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1 **Title: Modelling the climatic niche of turtles: a deep-time perspective**

2

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27 **Abstract**

28 Ectotherms have close physiological ties with the thermal environment; consequently, the
29 impact of future climate change on their biogeographic distributions is of major interest. Here,
30 we use the modern and deep-time fossil record of testudines (turtles, tortoises and terrapins)
31 to provide the first test of climate on the niche limits of both extant and extinct (Late
32 Cretaceous, Maastrichtian) taxa. Ecological niche models are used to assess niche overlap
33 in model projections for key testudine ecotypes and families. An ordination framework is
34 applied to quantify metrics of niche change (stability, expansion and unfilling) between the
35 Maastrichtian and present-day. Results indicate that niche stability over evolutionary
36 timescales varies between testudine clades. Groups that originated in the early Cretaceous
37 show climatic niche stability, whereas those diversifying towards the end of the Cretaceous
38 display larger niche expansion towards the modern. Temperature is the dominant driver of
39 modern and past distributions, while precipitation is important for freshwater turtle ranges.
40 Our findings demonstrate that testudines were able to occupy warmer climates than present
41 day in the geological record. However, the projected rate and magnitude of future
42 environmental change, in concert with other conservation threats, presents challenges for
43 acclimation or adaptation.

44

45 **Keywords:** Testudine, ecological niche model, niche stability, Late Cretaceous

46

47 **Introduction**

48 Global climate change over the last century has altered rainfall patterns and produced
49 warming not observed for millennia. Future scenarios predict an increase in global
50 temperature, relative to the pre-industrial era which will likely exceed 1.5 - 2° C by 2100 (1).
51 Climate plays a major role in determining biogeographic distributions (2,3) and, consequently,
52 recent global environmental change has caused geographic range shifts in numerous
53 species. However, large differences in the capacity of organisms to adapt or acclimatize have
54 been recognised (4). The impact of climate is expected to be especially important for terrestrial
55 and freshwater ectotherms, such as amphibians and reptiles, whose body temperatures are
56 tightly linked to their external environment (5,6). The potential impacts of climate change on

57 these animals have received considerable attention, and the ability to cope with local shifts
58 in temperature and precipitation is expected to vary between taxa (7-9).

59 Forecasting future responses to climate change is challenging. The fossil record offers long-
60 term distributional, ecological and species-richness data that provide critical information for
61 elucidating the effects of changing climate on paleobiogeographic patterns, thereby informing
62 our understanding of future ecological response (10-12). A fundamental assumption of using
63 the fossil record for this purpose is that the climatic niche occupied by an organism has
64 remained stable through space and time (13). However, the assumption of climatic niche
65 stability has frequently been questioned given the long-term potential for evolutionary
66 adaptation (14). Ordination techniques and ecological niche models (ENMs) can be used to
67 quantify climatic niches and niche stability by relating species occurrence records with climate
68 variables (15,16). These methods have been used to assess niche dynamics over Quaternary
69 and Neogene timescales (17-19), but application to the deep-time fossil record remains
70 limited (20,21). In this study we use the term niche to refer to the multivariate space of climate
71 variables that best corresponds to observed taxon distributions and the associated
72 distribution of potential abiotically suitable habitats (22).

73 Turtles, tortoises and terrapins (collectively termed testudines) originated in the Late Triassic
74 (~ 220 Ma) (23) and have persisted through a wide range of changing climates. Of 335
75 recognized modern species, 40% are regarded as globally threatened or endangered (24).
76 Alongside overexploitation and habitat loss, climate change is a significant threat to their
77 conservation status with ontogenetic growth rates, species abundance and geographical
78 ranges all predicted to decline under future climate scenarios (25,26). Temperature places
79 strong physiological constraints on testudine activity patterns and regulates sex-
80 determination of offspring (27). Freshwater species distributions are closely linked with
81 precipitation due to their dependence on standing water availability (5,28). Understanding
82 how future environmental change may affect the group is therefore crucial for informing
83 adaptive conservation management strategies.

