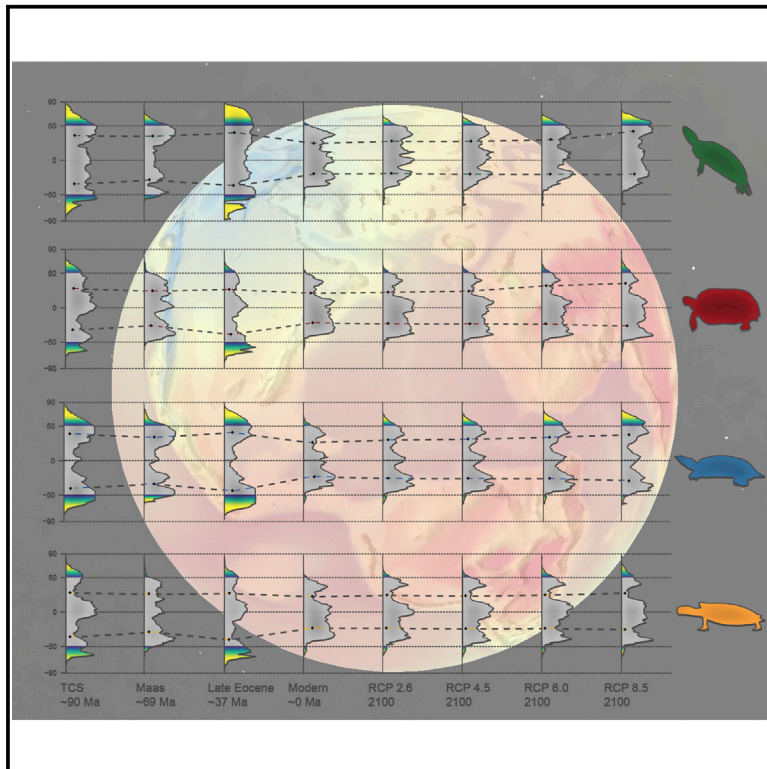


Current Biology

100 million years of turtle paleoniche dynamics enable the prediction of latitudinal range shifts in a warming world

Graphical abstract



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In brief

Chiarenza et al. examine the biogeographic patterns of non-marine turtles over the last 100 million years. Projections from ecological niche models to future climate scenarios indicate that areas currently hosting many turtle taxa would be adversely impacted by high temperatures, whereas high latitude regions could witness species-richness increases.

Highlights

- Non-marine turtles invaded higher paleolatitudes several times in the past
- Non-marine turtles reached their highest latitudes in the Cenomanian and Eocene
- Occupation of high paleolatitudes is projected at extreme emission scenarios
- Human occupation at high latitudes may prevent turtle adaptation to climate change

Article

100 million years of turtle paleoniche dynamics enable the prediction of latitudinal range shifts in a warming world

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SUMMARY

Past responses to environmental change provide vital baseline data for estimating the potential resilience of extant taxa to future change. Here, we investigate the latitudinal range contraction that terrestrial and freshwater turtles (Testudinata) experienced from the Late Cretaceous to the Paleogene (100.5–23.03 mya) in response to major climatic changes. We apply ecological niche modeling (ENM) to reconstruct turtle niches, using ancient and modern distribution data, paleogeographic reconstructions, and the HadCM3L climate model to quantify their range shifts in the Cretaceous and late Eocene. We then use the insights provided by these models to infer their probable ecological responses to future climate scenarios at different representative concentration pathways (RCPs 4.5 and 8.5 for 2100), which project globally increased temperatures and spreading arid biomes at lower to mid-latitudes. We show that turtle ranges are predicted to expand poleward in the Northern Hemisphere, with decreased habitat suitability at lower latitudes, inverting a trend of latitudinal range contraction that has been prevalent since the Eocene. Trionychids and freshwater turtles can more easily track their niches than Testudinidae and other terrestrial groups. However, habitat destruction and fragmentation at higher latitudes will probably reduce the capability of turtles and tortoises to cope with future climate changes.

INTRODUCTION

Climate models indicate that 21st century climate change will lead to increases in global temperature that are likely to exceed 1.5°C–2°C relative to the pre-industrial era, accompanied by major changes in precipitation regimes.¹ Associated environmental change will impact the geographic distributions of organisms, resulting in range shifts, contractions, expansions, extirpations, extinctions, and fragmentations.^{2–4} Although environmental niches are dynamic and can shift over time,⁵ the rate and

magnitude of anthropogenic climate change represents a significant challenge for ecological adaptation and acclimation.^{6,7}

Ecological niche modeling (ENM), which relates species distributions to environmental variables,⁶ is used frequently to estimate geographic range changes under future climate scenarios.^{8,9} However, the recent past does not offer useful analogs for the conditions that are predicted for the next century, as current CO₂ levels are unprecedented in the last 3 million years.^{10–13} By contrast, the deep time record, which includes climates substantially warmer than those of today, can provide

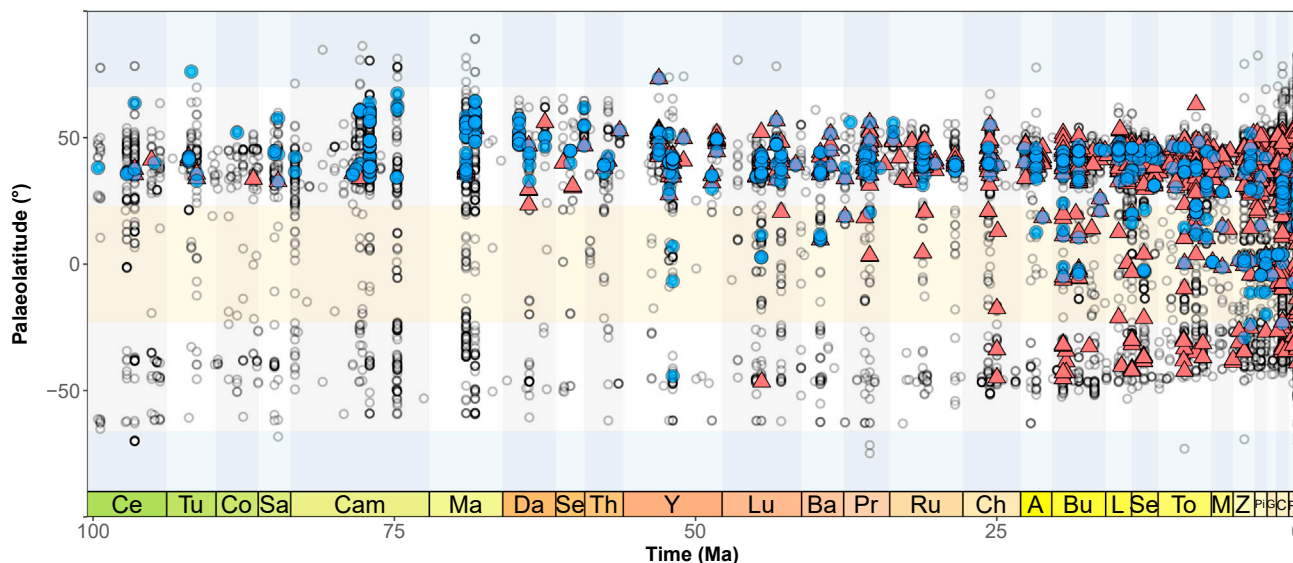


Figure 1. Paleolatitudinal distribution of non-marine turtles for the last 100 million years

Fossil occurrences in latitudinal space through time (Turonian to Recent) where blue circles represent Trionychidae and red triangles Testudinidae, whereas white circles are non-turtle tetrapod occurrences (used as a proxy of fossil sampling). Blue-shaded area represents the polar regions, and the orange-shaded area the tropical regions.

See also [Data S1](#).

valuable insights into potential future biogeographic scenarios, although acknowledging that these represent steady states rather than rapid environmental changes. Where extant taxa have closely related, ecologically analogous representatives the fossil record can be used to estimate the relative frequencies of niche stability or change through time,^{14–16} enabling better forecasts of the long-term response and resilience of clades to future environmental change.¹⁷ ENMs have rarely been applied to pre-Quaternary non-marine ecosystems but are now more frequently used by vertebrate paleontologists, having been applied to non-avian dinosaur extinction^{18,19} and biogeography,²⁰ Neogene horse diversification,²¹ paleolatitudinal range shifts in Cenozoic birds,²² and climatic niche conservation in Cretaceous turtles.²³

Sea turtles, tortoises, and terrapins (Testudinata: referred to as “turtles” collectively hereafter) are represented by ~356 extant species²⁴ and are globally distributed in freshwater, terrestrial, and marine biomes, providing key ecosystem services across wide-ranging habitat types.²⁵ As ectotherms, the tight association between their niche limits and climate is well established.^{26,27} An extensive fossil record with good biogeographic coverage^{28–30} allows a robust assessment of long-term niche responses to global environmental change.^{23,31} Approximately 41% of extant turtle species are globally threatened or endangered, and climate change—together with overexploitation and habitat fragmentation/loss—poses a significant conservation challenge.²⁴ Currently, the potential for ectotherms to adapt to the present rate of climate change remains uncertain,³² but turtle abundance, distributions, and nesting ranges are predicted to shift or contract under future climate scenarios.^{33–35} Throughout the Cenozoic, a gradual cooling³⁶ has been interpreted as a main driver of declining non-marine turtle diversity in the higher latitudes they occupied during the Late Cretaceous and

Paleogene,^{29,30} to the almost exclusively subtropical-equatorial ranges they thrive in today.³⁷ With our climate system heading toward warmer average temperatures,³⁸ the question of whether the long-established trend of equatorial migration for turtles might be inverted poses a serious threat for the conservation of these taxa, a question that can only be addressed empirically with the direct, long-term record provided by their fossil record.

