As the absolute number of divergence events generally increased with time (Antonelli et al., 2018; Klaus et al., 2016), we assessed temporal shifts rather than the absolute values of dispersal events using change point analysis in the R package 'ecp' (James & Matteson, 2014). In addition, we created subsets based on four vertebrate classes (mammals, birds, reptiles and amphibians), and used the Wilcoxon rank sum test and chi-square test to explore whether the dispersal events varied spatially and temporally among taxonomic groups.

In addition, we projected the geographical ranges from where the endemic TP species originated on the map by counting the incidence of their sister clades identified from the DEC models (Supporting Information Figure S1.4). In brief, we first identified non-TP sister clades that diverged from a common ancestor and shared a common ancestral range with the endemic TP species in the DEC models. Then, we mapped the distribution of each sister clade by merging the geographical ranges of its descendants. Finally, we generated a possibility map of source areas for endemic TP species by counting the incidence of non-TP sister clades in an equal-area grid cell of 110 km × 110 km in the Behrmann projection. To test whether the source areas of endemic TP species varied across taxonomic groups and differed in time, we created subsets based on (a) different vertebrate classes (mammals, birds, reptiles and amphibians), and (b) different time intervals according to the time points at which the frequency of dispersal events changed.

2.4 | Potential drivers of the source area of endemic TP species

We explored the relative effects of geographical distance, elevation difference and climatic dissimilarity (temperature and precipitation) on the source area of endemic TP species (Supporting

Information Figure S1.5a–d). Elevation data with a spatial resolution of one arc minute were downloaded from the National Centers for Environmental Information (https://www.ngdc.noaa.gov/mgg/global/relief/ETOPO1/data/). Climate data were derived from the WORLDCLIM dataset (c. 1 km × 1 km resolution; Hijmans et al., 2005). We analysed temperature-related variables (BIO 1–BIO 11) and precipitation-related variables (BIO 12–BIO 19) in two principal component analyses. As the first three principal component axes accounted for 94.1% of the total variations in temperature-related variables, and 92.0% of variations in precipitation-related variables (Supporting Information Table S1.3), we calculated temperature dissimilarity and precipitation dissimilarity using the Euclidean distance in the three-dimensional space. Since we assume that the endemic TP species originated from areas outside the TP, we considered the TP a homogeneous region and compared each grid cell outside the TP with the TP average to disentangle the factors underlying the origins of endemic TP species. This approach is feasible because the environmental conditions were largely consistent within the TP but remarkably different from surrounding regions (Supporting Information Figure S1.6). Thus, we calculated elevation difference and climatic dissimilarity between each grid cell outside the TP and the average values of grid cells within the TP. The geographical distance was calculated from the centre of each grid cell to the TP boundary using Euclidean distance.

2.5 | Statistical models

We used generalized linear mixed models (GLMMs) with a Poisson distribution to test the geographical and environmental effects on the source area of endemic TP species in the R package 'lme4' (Bates et al., 2015). We fit models for the source area of four individual vertebrate classes (amphibians, reptiles, birds and mammals) as well as for all the vertebrate species combined. The fixed effects were geographical distance, elevation difference, temperature dissimilarity and precipitation dissimilarity. The random effects included the regional species richness (or species richness for each taxonomic group; Supporting Information Figure S1.5e–i) and zoogeographical regions (Supporting Information Figure S1.5j). The geographical distance was natural log-transformed, and the regional species richness was natural log $(x + 1)$ transformed to improve linearity. All continuous variables were standardized to a mean of 0 and SD of 1, allowing direct comparison of the effect sizes. The Pearson correlation coefficients between all fixed factors were lower than .7 (Supporting Information Figure S1.7). Given that the endemic TP species were thought to originate from surrounding regions, we restricted the statistical analyses to the grid cells within a geographical distance of 3,000 km from the TP, which covered all source area hotspots of endemic TP species (Supporting Information Figure S1.8). To test whether the different inputs of grid cells affected our findings, we repeated our models using two alternative geographical distances of 2,000 and 4,000 km (Supporting Information Figure S1.8). We conducted GLMMs with all possible combinations of the variables in the

R package 'MuMIn' (Bartoń, 2019), and used corrected Akaike's information criterion (AICc) scores to determine the best model (with the lowest AICc values). We calculated marginal R^2 (accounting for fixed effects) and conditional R^2 (accounting for fixed and random effects) to assess the relative importance of fixed and random effects.