84 The Late Cretaceous (~72.1 – 66.0 Ma) record of testudines provides a model system for
85 testing possible testudine response to a future warmer climate. This interval was warmer than
86 present, with a reduced equator-to-pole temperature gradient due to higher polar
87 temperatures, fewer seasonal extremes and greater precipitation (29). Well calibrated global
88 climate model simulations and a broad distribution of climate proxy data for model validation

89 provide a good understanding of palaeoclimatic conditions (30,31). The fossil record of
90 testudines has a wide geographic coverage that exceeds modern day distributions. The
91 largest number of fossils can be found in the last two million years of the Maastrichtian (~
92 72.1 – 66.0 Ma) (32-34). To test for the impact of climate on testudine niche limits we use
93 ENMs to estimate the modern and Maastrichtian niches and calculate the overlap between
94 model projections. We identify non-analogous climates and apply an ordination framework to
95 quantify metrics of niche unfilling (niche space occurring only in the Maastrichtian), expansion
96 (niche space occurring only in the modern), stability (niche space occurring in both time
97 periods), and test for niche equivalency (*sensu* 15). Our study focuses on two extant testudine
98 freshwater families with pre-Maastrichtian origins (Trionychidae and Chelydridae) and two
99 ecotypes (freshwater, representing a wide range of families, and terrestrial, representing
100 Testudinidae and the extinct Nanhsiungchelyidae (SI 1 Table 6), rather than identifying
101 species-level ecological traits. We use these families and ecotypes as proxies of the species
102 and the roles that they fulfil within an ecosystem and how the availability of potential suitable
103 climate space changes, or remains stable, for these over time. This study provides the first
104 application of ENMs and ordination methods to quantify the climatic niche dynamics of any
105 Mesozoic vertebrate group. The application of these techniques to deep-time distributions
106 provides baseline data for testudine niche limits in a past greenhouse which can inform our
107 understanding of long-term ectotherm biogeographic response under fundamentally different
108 climatic regimes to today, both in the past and under future scenarios.

109

110 **Methods**

111 **Testudine occurrence data**

112 Modern testudine occurrence data were taken from the World Turtle Database (35). Fossil
113 occurrence data were downloaded from the Paleobiology Database (PBDB; paleodb.org)
114 through the Fossilworks portal (fossilworks.org) on September 3rd 2015, using the search
115 terms Testudinata and Cretaceous. The fossil data (major contributors - 36) were restricted
116 by removal of ichnotaxa (trace fossils), ootaxa (fossil eggs) and marine taxa, then subsetted
117 to include only those occurrences falling between 66–72.1 Ma, leaving a dataset of
118 Maastrichtian non-marine turtles comprising 877 taxonomic occurrences (743 identified at
119 least to family level) in 321 PBDB collections (S2 Dataset 1). Due to limitations in the number
120 of fossils identified to genera or species, we based our analyses on family-level identifications

121 (referred to herein as taxonomic) and ecotype level (fully terrestrial or freshwater). This
122 allowed for a comparison of family-specific niche traits with those of more generalist
123 ecological groups. The fossil record represents a complex mixture of preservational and
124 sampling biases (e.g., temporal variation in sedimentary rock volume, accessibility and
125 sampling effort) (37). Biases inherent in the Maastrichtian testudine fossil record result in a
126 set of available fossil occurrences that likely underestimate past global distributions and thus
127 potential climate niche space. However, the Maastrichtian is well sampled in comparison to
128 other stages of the Cretaceous and even younger parts of the geological record. The
129 geographic spread of Maastrichtian testudine occurrences covers all continents except
130 Australia and Antarctica (S2 Dataset 1) and matches that of other tetrapod clades except for
131 the apparently genuine absence of turtles at high-latitudes (33). Moreover the turtle carapace
132 is highly durable and more likely to be preserved than the majority of other vertebrate skeletal
133 elements (33,38).