Here, we use ENMs in combination with occurrences of Testudinata (the crown clade Testudines and their extinct relatives) to assess climatic niche occupation in multivariate space during three hyperthermal episodes over the last 100 million years. We focus on the Late Cretaceous–Paleogene interval (100.5–23.03 Ma), which witnessed a major transition from greenhouse to icehouse conditions and coincided with high taxon richness.^{28,30} Previous work has demonstrated a Cenozoic latitudinal range contraction (Figure 1) occurring in the last 40 million years for turtles³⁰ and that temperature is the primary factor affecting turtle distributions over geologic time, with precipitation a secondary factor in defining the paleoenvironmental niches of freshwater and terrestrial turtle ecotypes.²³ Here, we use different turtle “ecotypes” (defined as a group of organisms adapted to particular environmental conditions) and taxonomic families as proxies for the roles and taxa that they represent within an ecosystem, respectively. We focused on two extant testudinate families (Trionychidae and Testudinidae) and two ecotypes (freshwater and terrestrial), the latter representing a wider range of families, rather than identifying species-level ecological traits. These groups can be used as proxies of the species in their ecosystems and how their climate space changes through time and space, as shown previously.²³ Paleoenvironmental niches for each clade and ecotype were reconstructed for three specified time slices, based on past climate models that include combinations of seasonal precipitation

and temperature estimates. We then use these reconstructed greenhouse-world paleoniches to predict turtle ranges under 2100 emission climate scenarios (representative concentration pathway [RCP] 2.6–8.5³⁹) by estimating the future distribution of suitable habitable space. This novel application of ENM methods allows us to leverage information on the response of this widespread, long-lived clade to past environmental perturbations, demonstrating how deep time data can make a critical contribution to predicting the responses of extant taxa to anthropogenic climate change, thereby informing ongoing conservation efforts.⁴⁰

RESULTS

Modern climatic niche characterization for non-marine turtles

Our study focuses on four categories of extant turtles (Figure 2) that are also represented by rich Late Cretaceous–Eocene fossil records.²³ These include two taxonomic groups and two ecotypes. The two taxonomic categories are Trionychidae and “Testudinidae” (the latter informally including stem-testudinoids, with the first, unambiguous record of this “family-level” clade from the early Paleocene of China⁴¹), and the two ecotypes encompass taxa living in either freshwater habitats (freshwater ecotype) or on land (terrestrial ecotype: the latter including the tortoise-like Cretaceous Nanhsiungchelyidae) (for a complete list of the genera included in each category, see Data S1).

ENMs were built based on seasonal temperatures (cold/warm seasons) and precipitation (dry/wet seasons), using the HadCM3BL-M2.1aD model for paleoclimatic, modern, and future climatic layers (STAR Methods). Modern niche stability in multivariate space from modern to the Maastrichtian was tested previously.²³ We implemented the same approach extending these earlier analyses to an updated Maastrichtian record, and the Turonian–Santonian and Bartonian–Priabonian (BP) intervals (Figure 3). Our results are consistent with the findings of Waterson et al.,²³ with an absence of climatic niche invasion and support for niche stability from the past to modern time slices, with statistically significant ($p < 0.05$) niche equivalency⁴² only for Testudinidae. Ecotypes capture a higher proportion of the reconstructed multivariate climatic space, likely due to the higher number of occurrences, as more genera are included in these subgroups (Figure 3), whereas the higher proportion of niche unfilling is likely due to the low absolute number of occurrences from the turtle fossil record. Nonetheless, the lack of significant niche invasion, and the strong overlap of palaeoniches and extant niches with minimal centroid niche displacement (Figure 3), allows for backward projection of these ENMs into deep time with an ensemble approach.^{19,40,43} The number of climatically unique modern occurrences used for model calibration is 724 for Trionychidae, 1,319 for Testudinidae, 2,415 for the freshwater ecotype, and 700 for the terrestrial ecotype. The discriminatory capacity of the model was evaluated using area under the curve scores (AUC > 0.9 for all models; see STAR Methods for additional metrics used).

For trionychids, temperature of the warmest quarter is the most important variable under all three ENMs used in the ensemble, with a 65% contribution for Maxent, 40% for surface range envelope (SRE, the “bioclim” algorithm in biomod2⁴⁴), and

48% for random forest (RF), followed by temperature of the coldest quarter (39% in SRE, 33% in RF, and 32% in Maxent). Precipitation of the wettest quarter contributes 34% in SRE, 24% in RF, and 31% in Maxent, whereas precipitation of the driest quarter accounts for the remaining 11% in SRE, 11% in RF, and 29% in Maxent.

For testudinids, temperature of the coldest quarter is the most important variable, with a 51% contribution for Maxent, 41% for SRE, and 49% for RF, followed by temperature of the warmest quarter (37% in SRE, 33% in RF, and 26% in Maxent). Precipitation of the wettest quarter contributes for 26% in SRE, 24% in RF, and 14% in Maxent, whereas precipitation of the driest quarter accounts for the remaining 11% in SRE, 11% in RF, and 4% in Maxent.

For the freshwater ecotype, precipitation of the driest quarter was the most important variable, with a 64% contribution for Maxent, 60% for SRE, and 64% for RF, followed by temperature of the coldest quarter (17% in SRE, 15% in RF, and 17% in Maxent) and temperature of the warmest quarter (12% in Maxent, 13% in RF, and 15% in SRE). Precipitation of the wettest quarter contributes the remaining 8% in SRE, 9% in RF, and 7% in Maxent.

For the terrestrial ecotype, temperature of the coldest quarter is the most important variable, with a 66% contribution for Maxent, 63% for SRE, and 59% for RF, followed by temperature of the warmest quarter (24% in SRE, 20% in RF, and 21% in Maxent) and precipitation of the wettest months (9% in Maxent, 14% in RF, and 10% in SRE). Precipitation of the driest quarter contributes the remaining 3% in SRE, 7% in RF, and 3% in Maxent.

Current habitat suitability (Figure 4) is higher in areas matching with current observations of non-marine turtle clades (Figures 2 and 4M–4P), except for some Australian territories, which are suitable under both binary thresholds used, but lack empirical observations for occurrences of Trionychidae, Testudinidae, and the terrestrial ecotype (turtles are absent there due to dispersal constraints^{45,46}).

Deep time niche dynamics for Cretaceous–Paleogene turtles

In order to reconstruct testudinate paleoniches, modern climatic niches calibrated on present-day data were projected to three past time slices: the Maastrichtian (Late Cretaceous, ~72–66 mya), the combined Turonian+Coniacian+Santonian interval (TCS; Late Cretaceous, ~94–84 mya), and the late Eocene (Paleogene, ~38–34 mya). During the Late Cretaceous, no non-analog climate regions are shared between the Maastrichtian and TCS intervals (Figure S5). The Himalayan region of Asia experiences a non-analog climate between the Maastrichtian, late Eocene, and present time slices (Figure S5). Modern climates are distinctly different from those of the late Eocene in the low latitudes of South America, Africa, and the Himalaya (Figures S5 and S6). Very few testudinate fossil occurrences (<10%) fall within these non-analog regions; therefore, the influence of these on ENM projections is expected to be minimal and these regions were not excluded from our analyses.

Habitat suitability (Figure 4) for Trionychidae and the freshwater ecotype is similar in broad distributional patterns, whereas “testudinid” habitat suitability is mostly similar to that of the terrestrial ecotype, although each of these categories captures

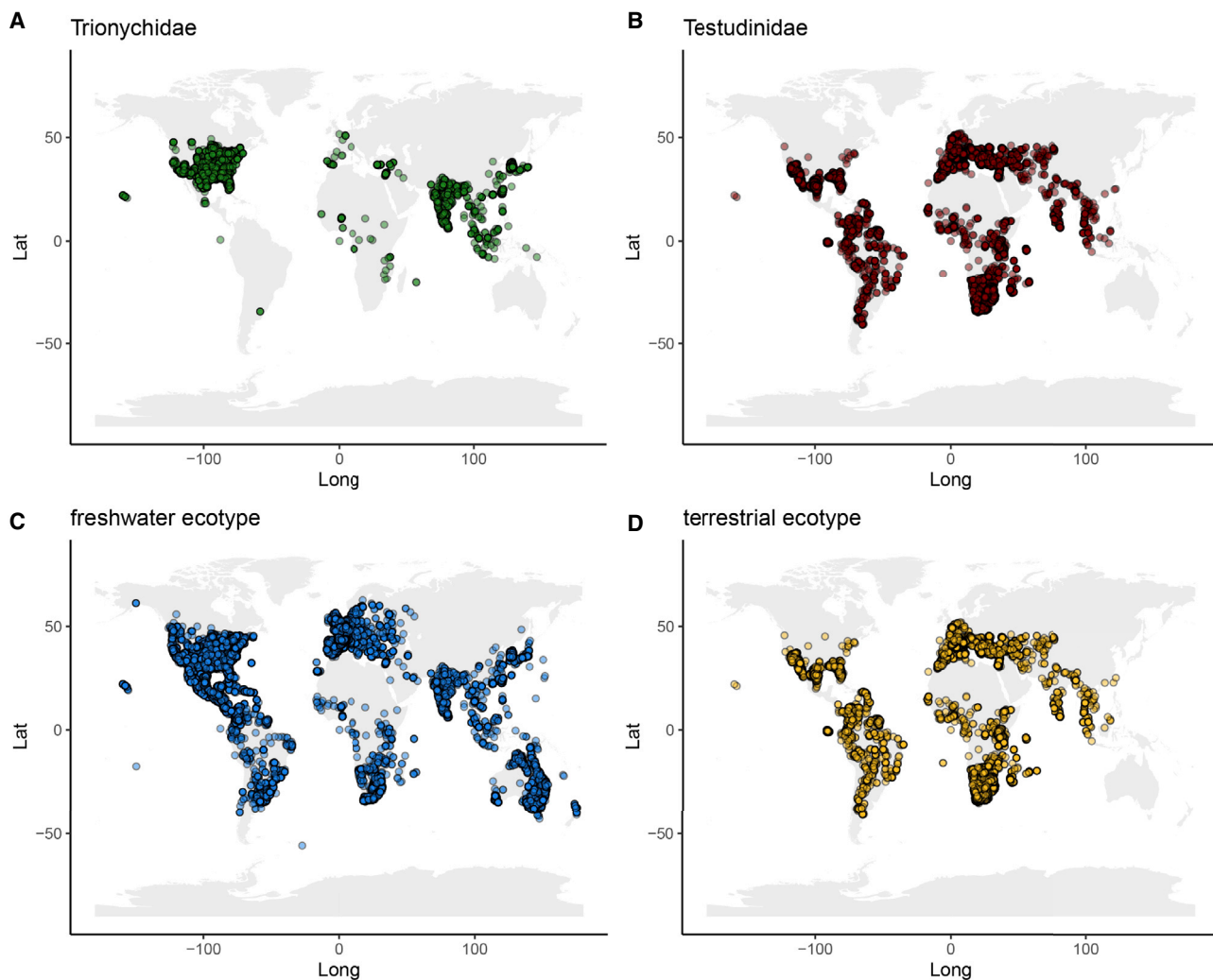


Figure 2. Modern distribution of non-marine turtles

Trionychidae are represented by green circles (A), Testudinidae by red circles (B), freshwater ecotype by blue circles (C), and terrestrial ecotype by yellow circles (D).