3 | RESULTS

3.1 | Spatio-temporal origins of endemic TP species

Our biogeographical analysis identified 128 independent dispersal events for species endemic to the TP in 48 mammal, 47 bird, 17 reptile and 16 amphibian clades (Figure 1a). The most important source region was South China, from where 31 endemic TP clades originated (Figure 1b; Supporting Information Table S1.4). Southeast Asia and Central Asia emerged as the second most important regions with 29 clades colonizing from these regions, followed by North China & Korea (16 clades), Euro-Siberia (14 clades) and West Asia (14 clades) (Supporting Information Table S1.4). According to the divergence time of endemic TP species from their sister clades, the earliest dispersal event occurred c. 55 Ma (Figure 1c), when *Cyrtodactylus tibetanus* diverged from its sister clade (Supporting Information Figure S1.9). Two sudden changes in the timing of dispersal events occurred 15 and 6 Ma (Figure 1c). Between 55–15 Ma, dispersal events were scarce (12 out of 128 cases, 9.4%). The main dispersal wave started 15 Ma, and most dispersal events occurred from 6 Ma onwards (91 cases, 71.1%).

3.2 | Cross-taxon comparison

The spatio-temporal origins of species endemic to the TP differed among vertebrate classes (Figure 1d,e). The earliest dispersal events were for reptiles (median = 8.1 Ma, Wilcoxon rank sum test, $p < .05$), followed by amphibians (4.5 Ma), birds (3.0 Ma) and mammals (1.7 Ma) (Figure 1d). Source regions for mammals were broadly consistent with those for birds, but both were significantly different from those for reptiles and amphibians (chi-square test, $p < .05$; Figure 1e; Supporting Information Table S1.5). Southeast Asia was the most important source region for birds and reptiles endemic to the TP, whereas mammals and amphibians predominantly colonized from Central Asia and South China, respectively (Figure 1e; Supporting Information Table S1.4). These findings were broadly consistent with our analysis of only the phylogenetic subsets with > 60% of species having molecular data (Supporting Information Figure S1.10). For example, the change points of the main dispersal for all terrestrial vertebrates occurred 15 and 7 Ma (Supporting Information Figure S1.10a), and the dispersal events for reptiles were significantly earlier than those for other taxa (Supporting Information Figure S1.10b). Similarly, source regions of species endemic to the TP showed significant differences among vertebrate classes (Supporting Information Figure S1.10c,d).