134 The use of higher taxa as a surrogates for specie data has been subject to debate (39),
135 though family or higher-level distributional data has been used to effectively describe the
136 environmental tolerances of some modern taxa (40,41). Use of family data to investigate
137 evolutionary processes in the fossil record is common as it increases the number, and
138 geographical coverage of occurrence data (42,43). The ecophysiological responses of
139 Trionychidae and Chelydridae species to contemporary climate is broadly conserved at the
140 family level and species within these families occupy similar habitats (44). Trionychidae and
141 Chelydridae are therefore considered a good surrogate for their associated species-level
142 traits.

143

144 **Climate data**

145 Modern climate variables were derived from UKMO Unified Model HadCM3; a fully coupled
146 Atmosphere-Ocean General Circulation model (46,47). The model has a surface resolution
147 of ~417 km x 278 km at the equator, reducing to 295 x 278 km at 45° latitude. A detailed
148 description of the GCM can be found within 48,49. Maastrichtian climate variables were
149 derived from UKMO Unified Model HadCM3L; identical to HadCM3 except for reduced spatial
150 resolution in the ocean component (31). A bilinear interpolation was applied to convert GCM
151 climate variables to 10 minute resolution. The GCM shows good broad agreement with proxy
152 data, however, in continental interiors proxy-model comparisons consistently report

153 conditions that are too extreme, i.e. cold winters and hot summers (47,48). Thus,
154 interpretation of niche analyses within these regions should thus be treated with caution.
155 Climate variables were chosen to reflect abiotic niche characteristics that have been shown
156 to be ecologically limiting to modern testudine distributions (26,28) and that can be feasibly
157 determined in the fossil record. Initially a larger number of temperature and precipitation-
158 related variables were considered (S1 Table 1). However, to reduce collinearity between
159 variables (49), we only retained combinations with a Pearson's pairwise correlation coefficient
160 $<|0.7|$. Three variables were used in the final niche analyses: mean temperature of the coldest
161 quarter and precipitation of the wettest and driest months.

162

163 **Niche modelling and quantifying niche change**

164 The MaxEnt ENM algorithm was used to model modern and Maastrichtian testudine climatic
165 niches as it is well-suited for use with presence-only occurrence data. Specifically, it
166 compares the climatic conditions at locations of occurrence records with randomly selected
167 points from a background extent to create maps of habitat suitability (50). A five-fold cross
168 validation procedure (51) was used to create global models for the modern and calculate area
169 under the curve (AUC) statistics (predictive performance measure). AUC values of 1 indicate
170 a perfect model prediction and 0.5 represents a no-better-than-random prediction (52).
171 Jackknife tests and % variable contribution were used to estimate variable importance.
172 Modern ENMs were projected onto Maastrichtian climate layers. A binomial test was used to
173 assess the ability of modern ENMs to predict Maastrichtian fossil occurrences. The same
174 procedure was repeated to produce Maastrichtian ENMs and project these to modern climate
175 layers. We used the Boyce Index (BI), with values ranging from -1 to 1, to assess the ability
176 of Maastrichtian ENMs to predict modern occurrences (53). Geographical niche overlap was
177 calculated between modern and Maastrichtian predictions (54) using both forward projection
178 models to the modern and backward projection to the Maastrichtian. Geographical niche
179 overlap ranges from 0 (no overlap) to 1 (identical predictions). Sensitivity analyses were
180 performed to assess the impact of training extent on MaxEnt ENMs (SI 1 Figures 12, 13 &
181 Table 7), and calibrations with modern species-level occurrence data for Trionychidae and
182 Chelydridae were compared to family-level analyses (SI 1 Figures 6 - 11).