See also [Figures S1–S4](#) and [Data S1](#).

different taxonomic content. In the late Eocene, habitat suitability is higher for freshwater turtles ([Figures 4I](#) and [4K](#)) in the paleotemperate regions and at lower-polar latitudes in both the Northern and Southern Hemispheres, with habitable regions in southern Alaska and Antarctica. Suitable habitats for testudinids and the terrestrial ecotype ([Figures 4J](#) and [4L](#)) are present in central and southern America, southern North America, sub-Saharan Africa, south-eastern Asia, and Australia, with some habitable areas along the northern coastlines of Antarctica. In the Maastrichtian, habitat suitability is higher for trionychids and the freshwater ecotype ([Figures 4E](#) and [4G](#)) in the paleotemperate regions of Eurasia and North America, with less extensive suitable areas in central South America, Africa, and the northern half of Australia. At this time, testudinids and the freshwater ecotype ([Figures 4F](#) and [4H](#)) have more suitable areas in tropical central America and Africa and south-eastern Asia, with suitable areas in southern Africa, South America, Australia, and northeastern

Antarctica also. The mid-Cretaceous TCS shows the broadest distribution of peak habitat suitability for trionychids and freshwater turtles in the northern paleotemperate regions of North America and Eurasia; the equatorial regions of Africa and South America; southern paleotemperate regions in India, Australia, Africa, and South America; and polar areas in Antarctica, Canada, and Alaska. By contrast, during this mid-Cretaceous interval testudinids and the terrestrial ecotype show more localized suitable areas in northern-central North America and Europe, central America, and along the coastlines of southern South America, Africa, Australia, and Antarctica.

Binomial tests ([Table 1](#)) show that ENMs were significantly better at predicting fossil occurrences than random expectations ($p < 0.05$), except for Cretaceous testudinid (Maastrichtian and TCS intervals), terrestrial ecotype (TCS, maximizing the sum of sensitivity and specificity [MaxSSS] threshold), and late Eocene categories. Trionychids and freshwater turtles show a high

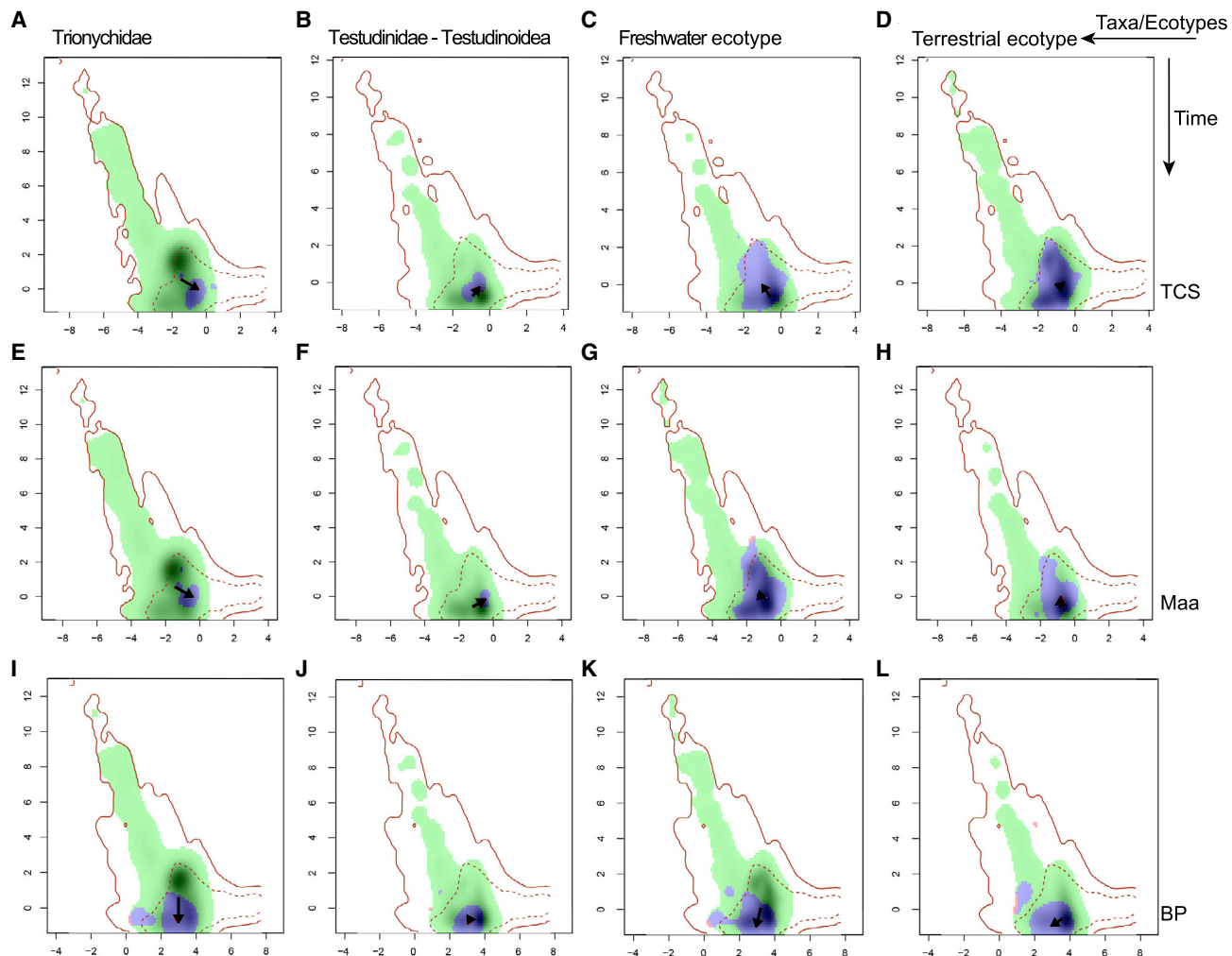


Figure 3. Evolution of non-marine turtles' niche in multivariate space

Figure showing the occupancy of modern species (gray, shaded gradient) and environmental availability in the study area (the solid red line shows 100% of available climates and dashed line shows 50% most frequent available environmental conditions). Green color indicates the unfilled potential niche (modern group), blue colors the stable niche (common between modern and past niches), and red pixels the expansion of the niche. Black arrows for the direction of niche displacement. (A–D) TCS, Turonian-Coniacian-Santonian (“mid” Cretaceous); (E–H) Maa, Maastrichtian (“latest” Cretaceous); (I–L) BP, Bartonian-Priabonian (late Eocene).

See also [Figures S5 and S6](#) and [Data S1](#).

success rate for predicting fossil occurrences from ENMs (>70%) for TCS and late Eocene intervals under both thresholds. Freshwater turtles show a high success rate (94.1%) for the Maastrichtian only under the least training presence (LTP) threshold, whereas it is lower with the MaxSSS threshold (46.6%). Our results suggest greater niche stability between the modern and TCS and late Eocene for the freshwater ecotype, compared with the Maastrichtian, whereas broad inferences based on testudinids can only be drawn from comparison with their late Eocene climatic space.

Turtle environmental niches under future climate scenarios

ENM future projections show regional differences in the relative increase and decrease of climatically suitable habitat under the RCP 4.5 (~2.5°C global warming level) and RCP 8.5 (~4.5°C

global warming level) scenarios at 2100 ([Figures 4Q–4X](#)). Trionychids modeled under RCP 4.5 ([Figure 4Q](#)) show expansion of suitable habitat in northern Europe, and warmer temperatures facilitated northward expansion of suitable habitat in central and western parts of North America. Conversely, warmer and drier climates in southern Europe are expected to result in a future loss of environmental suitability for this freshwater family ([Figure 4Q](#)). The higher warming RCP 8.5 scenario ([Figure 4U](#)) drives a northward expansion in North America, Europe, and central Asia, whereas causing habitat loss in central Africa, South America, and southern India.

Testudinid-modeled RCP 4.5 ([Figure 4R](#)) shows minimal expansion of suitable habitats in northern Europe but that warmer and drier climates are expected to cause worldwide habitat loss, with particularly strong habitat reduction and fragmentation in South