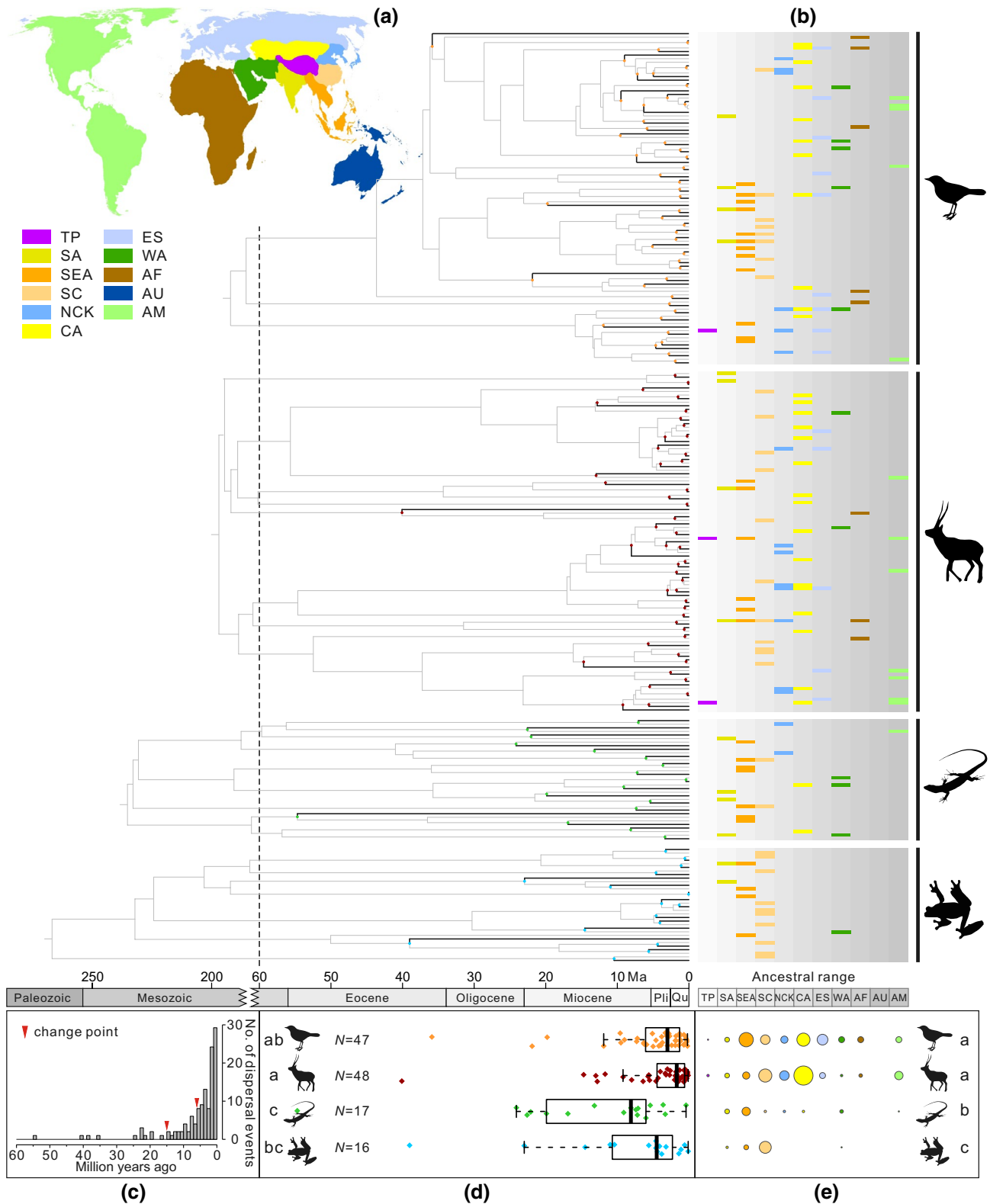
FIGURE 1 Dispersal events of terrestrial vertebrates endemic to the Tibetan Plateau (TP). (a) Black branches are clades endemic to the TP, and grey branches indicate their sister clades. Pli = Pliocene; Qu = Quaternary. Divergence events are highlighted at nodes with different colours representing different vertebrate classes. (b) Colour bars at tips indicate the ancestral range of endemic TP species and their sister clades. Colours denote 11 predefined zoogeographical regions consistent with the inset map (Eckert IV projection). (c) Histograms of total dispersal events within 1-Myr time bins. (d) Boxplots showing the temporal distribution of dispersal events across four vertebrate classes. Boxes show the median and 25th and 75th percentiles. Letters indicate significant differences among vertebrate classes (Wilcoxon rank sum test, $p < .05$). (e) Incidence of ancestral range of clades endemic to the TP among different vertebrate classes. Symbols are sized proportional to incidence and coloured as per panel (b) and the inset map. Letters indicate significant differences (chi-square test, $p < .05$). Abbreviations: TP = Tibetan Plateau; SA = South Asia; SEA = Southeast Asia; SC = South China; NCK = North China & Korea; CA = Central Asia; ES = Euro-Siberia; WA = West Asia; AF = Africa; AU = Australia; AM = the Americas [Colour figure can be viewed at wileyonlinelibrary.com]

3.3 | Taxonomic variation in source areas of endemic TP species

When the source areas of endemic TP species were spatially mapped, the Hengduan Mountains, the Himalayas, and Central Asia were the most important source areas for all vertebrates (Figure 2a). However, some incongruence in the hotspots of source areas emerged among vertebrate classes (e.g. Central Asia for mammals, Hengduan Mountains and the Himalayas for birds, the west Himalayas for reptiles and Hengduan Mountains for amphibians; Figure 2b–e). Overall, the spatial correlation between source areas for mammals and birds ranked the highest (Spearman's $r = .76$), whereas those between endotherms and ectotherms were relatively low (Spearman's r ranged from .18 to .39; Supporting Information Figure S1.11).