183 Non-analogue climates occur over time due to climate change and result in unreliable
184 projections of ENMs. We identify the presence of non-analogue climates using the ExDet

185 software package which measures the similarity of variables between time slices by
186 accounting for deviation from the mean and correlation between variables (55). Measures of
187 niche margin dynamics (unfilling, expansion and stability) and environmental niche overlap
188 between the time slices were quantified using an ordination framework that compares the
189 environmental attributes at sites of organism occurrence, in different locations or at different
190 time periods (16). The framework uses a principal components analysis (PCA); niche
191 quantification analyses are performed within the first two PCA axes (56). We used a pooled-
192 range approach (15,16) where analyses are made relative to the entire climate niche
193 occupied in both time periods. We also used this framework to test for statistical significance
194 of niche similarity and equivalency. Niche similarity assesses whether occupied climatic
195 niches in two time periods are more similar than would be expected by chance and niche
196 equivalency tests for whether climatic niches in two time periods are effectively identical (16).
197 These analyses were conducted in environmental space and provide a comparison to ENM
198 analyses in geographical space. All ENM and ordination analyses were performed in the R
199 statistics package (version 3.2.1) using the dismo and ecospat packages (57).

200

201 **Results**

202 **Drivers of testudine climatic niches today and in the Maastrichtian**

203 Mean AUC values for test data in the modern and Maastrichtian cross-validation ENMs were
204 moderate to high (Modern; Trionychidae: 0.83, Chelydridae: 0.92, terrestrial: 0.79,
205 freshwater: 0.69, and Maastrichtian; Trionychidae: 0.94, Chelydridae: 0.98, terrestrial: 0.91,
206 freshwater: 0.87) indicating that all models successfully discriminated presence of the
207 organisms from background locations. As expected, AUC values were lower for ecotypes
208 compared to the taxonomic ENMs, as ecotypes include multiple testudine families, including
209 some with more generalist ecological preferences. Temperature of the coldest quarter was
210 the most important variable to modern ENM fit for Trionychidae (46.8 %), freshwater (61.8
211 %) and terrestrial (74.6 %) ecotypes, based on MaxEnt mean % variable contribution and
212 jackknife estimates. The explanative power of temperature was greatest for the terrestrial
213 ecotype; this is expected as the presence of standing water (and thus precipitation) is less
214 critical for terrestrial testudines primarily exploiting land environments. The precipitation-
215 related variables showed significant importance for the freshwater ecotype (37.2 %) and
216 taxonomic ENMs (Trionychidae = 53.2 %, Chelydridae = 83.4 %), with precipitation of the

217 driest month the most important variable overall for Chelydridae (61.9 %). Temperature of
218 the coldest quarter was the most important variable to Maastrichtian model fit for all testudine
219 ENMs (Trionychidae = 80.2 %, Chelydridae = 66.9 %, freshwater = 65.2 %, terrestrial = 60.9
220 %). The precipitation-related variables combined also showed significant explanative power
221 for both ecotype and taxonomic ENMs (terrestrial = 39.0 %, freshwater = 34.9 %, Chelydridae
222 = 33.1 %, Trionychidae = 19.7 % (SI 1 Figure 2).

223 Sensitivity analyses highlight that ENM training extent has a significant impact on modern
224 ENM projections (SI 1 Figures 12 & 13). Modern ENMs with a global training extent better
225 predicted modern testudine occurrences (SI 1 Tables 2 & 7), therefore results herein focus
226 on these. Modelled modern environmental suitability at the family level is driven largely by
227 the widest ranging species in Trionychidae and Chelydridae (SI 1 Figures 6-11). This
228 suggests that using family-level occurrence data to predict suitable climate space in the past
229 will likely identify the widest range of potential abiotically suitable habitat for these taxonomic
230 groups.