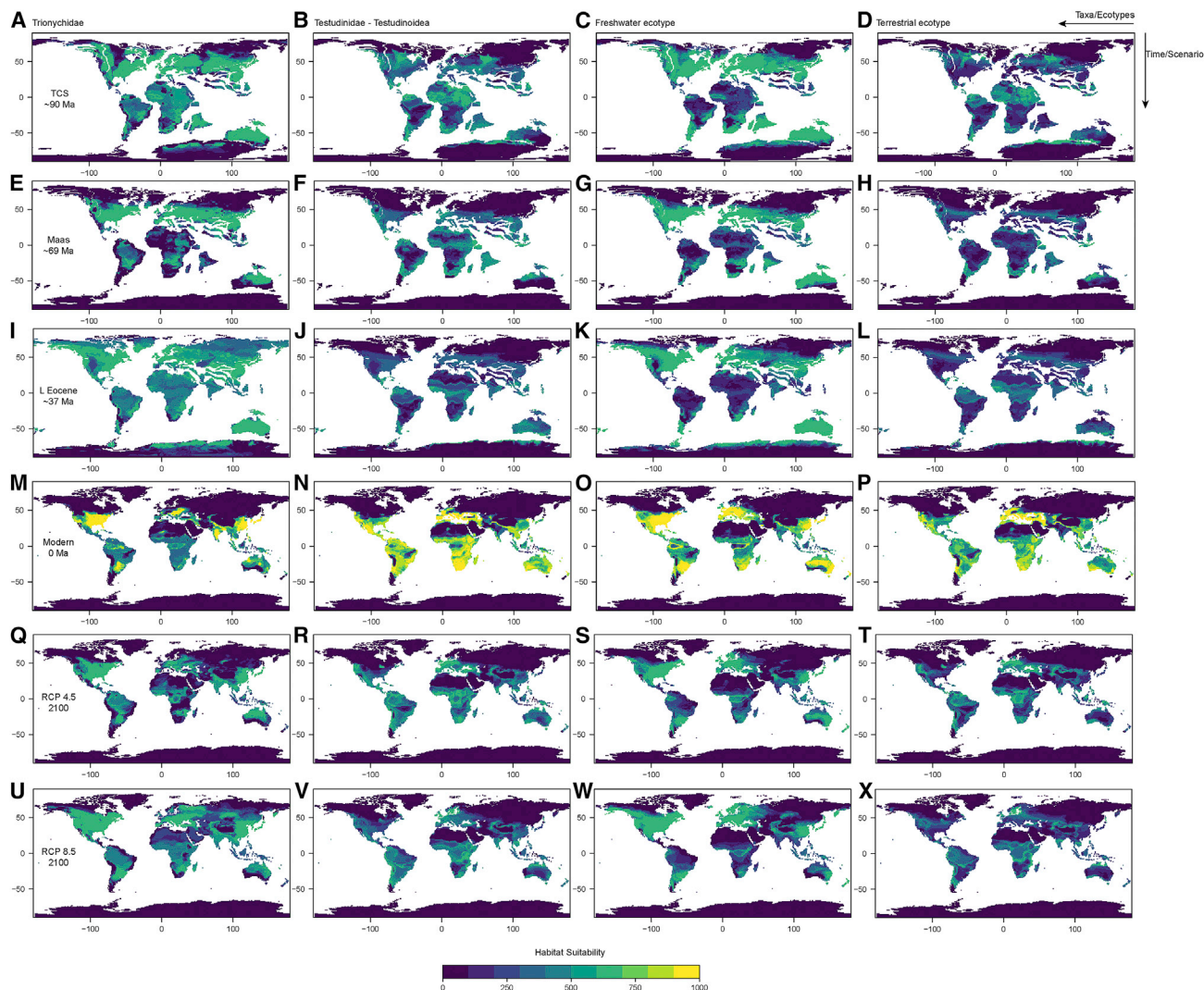


Figure 4. Ensemble ecological niche models projected globally for the four groups of non-marine turtles investigated in this study

Dark blue color (viridis scale) represents low level of habitat suitability (0), whereas yellow color represents high habitat suitability (1,000). Ecological niche models are trained on the present record and modern GCMs control (M–P) and are then projected to past (A–L) and future (Q–X).

See also [Figures S5](#) and [S6](#) and [Data S1](#).

America, Africa, southeast Asia, and Australia, which becomes more severe under RCP 8.5 (Figure 4V). Under an RCP 4.5 scenario, freshwater turtles (Figure 4O) gain suitable habitats in northwestern and northeastern North America and Europe, with some habitat loss in southwestern North America and west-central Asia. Important reduction in suitable habitats occurs in the southern continents (South America, Africa, and Australia), which in response to RCP 8.5 only preserve suitable areas in the southern-most regions of these landmasses.

Compared with its modern distribution, the terrestrial ecotype RCP 4.5 projections (Figure 4T) show northward range expansion throughout North America and in northern Europe, but aridification of the tropical bands leads to substantial habitat loss in central America, most of Africa, south-eastern Asia, and most of Australia, and suitable habitats remain only at latitudinally extreme locations (e.g., northern Europe, southern-most

Australia, and South America) under a more extreme RCP 8.5 scenario (Figure 4X).

Climatically driven latitudinal shift in non-marine turtles

In today's world, climatically habitable areas for non-marine Testudinata range between 0° and 66° latitude in both hemispheres (Figure 5). A modern habitat suitability gradient for trionychids (Figure 5A) peaks in the equatorial band (~4°) with comparably high suitable areas at 40° N and 25° S. Minor habitable suitable areas beyond the 50° in both hemispheres are present above 58° N and 65° S. Centroids of habitat suitability are located at 25° N and 20° S. During the late Eocene, habitat suitability for trionychids was greater at higher latitudes and decreased at the equator (centroids of habitat suitability at 42° N and 40° S) and extended up to the polar latitudes, reaching absolute peaks across 50° in both hemispheres, with high peaks of suitable

Table 1. Results of binomial tests between predicted and real fossil occurrences

Group	TCS (MaxSSS)	TCS (LTP)	Maa (MaxSSS)	Maa (LTP)	BP (MaxSSS)	BP (LTP)
Trionychidae	88.6 ^a	88.6 ^a	46.2 ^a	52.1 ^a	88.7 ^a	96.2 ^a
Testudinidae (<i>sensu lato</i>)	16.7 (n.s.)	41.7 (n.s.)	–	–	–	37.8 ^a
Freshwater	94.5 ^a	96.3 ^a	46.6 ^a	94.1 ^a	70 ^a	77.6 ^a
Terrestrial	16 (n.s.)	38 ^a	5.9 ^a	25.2 ^a	–	3.1 (n.s.)

^aStatistically significant ($p < 0.05$)

habitats up to 75° N and 70° S. In the Maastrichtian, habitable areas are available from pole to pole, with absolute peaks of habitat suitability located at 46° N and 48° S and centroids at 38° N and 30° S. Polar habitat suitability is present up to 74° N and 70° S during this time interval. In the TCS, peaks of habitat suitability are reached at 50° N and 60° S, with centroids at 35° in both hemispheres and a substantial amount of suitable habitat at polar latitudes. Future projections show a dynamic increase in the latitudinal range, which is particularly substantial in the Northern Hemisphere, with an increase of the centroid to 45° N and the presence of substantial habitable area between 60° N and 75° N. Future climate warming will lead to an increase in climatically suitable habitats for testudinid turtles particularly in the Northern Hemisphere. Niche changes in response to RCP 8.5 shows a peak at 60° N and a Southern Hemisphere peak at 24° S. Suitable habitats are present at high latitudes up to 80° N and 67° S, with centroids shifting up to 45° N and 23° S.

Modern testudinids (Figure 5B) show higher habitat suitability around the equatorial band and the Southern Hemisphere, with peaks at 6° N and 30° S, and centroids at 20° N and 25° S. In the late Eocene, testudinid habitat suitability extends to the poles, with a peak at 61° S and centroids shifting to 28° N and 40° S. In the Maastrichtian, habitat suitability for the terrestrial ecotype is higher in the paleotemperate band and across the equator, with suitable habitats up to 70° N and centroids shifting slightly from the modern at 27° in both hemispheres. During the TCS interval, habitat suitability is higher across the equatorial band but extends to the poles with substantial suitable habitats up to 70° in both hemispheres and with centroids at ~31° in both hemispheres. Future climate change scenarios imply an extension in latitudinal range, with suitability peaks in response to high warming at 11° N, 40° N, and 41° S, centroids at 35° N and 28° S, and suitable polar habitats in the Northern Hemisphere up to 80° N and 70° S.

Modern freshwater turtles peak (Figure 5C) in habitat suitability at 30° S with centroids at 24° N and 28° S, stretching latitudinally between 66° N and 68° S. During the late Eocene, climatic suitability extends into polar latitudes at 55° N and 69° S and decrease around the equator, with centroids shifting up to 43° N and 46° S and highly suitable habitat up to 75° in both hemispheres and then declining gently poleward. In the Maastrichtian, habitat suitability peaks for freshwater turtles are reached at 42° N and 47° S, decreasing around the equator with centroids shifting at 34° N and 38° S. Suitable habitats are present up to 77° N and 71° S. During the TCS interval, suitability peaks are at 47° N and 58° S, with centroids at 39° N and 40° S and suitable habitats up to 83° N and 85° S. Future warming will lead to an increase in climatically suitable habitats for freshwater turtles,

particularly in the Northern Hemisphere, with a peak at 61° in the Northern Hemisphere and an absolute peak at 44° S. Centroids shift up to 39° N and 32° S.

Modern climatic suitability for the terrestrial ecotype (Figure 4D) is higher around the equator and in the Southern Hemisphere at 36°, with centroids at 25° N and 22° S. In the late Eocene habitability extends to the poles, with an absolute peak at 69° S, high suitability at 60° N, and centroids shifting up to 25° N and 47° S. In the Maastrichtian habitat, suitability is highest at 41° N and centroids at 28° N and 32° S. In the TCS interval, habitat suitability is highest around the equator, with centroids at 32° N and 36° S, but high peaks of suitability are present between 73° N and 59° N and at 68° S. In the future, the climatic suitability gradient is projected to flatten around the equator and increase at polar latitudes, particularly in the Northern Hemisphere, where for RCP 8.5, suitable habitats are present up to 75°, with centroids at 28° in both hemispheres.

DISCUSSION

Environmental-driven niche shifts in response to a cooling world

A latitudinal shift toward the equator occurred in the distribution of non-marine turtles during the last 100 million years, likely due to declining temperature during the transition from a greenhouse to an icehouse world.^{28,30,47} Significant differences in habitat suitability occur between North America and Asia in the Late Cretaceous: these might explain differences in assemblage composition,⁴⁸ which have been attributed to a combination of complex geography, changing climatic conditions and their implications for clade dispersal.⁴⁹ The transition from high temperatures in the Cretaceous to a cooler, drier late Eocene climate coincides with major shifts in freshwater and terrestrial turtle niche limits (Figures 4 and 5). Environmental change during the late Eocene triggered the appearance of biomes with lower diversity and more open structures^{50–52} in contrast to the Late Cretaceous temperate forests that dominated northern mid-latitudes.^{53,54} By the late Eocene, turtles occupied a greater variety of biomes, including grasslands, dry shrubland, savanna, and tropical forest. Although some taxa shifted their ranges to track suitable environmental space, others adapted to changing climate conditions and exploited novel habitats over a greater latitudinal range (Figures 4 and 5). Better ENM predictivity from the modern to the late Eocene for the terrestrial ecotype (Figures 3J, 3L, 4J, and 4L) suggests that present-day environmental tolerances are closer to those of the late Eocene. This is consistent with evidence that this interval coincided with the initial diversification of testudinids (i.e., tortoises⁵⁵); high genus