3.4 | Temporal variation in source areas of endemic TP species

When the source areas of endemic TP species were mapped along different time intervals (55–15, 15–6 and 6–0 Ma) according to the times of sudden change in dispersal events (Figure 1c), we found that the geographical origins of endemic TP species varied through time (Figure 3). Southeast Asia and the Himalayas were the most important source areas earlier, from 55 to 15 Ma (Figure 3a), whereas the Hengduan Mountains and Central Asia were most important from 15 to 6 Ma (Figure 3b). From 6 Ma onwards, the Hengduan Mountains acted as the primary source area of endemic TP species (Figure 3c).

3.5 | Potential drivers of source areas of endemic TP species

The fixed effects of the best GLMM explained 19% of the geographical variation in the source area of endemic TP species ($R^2_{marginal}$), with elevation difference exhibiting the strongest effect, followed by geographical distance (Table 1). This result was robust despite differences in the spatial extent of grid cells (Supporting Information Figure S1.12). The combination of fixed effects and random effects explained 87% of the variation ($R^2_{conditional}$), indicating that biological and geographical random effects also explain a substantial proportion (c. 68%) of the geographical variation in the source areas (Table 1). The relative effects of geographical factors and environmental dissimilarity varied among taxa. Elevation difference had the most important effect on the source area of mammals, whereas geographical distance was more influential to birds, reptiles and amphibians (Figure 4; Supporting Information Table S1.6).

4 | DISCUSSION

4.1 | Temporal origin of endemic TP species

We demonstrated that the dispersal events of endemic TP species occurred first at the beginning of the Eocene (c. 55 Ma) and started to

increase around the middle Miocene (c. 15 Ma; Figure 1c). Previous reviews based on a biogeographical synthesis of multiple TP vertebrates have proposed that the TP species diverged from their sister clades no earlier than c. 9–7 Ma (Päckert et al., 2015; Yang et al., 2009). According to our results, although early colonization events (55–15 Ma) were scarce (12 out of 128 cases), it is clear that the majority of 'into TP' dispersal events occurred at least by 15 Ma. Evidence supporting a much earlier origin for endemic TP species is accumulating (Mosbrugger et al., 2018 and references therein). Most recently, a synthesis of biogeographical histories of the alpine flora suggested that cold-adapted species had started to colonize the TP from neighbouring regions in the early Miocene (c. 23–16 Ma; Ding et al., 2020), which corroborates our findings.

The temporal variation in dispersal events was probably influenced by differences in geological and climatic history. The earliest dispersal event of endemic TP species coincides roughly with the timing of the Indo–Asian collision and initial emergence of the TP (Botsyun et al., 2019; Royden et al., 2008) and is consistent with the previous phylogeography of the gekkonid genus *Cyrtodactylus* (Agarwal et al., 2014). Dispersal events continuously increased since the middle Miocene (c. 15 Ma). This timeline is almost concurrent with the enhancement of the monsoon system (Sun & Wang, 2005) and the onset of aridification of the Asian interior (Miao et al., 2012). These climatic changes likely restructured the habitats for species (e.g. the desert-to-steppe biome change in Central Asia; Barbolini et al., 2020) and thus, facilitated the dispersal events into the TP from surrounding regions (Ding et al., 2020; Pisano et al., 2015). Furthermore, we recorded a sharp increase in dispersal events from the late Miocene (c. 6 Ma) onwards, supporting the hypothesis that this was an important time for 'into TP' dispersal events. This trend has been previously demonstrated by phylogeographical (Päckert et al., 2015) and palaeontological (Li et al., 2018; Li & Wang, 2015) studies and other evidence from fishes (Ma et al., 2015) and plants (Hauenschild et al., 2017). This timing highlights the importance of the latest uplift of the TP edge (e.g. the Hengduan Mountains and Qilian Mountains) and glaciation cycling in shaping the vicariance of clades between the TP and surrounding regions (Ding et al., 2020; Lei et al., 2014; Muellner-Riehl, 2019).