231

232 **Testing niche stability**

233 Modern ENMs were projected to Maastrichtian climate layers (backward projection models)
234 and Maastrichtian ENMs to modern climate layers (forward projection models), to test for
235 stability in climate niches between the two time periods. Modern ENM projections were
236 statistically significant for the freshwater ecotype and taxonomic ENMs (binomial test results,
237 $p < 0.01$ at all three omission thresholds: SI 1 Table 2), suggesting stability in the climatic
238 drivers of the niche between the modern and the Maastrichtian for these groups (Figure 1).
239 In contrast, a non-significant result for the terrestrial ecotype at the 50 % omission threshold
240 suggests this climatic niche is less stable ($p = 0.09$). Maastrichtian ENM projections (SI 1
241 Figure 2) showed poorer predictive performance than modern ENMs, which may be a result
242 of fewer occurrences in the Maastrichtian compared to the modern for ENM calibrations.
243 Model predictive power may also be influenced by taxonomic differences in environmental
244 tolerances (i.e. species vs family level, Figures SI 1 6-11). Average Boyce indices were all
245 negative (SI 1 Table 3), suggesting model predictions of modern testudine occurrence data
246 are no better than random. Chelydridae (BI: -0.24) and terrestrial ecotype (BI: -0.37) scores
247 are most negative and indicate predictions of low suitability where presence is more frequent.
248 Backward projection models (BP) generally showed higher geographic niche overlap (defined

249 between 0 and 1, with 1 being identical) than forward projection models (FP). Freshwater
250 ecotype models showed highest mean geographical niche overlap (BP: 0.66, FP: 0.65),
251 followed by Trionychidae (BP: 0.51, FP: 0.44), Chelydridae (BP: 0.50, FP: 0.32) and terrestrial
252 (BP: 0.40, FP: 0.54). Environmental niche overlap was 0.36 for Trionychidae, 0.30 for
253 Chelydridae, 0.26 for the freshwater ecotype and 0.17 for the terrestrial ecotype.
254 Environmental niche overlap scores are expected to be lower than geographical niche
255 overlap scores because geographical niche overlap compares how ENM predictions of
256 suitable areas overlap on the landscape, while environmental niche overlap quantifies
257 observed overlap of occurrences in environmental space, thus not including those areas that
258 are suitable but unoccupied.

259 Change in niche margins within environmental space varies between the testudine groups
260 (Figure 2). The freshwater ecotype displays high stability (90 %) and minimal expansion (10
261 %). Trionychidae shows stability (67 %) but also significant expansion (~31 %). In contrast,
262 expansion is higher for Chelydridae (72 %), with some stability (28 %). The terrestrial ecotype
263 shows the greatest expansion (77 %) and lowest stability (23 %). Measures of niche unfilling
264 were low or non-existent for all groups except for the terrestrial ecotype (12%). Tests for niche
265 similarity were statistically significant for Trionychidae, Chelydridae and the freshwater
266 ecotype but not statistically significant for the terrestrial ecotype (i.e. the hypothesis that the
267 Maastrichtian and modern niches are no more similar than by chance cannot be rejected) (SI
268 1 Table 5). Tests for niche equivalency showed observed environmental overlaps were lower
269 than 95 % of simulated overlaps, rejecting the hypothesis of niche equivalency for all
270 testudine groups. Overall, this shows that, with the exception of the terrestrial ecotype, the
271 testudine groups occupy environmental niches that are similar but not identical between the
272 modern and Maastrichtian (SI 1 Table 5 & Figure 14). Change of the terrestrial ecotype niche
273 centre was primarily along environmental gradient 2, (Figure 2 & SI 1 Figure 15), suggesting
274 that shifts in both temperature and precipitation influence the climatic niche change of
275 terrestrial testudines from the Maastrichtian to the modern.

276 Grid cells with at least one variable outside of the univariate range are confined to the low
277 latitudes of South America, Africa, India and southern Asia (Figure 3). Temperature of the
278 coldest quarter is most influential to type 1 novelty (SI 1, Figure 3). Very few Maastrichtian
279 testudine fossil occurrences fall within the non-analogue regions (five freshwater ecotype
280 occurrences, S2 Dataset 1); therefore, the influence of these areas on the model is expected
281 to be minimal and these regions were not excluded from our niche analyses. Environmental

282 and occurrence data for the Maastrichtian represent a longer time period than does the
283 modern data. This time-averaging increases the likelihood of sampling a greater proportion
284 of the potential niche space. However our analyses show that Maastrichtian turtles occur
285 predominantly within areas of suitable climate space, thus this does not appear to have
286 affected our data set.