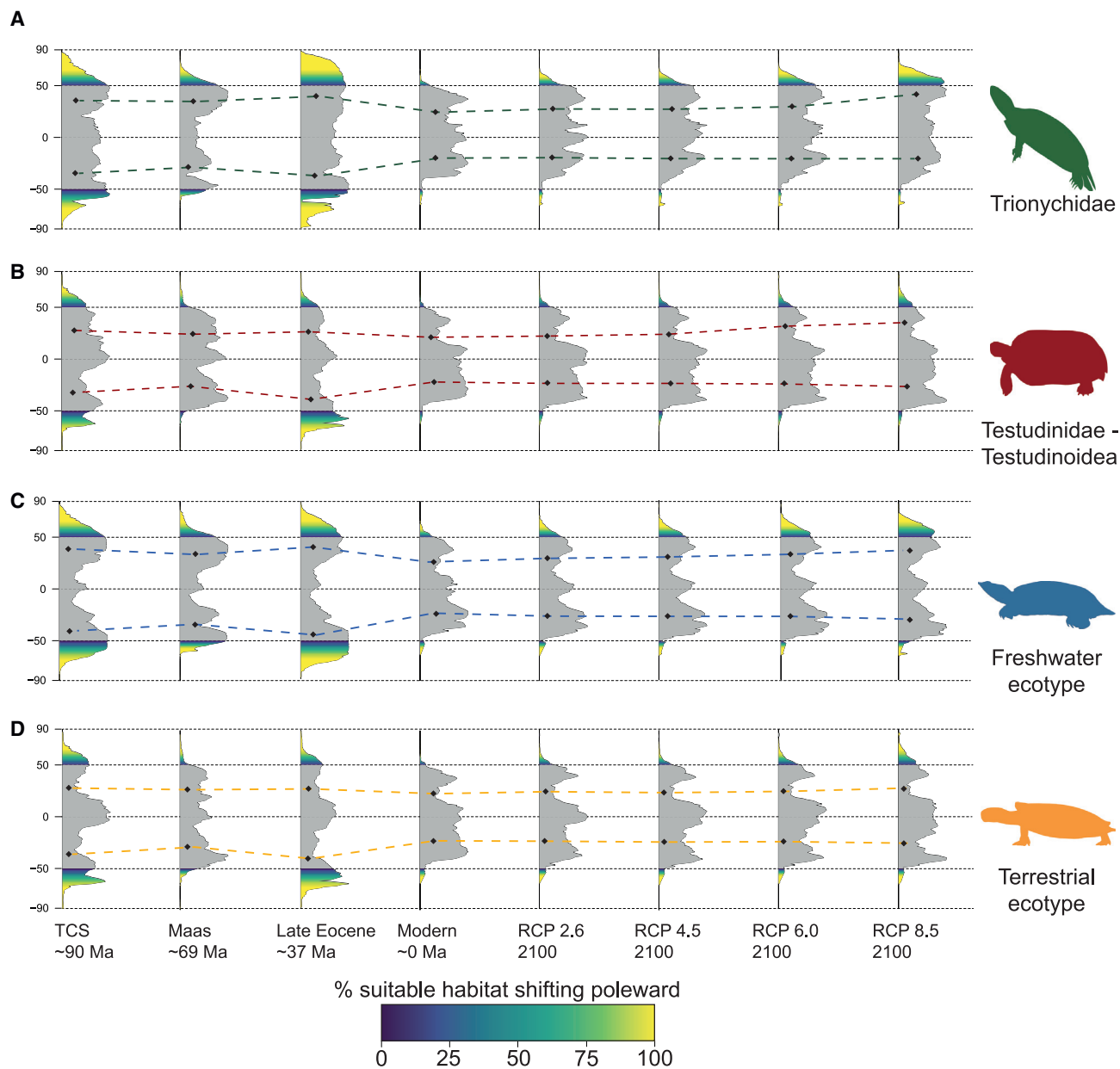


Figure 5. Latitudinal climatically suitable gradient for non-marine turtles

Paleolatitudinal range dynamics in available climatic niche space is symbolized by centroids (black diamonds); dashed lines represent the paleolatitudinal fluctuations for the four groups investigated in this study (A, Trionychidae, green; B, Testudinidae, red; C, blue, freshwater ecotype, blue; D, terrestrial ecotype, yellow). Amount of suitable habitat beyond 50° is highlighted with a viridis legend (values transformed in percentages from outputs shown in Figure 4). See also Figures S5 and S6 and Data S1.

richness in North America, Asia, and Europe;³⁰ and the occupation of novel environmental space by the clade (Testudinidae).²³ The presence of ectothermic reptiles, including turtles, in high latitude vertebrate assemblages coincides with the warmest periods of the Paleogene,^{30,56–58} highlighting that species can migrate in response to climatic change if given sufficient time and adequate dispersal corridors.

The latitudinal distribution we see in the modern, with an equatorially rich community of non-marine turtles, might have started in the latter part of the Eocene, being affected by the onset of

polar glaciation and subsequent climate change during the Oligocene.⁵⁹ Decreases in aquatic amphibian and reptile diversity occurred at the Eocene-Oligocene (E/O) boundary (33.9 Ma), including the extinction of the last stem cryptodiran lineages,⁶⁰ with varying changes in richness among turtles in different geographic regions³⁰ and sharp declines in non-marine crocodylian biodiversity at temperate paleolatitudes.⁴⁷ Losses in turtle species richness have been ascribed to increased aridity and reduction in the extent of permanent water bodies in North American biomes^{30,60,61} and occurred together with decreases

in terrestrial squamate diversity in North America and Europe, which might be attributed to lower temperatures.⁶² Changes in precipitation regimes and seasonality,⁶³ as well as major orographic events during the Paleogene (e.g., regional uplift and closure of the Western Interior Seaway in North America), likely led to shifts in the distribution of water bodies on land. Our results confirm quantitatively that in the absence of habitat fragmentation or direct human impacts, environmental variables exert the largest impact on extant non-marine turtle distributions.³⁷

Clade-level patterns of niche change

Estimation of paleodistributions for trionychids suggest some stability in their temperature and precipitation limits in comparison with their extant relatives (Figures 3 and 4), with higher overlap between the present and the late Eocene, as did previous analyses comparing the family's present-day niche limits with those of the Maastrichtian.²³ Testudinids show stability in their climate limits back to the late Eocene (Figure 3), but since Cretaceous testudinoids (including Lindholmemydidae and Emydidae, which are considered mostly freshwater taxa) likely had more different ecologies and broader climate limits than modern-day testudinids (which are primarily terrestrial; Figure 1), the overlap between the modern and TCS/Maastrichtian testudinid niches is more limited than with late Eocene ones. Trionychid ancestral distribution estimates show some stability in the environmental niche occupied between the present and Maastrichtian²³ (Figures 4B, 4F, 4J, and 4N). Trionychia is an early-diverging cryptodire lineage (originating >145 Ma) and Trionychidae originated in the late Albian⁶⁴ (~113.0–100.5 Ma).⁶⁴ Therefore, its distribution had expanded to occupy a significant climatic range by the Late Cretaceous. The importance of the temperature of the warmest season and the precipitation of the driest season in ENM fits for the trionychid and freshwater ecotypes suggest that warm and arid conditions have a strong influence on the distributions of these taxa, with the possibility of freshwater taxa occupying environments with warmer temperatures relative to the present day, but with rainfall an important limiting factor (likely for thermoregulatory reasons). This interpretation is consistent with the thermoregulatory behavioral adaptations of these taxa, including the use of water by freshwater turtles to buffer higher temperatures.^{26,65} By contrast, testudinids and fossil terrestrial ecotypes are more strongly constrained by the temperature of the coldest quarter, showing the stronger thermophysiological constraints exerted on these primarily terrestrial groups of ectotherms.^{66,67}

Poorer modeling performance between paleodistribution estimates for the terrestrial ecotype (testudinoids and the tortoise-like nanhsiungchelyids) may indicate niche shifts during the Late Cretaceous and after the Miocene⁶⁸ or due to the phylogenetic distance of stem-testudinoids from the crown group (Testudinidae), confirming previous suggestions that some extinct terrestrial turtles (Nanhsiungchelyidae) had higher temperature tolerances than extant testudinids.²³ Stem-testudinoids originated in Asia and modern terrestrial testudinoids (including Testudinidae) diversified after the Cretaceous-Paleogene (K/Pg) boundary (~66.0 Ma), during pronounced Paleogene warm periods (Paleogene hyperthermals and the early Eocene Climatic Optimum)⁵⁷ and likely underwent long-

range dispersal during the Paleocene or early Eocene via northern land masses.^{69,70}

Turtle ENM projections indicate some niche stability with minimal or absent niche invasion between the Late Cretaceous, late Eocene, and the Recent (Figure 3). Our findings corroborate the idea that clades stay close to their ancestral environmental niche, but as novel conditions arise during evolutionary history, the appearance of new available conditions (giving clades access to new areas of environmental space) can drive adaptation in some lineages.⁷¹ Moreover, the extant testudinid distributions used to reconstruct paleoniches are weighted by species that diversified in, and continue to occupy, arid environments. Terrestrial tortoises representing deeper nodes in the phylogeny occurred in wetter environments during the Eocene and today; thus, the mismatch between testudinid fossils and ancestral estimates is expected, as the late Eocene captures a time of diversification within Testudinidae and the broader terrestrial ecotype, as well as differences in habitat occupation between Eocene and recent taxa.

Paleobiological implications for the conservation of non-marine turtle habitats

In response to the most extreme RCP 8.5 emission scenario, global surface temperature change is projected to exceed 4°C (relative to 1850–1900) by the end of the century (2081–2100).² ENM future predictions (RCP 4.5–8.5) suggest poleward shifts of climatically suitable areas for all turtle groups in the Northern Hemisphere in response to global warming (Figure 4). The above average warming of higher latitudes may therefore lead to poleward range expansion for turtles in the Northern Hemisphere and some regional range contractions as a result of changing precipitation and temperature regimes (Figure 5). Range expansions toward higher latitudes, particularly in northeastern North America, are largely consistent with ENM projections to 2,080 climate scenarios for freshwater and terrestrial turtles at the species level.³³

Reptile species occupying current high temperature regions have been identified to be at high extinction risk in response to future temperature increases⁷² with Warren et al.⁷³ estimating that 14% of taxa will experience a 50% niche loss at 4°C of temperature rise and 52% at 4.5°C. Our results show that while range expansion for the terrestrial ecotype is predicted in northern Europe (Figure 4), range contractions are predicted in central Africa, south-eastern Europe, and northern and southern parts of South America as these regions become warmer and drier (Figure 4).