4.2 | Geographical origin of endemic TP species

Species endemic to the TP originated from various zoogeographical regions (Figure 1b,e), with the Hengduan Mountains, Himalayas, and Central Asia emerging as the most important source areas (Figure 2). The importance of the Hengduan Mountains and Himalayas was expected because these regions are closely connected to the TP and share the most similar environments and orogenetic histories (Favre et al., 2015). From an evolutionary perspective, the Hengduan Mountains and Himalayas acted as species pumps from which multiple lineages on the TP originated (Ding et al., 2020; Päckert et al., 2015) and, thus, share the majority of extant species with the TP (He et al., 2017). Unexpectedly, the relatively distant Central Asian region was also identified as a key source area of endemic TP species (Figures 1e and 2a), in particular for mammals and birds
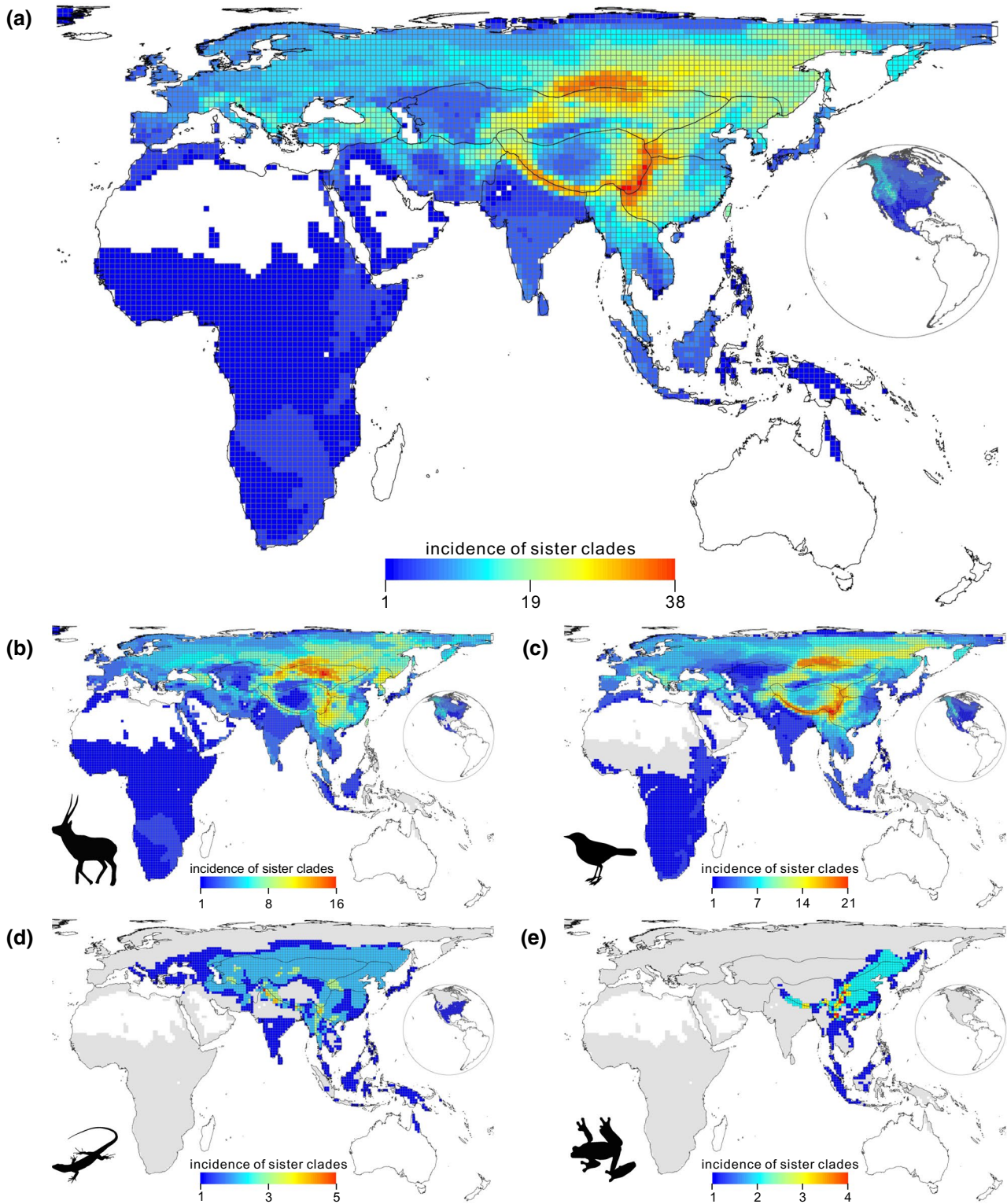
FIGURE 2 Geographical variation in the source area of endemic Tibetan Plateau (TP) species for (a) all terrestrial vertebrates, (b) mammals, (c) birds, (d) reptiles and (e) amphibians. The source area of endemic TP species was calculated by counting the incidence of non-TP sister clades in 110 km × 110 km grid cells. Grey areas within the land indicate the absence of species in a particular taxonomic group [Colour figure can be viewed at wileyonlinelibrary.com]
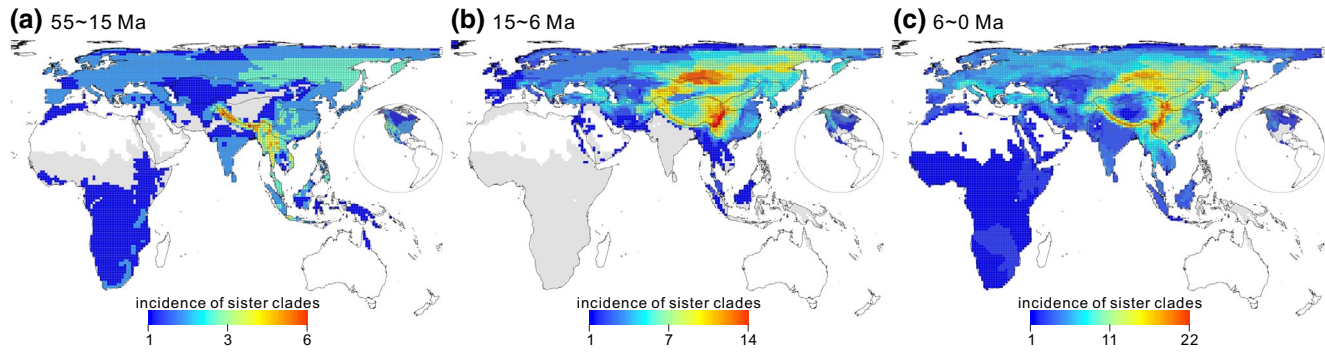
FIGURE 3 Geographical variation in the source area of endemic Tibetan Plateau (TP) species during three time periods. The source area of endemic TP species was calculated by counting the incidence of non-TP sister clades in 110 km × 110 km grid cells. The periods were defined according to points of sudden change at 15 and 6 Ma [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Coefficient estimates from generalized linear mixed models explaining the geographical variation in the source area of terrestrial vertebrates endemic to the Tibetan Plateau (TP)

	β (SE)	95% CI
Intercept	2.33 (.171)	(1.997, 2.669)
Fixed effects		
Geographical distance	−.14 (.008)	(−.152, −.12)
Elevation difference	−.22 (.007)	(−.232, −.203)
Temperature dissimilarity	.05 (.015)	(.022, .079)
Precipitation dissimilarity	−.04 (.01)	(−.06, −.022)
Random effects		
Regional species richness	.36	
Zoogeographical regions	.45	
Goodness-of-fit statistics		
Marginal R^2	.19	
Conditional R^2	.87	

Note: The source area of endemic TP species is calculated by counting the incidence of non-TP sister clades. Fixed effects are indicated by standardized coefficients with 95% confidence intervals (CI). Random effects are shown as one standard deviation. Marginal R^2 indicates variation explained by fixed effects, and conditional R^2 indicates variation explained by fixed and random effects. All estimates are significant ($p < .01$).

(Figure 2b,c). Although several vertebrates (Guo & Wang, 2007; Li et al., 2018; Li & Wang, 2015) and plants (Hauenschild et al., 2017; Zhang et al., 2016) have been proposed to have originated from Central Asia, few previous studies considered this to be a common pattern (Wen et al., 2014). Our results, based on nearly all terrestrial vertebrates endemic to the TP, support the importance of Central Asia and highlight the role of the northern dispersal route for biotic interchange between the TP and temperate Asia.

Elevation and geographical distance have significant effects on the source areas of endemic TP species (Table 1), which corroborates previous findings that endemic TP species were likely to colonize from neighbouring areas that were ecologically similar to the TP

(Hu, Broennimann, et al., 2016; Wan et al., 2018). Notably, biological and geographical random effects explained a substantial proportion (*c.* 68%) of the variation in the source areas of endemic TP species, threefold higher than the variation explained by the fixed effects (Table 1). This finding indicated that the source areas of endemic TP species cannot be fully explained by the ecological factors measured in the analysis alone, but may also be significantly explained by biological and historical factors. For example, the importance of regional species richness in model fitting confirmed that endemic TP species are more likely to originate from areas with higher biodiversity (Table 1), such as the Hengduan Mountains and Himalayas (Figure 2). Furthermore, the strong predictive power of biogeographical regions corroborates our findings regarding geographical variation in source areas of endemic TP species and supports the key role of historical processes in shaping current biodiversity patterns (Hawkins et al., 2003).