Although warmer temperatures may make higher latitudes more suitable for testudinid and terrestrial turtles, similar to the conditions found during the Cretaceous-Paleogene, this reconfiguration may eradicate completely their suitable habitats at lower latitudes⁶⁷ (Figure 4), due to more constrained climatic adaptability and the limited ability to buffer warmer temperatures in terrestrial turtles. Conversely, range contraction is predicted for the freshwater ecotype in central Asia and southern Africa (Figure 4), reflecting shifts in temperature and precipitation regimes. On the other hand, the wider niche space occupied by the freshwater ecotype (Figure 3), possibly related to its presence in fluvio-lacustrine biotopes (with higher thermal inertia), may lessen the impact of this contraction across the lower latitude areas of its total range. However, it is important to note that future precipitation projections are much less certain than temperature projections⁷⁴

and indicate changes in the timing and amount of precipitation.³⁸ Importantly, for these groups, the global water cycle is expected to show non-uniform changes in response to further warming and the contrasts between wet and dry regions and seasons are predicted to increase, whereas at the same time, more water will be needed for human adaptation (for energy and crop production). Freshwater taxa will likely be most vulnerable in mid-latitude and subtropical dry regions, which are forecast to experience further decreases in precipitation by 2100^{1,38} and might suffer substantial reductions in species richness and geographic range as a result. These areas (e.g., the south-eastern USA and south-east Asia) are areas of high modern turtle richness; hence, the effects on overall clade diversity will be severe. Moreover, our data do not consider other human impacts on turtle vulnerability to climate change, such as increases in habitat destruction, land use change, and water pollution, which are also key drivers in the loss and degradation of ecosystems.¹

Over the course of their extensive evolutionary history, turtles have successfully endured two mass extinction events and significant episodes of global environmental change, including both global greenhouse and icehouse conditions.^{28–30} However, the ability of this geographically widespread and ecologically varied vertebrate clade to adapt to geologically unprecedented rates of climate change or to track suitable environmental conditions at adequate speed is unknown. The work presented here demonstrates that the most vulnerable taxa currently occupy areas that will experience increases in both temperature and aridity over the coming century. The combination of habitat fragmentation and loss, high density human populations in temperate latitudes that exert strong dispersal constraints and shifting temperature and precipitation patterns will further exacerbate the risks to vulnerable species as migration to more suitable climate spaces will be more challenging for this clade than in the geological past. A combination of historical baseline data and a greater understanding of turtle adaptation rates under rapid warming scenarios will be essential for informing conservation practice over the coming century.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2022.11.056>.

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AUTHOR CONTRIBUTIONS

P.M.B., D.N.S., and P.J.V. conceived the study, which was expanded and updated by A.A.C. P.J.V., D.B.N., P.A.H., and M.E.C. contributed data. A.A.C., A.M.W., P.A.H., D.N.S., P.J.V., C.Y., and S.V. analyzed the data. A.A.C., P.M.B., A.M.W., D.N.S., and P.A.H. wrote the first draft of the manuscript and interpreted the data, with further contributions from all other authors. All authors helped in the editing of the final manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

We support inclusive, diverse, and equitable conduct of research.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Climate variables used in ENM and ordination analyses	http://www.bridge.bris.ac.uk/resources/simulations	Chiarenza et al. ²⁰
Software and algorithms		
R script for ENM analyses	https://github.com/AlfioAlessandroChiarenza/100-million-years-of-turtle-palaeoniche-dynamics-future-climate-change.git	N/A
R package mapast V 0.1	https://rdr.io/github/macroecology/paleoMap/man/mapast-R-package.html	N/A
R package ggplot2 V 3.3.5	https://cran.r-project.org/web/packages/ggplot2/index.html	N/A
R package raster V 3.5-2	https://cran.r-project.org/web/packages/raster/index.html	N/A
R package biomod2 V 3.5.1	https://cran.r-project.org/web/packages/biomod2/index.html	N/A
R package ecospat V 3.3	https://cran.r-project.org/web/packages/ecospat/index.html	N/A
R package chronosphere V 0.4.1	https://cran.r-project.org/web/packages/chronosphere/index.html	N/A
R package rgbif V 3.7.2	https://cran.r-project.org/web/packages/rgbif/index.html	N/A

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Paul Barrett (p.barrett@nhm.ac.uk).

Materials availability

This study did not generate new unique materials.

Data and code availability

Climate variables used in ENM and ordination analyses for the modern and paleo- time intervals are available at: <http://www.bridge.bris.ac.uk/resources/simulations>. Paleogeography of the Maastrichtian, TCS and late Eocene continental configurations is based on the PALEOMAP plate rotation model¹⁰³ and are accessible via the R package macroecology/mapast.¹⁰⁴ Maastrichtian, TCS and late Eocene turtle paleorotations are based on rotation of recent present-day fossil bearing occurrences using the chronosphere¹⁰⁵ R package. All turtle occurrence data are available as Supplementary files at [Data S1](#).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Testudinate occurrence data

Modern testudinate occurrence data were taken from the Global Biodiversity Information Facility website (GBIF). Data were accessed via the R package rgbif,⁷⁵ using the entries for Testudinata, Trionychidae, and Testudinidae.⁷⁶ Genera in each family-level clade^{77,78} and ecotype categories were vetted and included according to information in The Reptile Database (reptile-database-reptarium.cz) and cross-checked with the World Turtle Database.²⁴ The occurrences were filtered for the “families”, genera (see [Figures S1–S4](#)), decimal longitude, and decimal latitude ([Data S1](#)), removing entries of fossil specimens and “preserved specimens”, to avoid mixing modern and past occurrences in the “modern training dataset”. Fossil occurrence data were downloaded from the Paleobiology Database (PBDB; <https://paleobiodb.org/#/>), using Trionychidae for the Turonian-Coniacian-Santonian (TCS) interval, Maastrichtian, and Bartonian–Priabonian (late Eocene) intervals. Fossil Testudinidae were downloaded for the Bartonian–Priabonian, while as a surrogate for this clade in the Cretaceous, the Testudinoidea entry (including testuninoids like Lindholmemydidae and

Emydidae) was used for the TCS and Maastrichtian interval. For the terrestrial ecotype, the tortoise-like Cretaceous Nanhsiungchelyidae were included. Entries assigned to freshwater, marine coastal, and brackish were excluded, while for the freshwater ecotype, terrestrial, marine, and coastal entries were excluded. The occurrence dataset in modern-day coordinates is available as [Data S1](#). A detailed description of the fossil data, and consideration of sampling and preservational biases, can be found in Waterson et al.²³ Modern and fossil occurrence records were geographically filtered in order to reduce occurrences to one per climate grid cell (corresponding to 18.5 x 18.5 km² at the equator) and to remove spatially autocorrelated data.⁷⁹ Genera included in each clade-level or ecotype categories were:

For Trionychidae ([Figure S1](#)), *Apalone*, *Amyda*, *Lissemys*, *Cycloderma*, *Pelodiscus*, *Rafetus*, *Trionyx*, *Palea*, *Nilssonina*, *Dogania*, *Cyclanorbis*, *Chitra*, *Pelochelys*; for Testudinidae ([Figure S2](#)), *Gopherus*, *Chersina*, *Stigmochelys*, *Kinixys*, *Chelonoidis*, *Homopus*, *Testudo*, *Psammobates*, *Indotestudo*, *Centrochelys*, *Chersobius*, *Geochelone*, *Manouria*, *Aldabrachelys*, *Pyxis*, *Malacochersus*, *Astrochelys*; for freshwater ecotype ([Figure S3](#)), *Carettochelys*, *Chelydra*, *Macrochelys*, *Dermatemys*, *Mauremys*, *Batagur*, *Callagur*, *Chinemys*, *Cistoclemmys*, *Cuora*, *Cyclemys*, *Geoclemys*, *Geoemyda*, *Hardella*, *Heosemys*, *Hieremys*, *Kachuga*, *Malayemys*, *Melanochelys*, *Morenia*, *Notochelys*, *Ocadia*, *Orlitia*, *Pyxidea*, *Rhinoclemmys*, *Sacalia*, *Siebenrockiella*, *Chrysemys*, *Clemmys*, *Deirochelys*, *Emydoidea*, *Emys*, *Graptemys*, *Malaclemys*, *Pseudemys*, *Terrapene*, *Trachemys*, *Kinosternon*, *Sternotherus*, *Claudius*, *Staurotypus*, *Platysternon*, *Cyclanorbis*, *Cycloderma*, *Lissemys*, *Chitra*, *Pelochelys*, *Amyda*, *Rafetus*, *Apalone*, *Nilssonina*, *Aspideretes*, *Pelodiscus*, *Palea*, *Dogania*, *Trionyx*, *Acanthochelys*, *Chelodina*, *Chelus*, *Elseya*, *Emydura*, *Hydromedusa*, *Phrynops*, *Platemys*, *Rheodytes*, *Pseudemys*, *Pelomedusa*, *Pelusios*, *Leucocephalon*, *Elusor*; for the terrestrial ecotype ([Figure S4](#)), *Geochelone*, *Indotestudo*, *Kinixys*, *Manouria*, *Pyxis*, *Testudo*, *Gopherus*, *Chersina*, *Stigmochelys*, *Chelonoidis*, *Homopus*, *Psammobates*, *Centrochelys*, *Chersobius*, *Aldabrachelys*, *Malacochersus*, *Astrochelys*. Turtle occurrences are available in csv format as [Data S1](#), with each tab in the spreadsheet containing specific taxonomic and temporal occurrences for non-marine turtles and binned as follows: modern Trionychidae ([Data S1A](#)); modern Testudinidae ([Data S1B](#)); modern freshwater ecotype ([Data S1C](#)); modern terrestrial ecotype ([Data S1D](#)); TCS Trionychidae ([Data S1E](#)); Maa Trionychidae ([Data S1F](#)); BP Trionychidae ([Data S1G](#)); TCS Testudinoidea ([Data S1H](#)); Maa Testudinoidea ([Data S1I](#)); BP Testudinoidea ([Data S1J](#)); TCS freshwater ecotype ([Data S1K](#)); Maa freshwater ecotype ([Data S1L](#)); BP freshwater ecotype ([Data S1M](#)); TCS terrestrial ecotype ([Data S1N](#)); Maa terrestrial ecotype ([Data S1O](#)); BP terrestrial ecotype ([Data S1P](#)).