4.3 | Historical effects on origins of endemic TP species

Our results demonstrated that the source areas of endemic TP species varied through time (Figure 3). Specifically, the early colonization events of endemic TP species predominately occurred from Southeast Asia and the Himalayas, and species colonizing from the Hengduan Mountains and Central Asia diverged more recently. These shifts strongly coincided both spatially and temporally with the TP uplift and regional climatic changes (Favre et al., 2015; Royden et al., 2008). Since the Eocene Indo–Asian collision (*c.* 55–50 Ma), the initial emergence of the TP could have promoted the development of new habitats characterized by warm and humid lowland environmental conditions (Deng et al., 2019), thus facilitating the colonization of Palaeogene-aged lineages into the TP via the southern route (Liu et al., 2019; Wu et al., 2019). By the middle Miocene (15.9–11.6 Ma), however, the Himalayas had nearly reached its present height and acted as a barrier to biotic interchange between the TP and South Asia (Deng & Ding, 2015). In contrast, the progressive uplift of the Tianshan Mountains (Charreau et al., 2009) and the
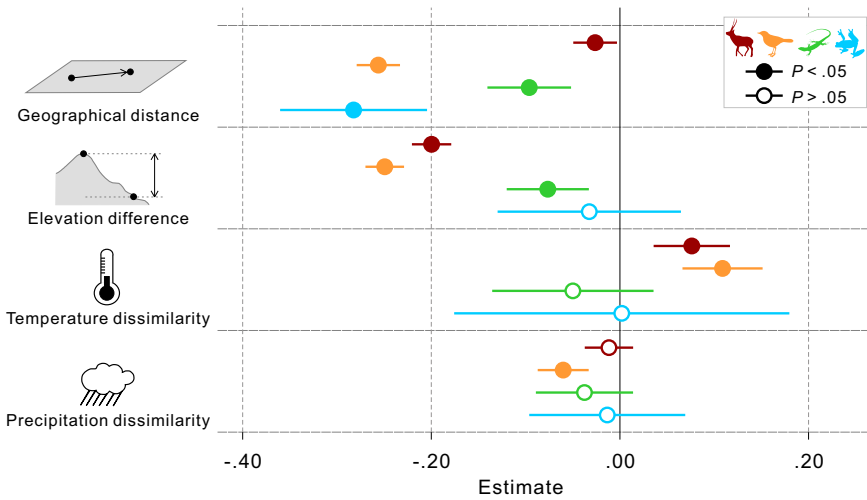
FIGURE 4 Regression coefficients and 95% confidence intervals for predicting the source area of endemic Tibetan Plateau species in generalized linear mixed models. Filled dots represent statistically significant relationships ($p < .05$). The full models are provided in Supporting Information Table S1.6 [Colour figure can be viewed at wileyonlinelibrary.com]

onset of aridification in the Asian interior (Miao et al., 2012) might have accelerated in situ speciation (Pisano et al., 2015; Solovyeva et al., 2018), which, coupled with the moderate topographical gradient of the northern route, could facilitate dispersal from Central Asia to the TP (Li & Wang, 2015). From the late Miocene onwards, the Hengduan Mountains became the only important source of endemic TP species (Figure 3). This timing corroborates a recent phylogenetic analysis of multiple clades of plants in the Hengduan Mountains, which showed that the Hengduan Mountains' uplift has driven in situ diversification since the late Miocene (*c.* 8 Ma; Xing & Ree, 2017). To sum up, the uplift of the TP and subsequent climate change over the past 50 Myr created novel ecological opportunities for species to colonize the TP via a variety of dispersal routes during different periods, which in turn created orographic barriers and climatic heterogeneity that facilitated vicariance (Favre et al., 2015; Mosbrugger et al., 2018).

4.4 | Cross-taxon comparison

The spatio-temporal origins of endemic TP species differed significantly among vertebrate classes. Geographically, most mammals and birds (endotherms) colonized the TP via the northern route, whereas reptiles and amphibians (ectotherms) rarely colonized from this route (Figure 1e). This incongruence can be explained by the endotherms having greater dispersal abilities (Stevens et al., 2014) and lower sensitivity to climatic conditions (Rolland & Salamin, 2016). A probable speciation mode for species colonizing via the northern route is that they reached the TP via long-distance dispersal and subsequently underwent vicariance owing to the climatic changes in the Asian interior. This mode was widely favoured by several mammals (Bannikova et al., 2018; Li et al., 2018; Li & Wang, 2015). In contrast, for species originating from the Hengduan Mountains and Himalayas, the dominant speciation mode presumably occurred via ecological segregation or vicariance caused by the uneven uplift of the TP (Päckert et al., 2015). Most reptiles (Agarwal et al., 2014) and amphibians (Che et al., 2010; Hofmann et al., 2017; Wu et al., 2020),

as well as many birds (Liu et al., 2016), might favour this speciation mode, which, along with high habitat heterogeneity in the Hengduan Mountains and the Himalayas, makes these regions important global biodiversity hotspots (Cai et al., 2020).

Another difference among taxa was that ectotherms colonized the TP earlier than endotherms (Figure 1d). Such a discrepancy was also found in the great American biotic interchange (Bacon et al., 2015) and Amazonian biotic interchange (Antonelli et al., 2018), and was explained by differences in biological factors among taxa, such as dispersal traits and life history strategies (Rolland & Salamin, 2016; Stevens et al., 2014). Alternatively, this difference might involve deep-time evolutionary processes, driven by orogenetic events and past climatic change during different periods (Mosbrugger et al., 2018). For instance, ectotherms colonized the TP earlier and more often via the southern route, whereas the endotherms colonized the TP predominantly via the northern route during a later period (compare Figure 2 and Figure 3). This shift coincided with the uplift of the TP in that the initial uplift occurred at the southern margin followed by northward and eastward uplift progression (Mulch & Chamberlain, 2006).

4.5 | Potential limitations

Our study potentially suffered from several limitations that should be addressed in future studies. First, there were uncertain placements of several species in the available phylogenetic tree owing to missing molecular data. Uncertain placement of some species in phylogenies might bias ancestral range estimates, and more comprehensive molecular data would further reinforce our understanding of the origins of endemic TP species. Furthermore, our analysis relied solely on a synthesis of molecular divergences of multiple lineages, but extinction events were not considered. Once a sister clade to TP species went extinct, the divergence time of endemic TP species would far pre-date the true colonization time (O'Dea et al., 2016). Thus, a temporal framework that incorporates molecular phylogenies and fossil data would better constrain biogeographical scenarios

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(Wu et al., 2019). Since the earliest vertebrate fossils found on the TP dated to the Oligocene (33.9–23 Ma; Deng et al., 2019), further exploration of fossil collections is necessary to facilitate a more comprehensive understanding of the spatio-temporal origins of the TP biota.

5 | CONCLUSION

The present work provides a comprehensive assessment of the spatio-temporal origins of endemic TP species based on a synthesis of their biogeographical histories. Our results revealed that terrestrial vertebrates endemic to the TP have colonized predominantly from the Hengduan Mountains, the Himalayas, and Central Asia since the early Eocene, and that the main colonization phase started 15 Ma and peaked from 6 Ma onwards. The source areas of endemic TP species can be predicted by elevation and geographical distance but were more likely shaped by historical events such as the uplift of the TP and regional climatic changes. Different vertebrate classes showed varied colonization modes according to the geological and climatic history. Our findings would be reinforced by integrating more comprehensive molecular data and fossil collections, as well as considering other taxa, which would further our understanding of the origin and evolution of life on the TP.

AUTHOR CONTRIBUTIONS

J. H. and H. J. designed the research; J. H., C. D. and J. Y. collected the data; J. H., S. L. and H. J. performed analyses; and J. H. and H. J. wrote the manuscript. All authors contributed to the final version of the manuscript.

DATA AVAILABILITY STATEMENT

The checklist of terrestrial vertebrates endemic to the TP is available as Supporting Information Appendix S3. Data regarding species geographical ranges, vertebrate phylogenies, elevation, climate, and species richness maps were derived from different online databases, as described in the Methods section. The data and R code supporting the findings of this study are available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.pk0p2ngmj).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.