Climate data

Modern climate variables were derived from versions of the UK Met Office (UKMO) Unified Model HadCM3; a fully coupled Atmosphere-Ocean General Circulation Model (AOGCM),^{80–82} Paleoenvironmental variables were calculated for three time slices from the Late Cretaceous–Paleogene interval: the Maastrichtian (Late Cretaceous, 72.1–66.0 mya), the combined Turonian+Coniacian+Santonian (TCS: Late Cretaceous; 93.9–83.6 mya), and the Bartonian–Priabonian (Paleogene, late Eocene; 41.3–33.9 mya). TCS, Maastrichtian, and late Eocene climate variables were derived from the UKMO Unified Model HadCM3L, specifically HadCM3BL-M2.1aD, which is identical to HadCM3 with the exception of lower spatial resolution in the ocean component.⁸³ Details of AOGCM boundary conditions for these time slices can be found in Lunt et al.⁸¹ and Farnsworth et al.⁸⁴ For a detailed description of the climate model resolution and processing of GCM output for niche analyses see Waterson et al.²³ Climate variables used for the 2100 scenario are based on different emission scenarios (RCP 2.6, 4.5, 6.0) up to the high-end representative concentration pathway (RCP) 8.5; one of a range of socio-economic scenarios for future climate modelling projections³⁹ used extensively in IPCC AR5.² The vegetation gross primary productivity estimates were derived from the TRIFFID vegetation module, which is part of the Hadley Centre model,⁸⁵ a coupled biogeography and biogeochemistry model that simulates the equilibrium distribution of 28 major natural biome types.⁸⁶ As a vegetational feedback system for this climate model, past vegetational patterns were produced using the vegetation model BIOME4; comparisons with paleobotanical proxy data for the relevant time slices were used to qualitatively validate BIOME4 reconstructions. A detailed description of BIOME4 and the model-data comparison and is provided in the [supplemental information](#). Further details on deep-time applications of this methodology for paleontological and paleobiogeographical studies can be found in Chiarenza et al.^{18–20,87} for the Mesozoic stages, and Waterson et al.²³ and Saupe et al.²² for the Cenozoic epochs. The predictive variables used in niche analyses were chosen to reflect the environmental factors that have been shown to be ecologically limiting to modern turtle distributions.^{26,33} We also selected variables that can be estimated using proxy evidence in the fossil record and AOGCM output. To reduce collinearity between considered variables, we retained combinations with a Pearson's pairwise correlation coefficient <|0.7| only. Based on these constraints, four variables were used in the final ENM analyses: mean temperature of the coldest and warmest quarters, mean precipitation of the wettest and driest quarters.^{20,22} The temperature and precipitation variables only (mean temperature of the coldest and warmest quarters, precipitation of the wettest and driest quarters) were also used for future ENM projections.

METHOD DETAILS

Ecological niche modelling

We ran Ecological Niche Models (ENM) for modern Trionychidae and Testudinidae, and for freshwater and terrestrial non-marine turtle ecotypes. We calibrated our models using their modern global distributions, and projected them into past and future climate scenarios, assuming niche conservatism.⁸⁸ For ENM analyses, an ensemble approach⁴³ was used. These analyses were run in R version 4.1.3 (R Core Team 2022) with the biomod2 package⁴⁴ for Ensemble modelling, using MaxEnt (maximum entropy algorithm^{89,90}), SRE (Surface Range Envelope, the 'Bioclim' algorithm in biomod2⁴⁴) and RF (Random Forest⁹¹); expanded discussion on ENM

can be found in Chiarenza et al.¹⁹ and the script with model settings for specific ENM algorithms and the ensemble modelling can be accessed as supplementary data. Model evaluation was assessed by means of Area Under Curve (AUC), TSS, and KAPPA estimators^{92,93} (see Chiarenza et al.¹⁹). Modern ENMs were projected to future (RCP 2.6–8.5) and past (TCS, Maastrichtian, and late Eocene) time slices. Multivariate climatic niches overlap between present and past occurrences were quantified using the R package *ecospat*⁹⁴ using 10,000 iterations for equivalency and similarity tests at a 100 value of grid resolution. Overlap was calculated between model projections. A binomial test was used to assess the statistical significance between ENM predictions and fossil occurrences in the relevant time slices.⁹⁵ We applied two thresholds to define environmentally suitable or unsuitable areas to assess model performance: (i) least training presence threshold (LTP, *sensu* Pearson et al.⁹⁶); and (ii) maximising the sum of sensitivity and specificity (MaxSSS⁹⁷) threshold, as performed by Saupe et al.²² with similar occurrence and experimental settings as used in this study. The presence of non-analogue climates (climate conditions that are outside the range over which a niche has been quantified; [Figures S5](#) and [S6](#)) was identified using the ExDet software package, which measures the similarity between time slices by accounting for deviation from the mean and correlation between variables.⁹⁸ Modern niches for turtle families and ecotypes were then projected to a 2100 climate scenario to quantify the distribution of future suitable turtle environmental space.

An ensemble model was created by using MaxEnt,⁹⁹ Random Forest, and SRE following the approach and settings in Chiarenza et al.¹⁹ For MaxEnt, a maximum iteration of 5000 was chosen.⁴⁴ Linear, quadratic, and product features were enabled. Other settings enabled were: linear+quadratic+product threshold (70), linear+quadratic threshold (10), hinge threshold (15), beta threshold (-1), beta categorical (-1), beta linear+quadratic+product (-1), beta hinge (-1), and default prevalence of 0.5 were set.⁴⁴ For the beta multiplier a value of 2 was chosen: the numeric default is 1, but a higher number gives a more spread-out distribution in the predictions; since a value >1 may be recommended for projections based on coarse occurrence data, like in fossil systems, to avoid overfitting. The Random Forest algorithm was implemented with 1000 trees. 50 subsampling replications with 1000 random pseudoabsences selected were performed.¹⁰⁰ Model evaluation was performed by means of AUC, TSS, and KAPPA estimators.^{92,93} The occurrences record was subsampled with a random split, using 70% of occurrences for calibration and 30% to evaluate the models' predictive accuracy. Prevalence (0.5), variable importance (0.5) was also set. Ensemble of all models were built by selecting all model outputs, based on TSS score, estimating the mean probabilities across predictions as an enabled feature and showing the proportional (default) probability mean weight decay.⁹³ A default (=0.05) significance level for estimating the confidence interval was set. As sensitivity analyses on climate data for ecological niche modelling, we quantified the type 1 novelty listing the variables included in non-analogue climates (see [Figures S5](#) and [S6](#) and relative captions). Script for ENM ensemble analyses is available as R script in.

QUANTIFICATION AND STATISTICAL ANALYSIS

We assessed the ability of past-projections of habitat suitability to correctly predict fossil occurrences using binomial tests¹⁰¹ with the R function `binomial_test()` from the package `ntbox`,¹⁰² following the methodology in Saupe et al.²² Binary models using both the LTP and MaxSSS thresholds were used (see [Table 1](#)). Success of prediction was presented as a percentage value of the probability (p) of successfully predicting occurrences according to the formula $p = \frac{n}{n+f}$ where n is the number of successfully predicted occurrences, and f is the number of failed predictions.

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Supplemental Information

**100 million years of turtle paleoniche
dynamics enable the prediction of latitudinal
range shifts in a warming world**

Alfio Alessandro Chiarenza, Amy M. Waterson, Daniela N. Schmidt, Paul J. Valdes, Chris Yesson, Patricia A. Holroyd, Margaret E. Collinson, Alexander Farnsworth, David B. Nicholson, Sara Varela, and Paul M. Barrett

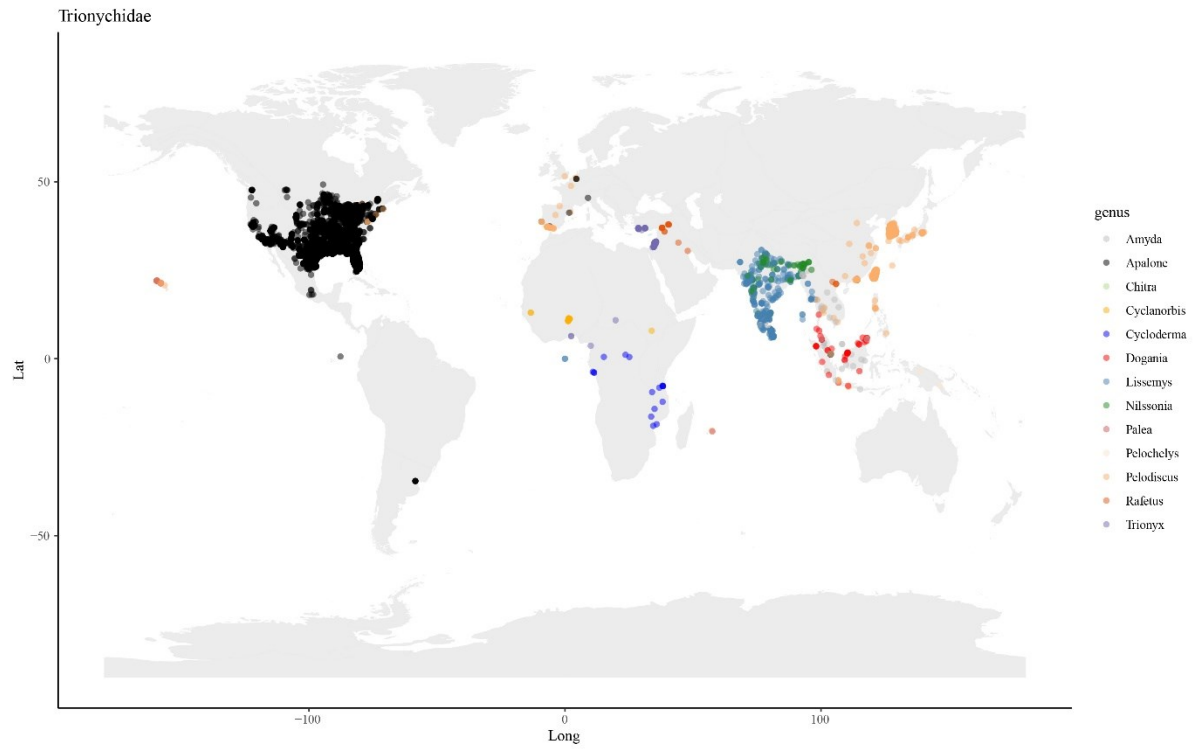


Figure S1. Map of occurrences for modern Trionychidae. Related to Figure 2. Included list contains genera attributed to this “family-level” clade.

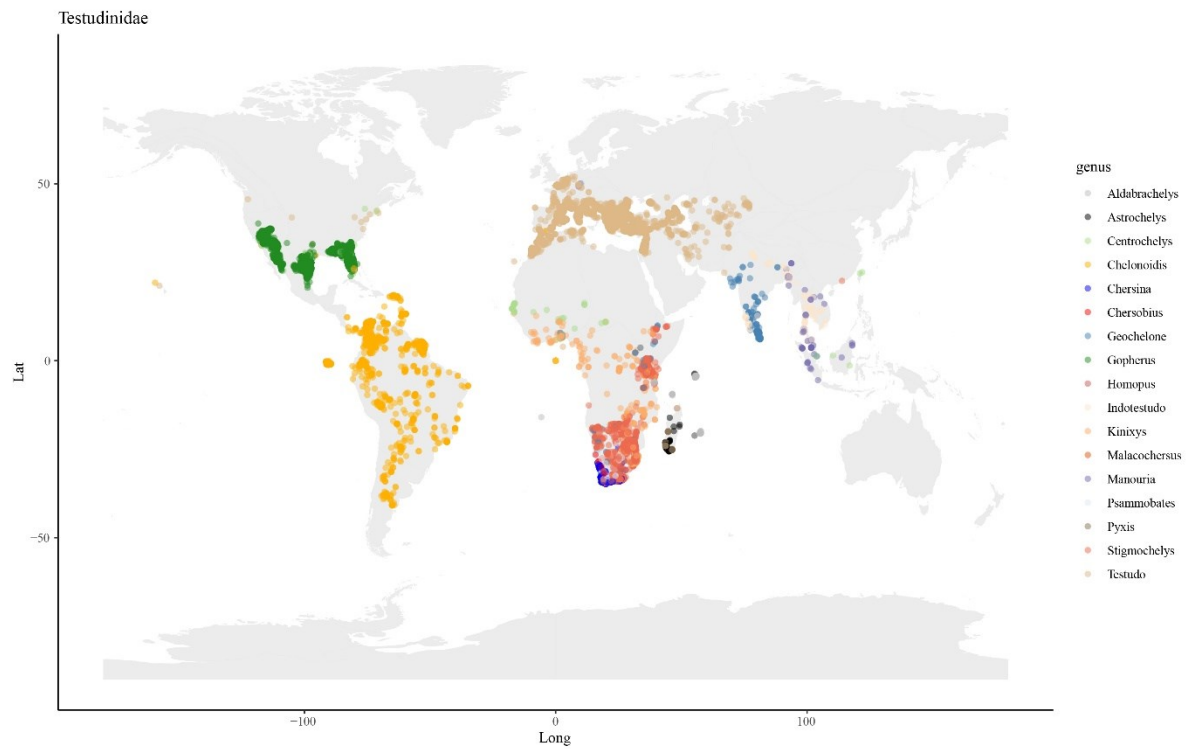


Fig. S2. Map of occurrences for modern Testudinidae. Related to Figure 2. Included list contains genera attributed to this “family-level” clade.

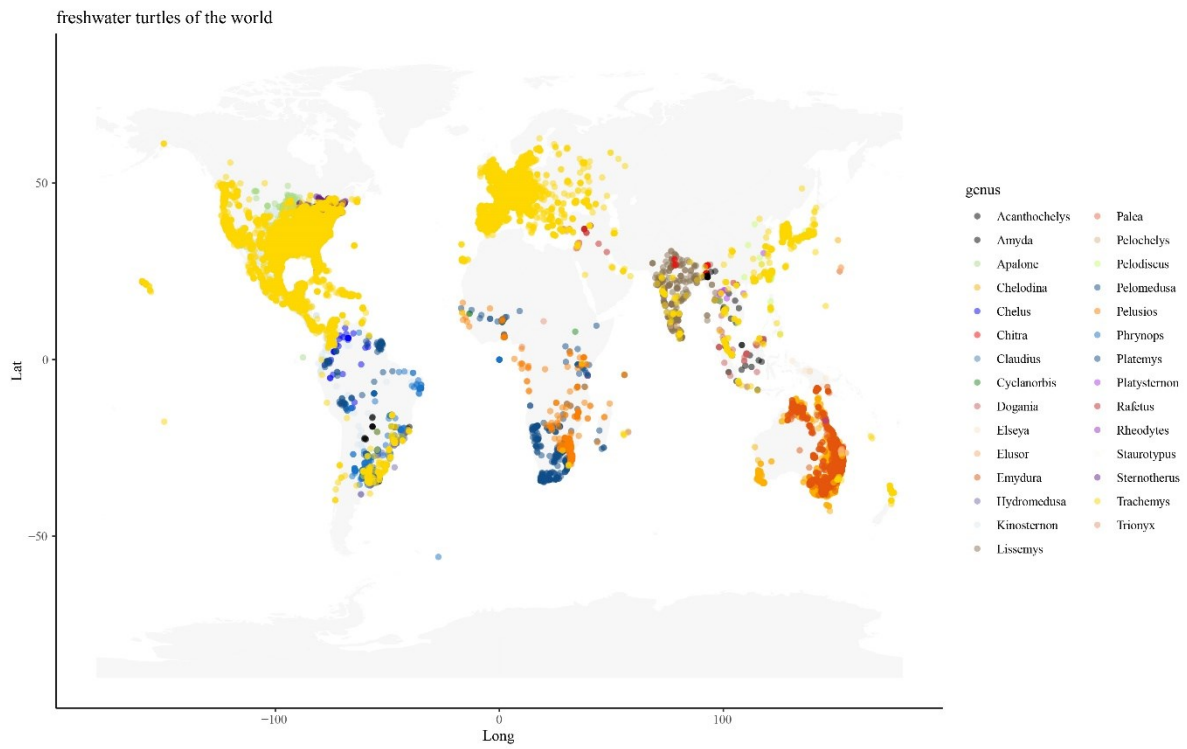


Figure S3. Map of occurrences for modern freshwater turtles. Related to Figure 2. Included list contains genera attributed to this ecotype.

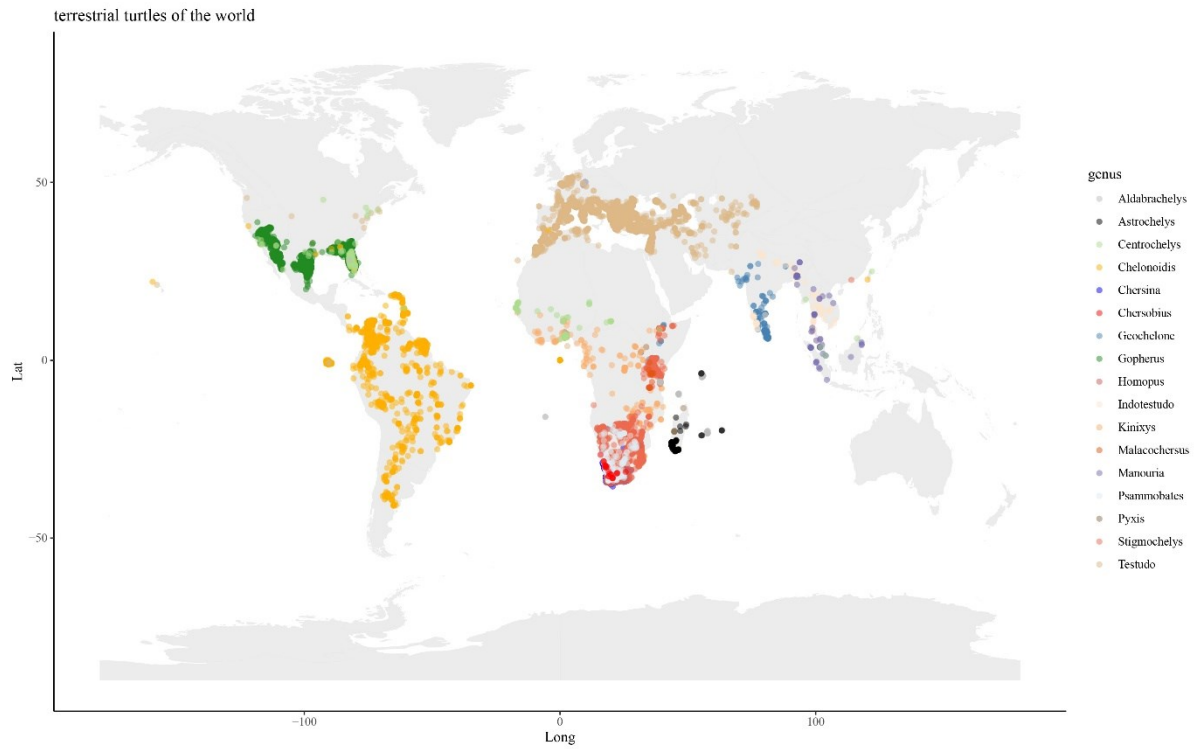


Figure S4. Map of occurrences for modern terrestrial turtles. Related to Figure 2. Included list contains genera attributed to this ecotype.

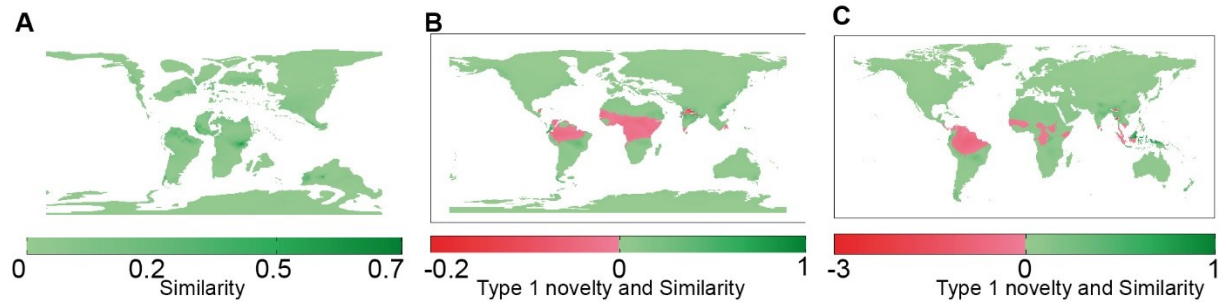


Figure S5. Availability of non-analogue climate space. Related to Figures 3, 4, 5. Comparison between: (A) the Cretaceous stages (Turonian-Coniacian-Santonian, Maastrichtian) and the present; late Eocene (Bartonian-Priabonian) and the present (B); the present and 2100 (RCP 2.6–8.5; C). Green = regions of similar climate variables (0 indicates maximum similarity), red = regions with at least one variable outside the univariate range (type 1 novelty). The more negative values the type 1 novelty, the less similar the climates are in these regions.

A



B



Figure S6. Climate variables most influential to type 1 novelty. Related to Figures 3, 4, 5. Type 1 novelty includes areas with at least one variable outside the univariate range of climate space in non-analogue climate regions, comparing the Cretaceous and recent (A) and the late Eocene and recent (B).