287

288 **Discussion**

289 ***The role of temperature and precipitation in testudine climatic niches***

290 Temperature explained most of the modelled habitat suitability in modern and Maastrichtian
291 ENMs, confirming that thermal limits are the primary constraints on climate niches at the
292 global scale (26,58). Temperature links directly to testudine thermal physiology and is
293 expected to place fundamental restrictions on distribution, as lethal temperatures exceed
294 those suitable for reproduction (59). We used temperature of the coldest quarter, thus ENM
295 results suggest a more equable climate system during the Late Cretaceous meant that even
296 high latitude temperatures were greater than testudine critical thermal minima. The relative
297 importance of temperature varies for different testudine groups as has been previously
298 suggested (60). Aquatic turtles appear to have lower and broader thermal limits than their
299 terrestrial counterparts; minimum voluntary temperatures are estimated ~15° C for terrestrial
300 testudinoids (tortoises) whereas some freshwater turtles can remain seasonally active in
301 water as low as 5° C (59). These physiological observations are supported by the greater
302 importance of temperature in modern terrestrial ecotype ENMs compared to the freshwater
303 groups. Precipitation-related variables were important in freshwater testudine ENMs,
304 highlighting the key role of rainfall for turtles occupying aquatic ecosystems, which use water
305 as a thermal buffer (27,61). Today the importance of precipitation was lowest for the terrestrial
306 ecotype, supporting prior findings that terrestrial testudinoids show links with precipitation,
307 but to a lesser extent than freshwater turtles due to their terrestrialised life histories (58,62).
308 The explanatory power of temperature is greater in Maastrichtian ENMs compared to the
309 modern, and precipitation shows significant contributions to Maastrichtian model fit in the
310 ecotype ENMs. Whereas this could be a preservational bias resulting from fewer testudine
311 occurrences in the Maastrichtian compared to the modern, it is important to note that land
312 environments were wetter in the Maastrichtian than in the present day (29,32). Therefore, the
313 relative importance of total precipitation may not have been as large during a warmer and

314 less seasonal global climate regime. Our results support the long-standing assumption that
315 the occurrence of reptilian ectotherms indicates warm climate (13,63). However, precipitation
316 is also critical in constraining the distributions of taxa that occupy freshwater environments.

317

318 ***Do climatic niches change over evolutionary timescales?***

319 Few studies have addressed vertebrate ectotherm niche stability over evolutionary
320 timescales (60,64). Our results suggest climatic niche stability over deep-time varies among
321 testudine groups. The freshwater ecotype and Trionychidae show highest overlap in forward
322 and backward ENM projections and significant niche margin stability between the
323 Maastrichtian and the modern, implying that similar ecological limits have applied to these
324 taxa for >70 million years. While the terrestrial ecotype and Chelydridae also displays niche
325 margin stability, greater expansion suggest that the niche margins have shifted in
326 environmental space between the two time periods for these groups (Figure 2). Although the
327 time interval sampled in the Cretaceous is longer than that sampled for the modern, and thus
328 should have greater potential for sampling niche spaces not represented in the modern,
329 Maastrichtian niches are smaller than those in the present. However this could result from
330 fewer sampled testudine occurrences in the Maastrichtian, which may represent a smaller
331 range of suitable climate space in comparison to the modern testudine data. Niche expansion
332 from the Maastrichtian to today for freshwater testudines is driven primarily by precipitation
333 variables (Figure 2 a – c). Warmer temperatures and greater evaporation generated a more
334 enhanced hydrological cycle in the Maastrichtian with continents that were ~15 % wetter than
335 present day (30). At the regional scale, however, some areas (south-west North America,
336 central South America, central and southern Africa and central and south-east Asia) show
337 higher wettest month rainfall today. These regions have high testudine species richness at
338 present (65) and suggest that changing precipitation patterns may have played a key role in
339 driving the expansion of freshwater turtle niche space between the Late Cretaceous and the
340 modern. Terrestrial ecotype niche expansion is in the direction of environmental gradient 2
341 (Figure 2d), further indicating that as well as precipitation, thermal limits are important
342 constraints on terrestrial testudines and likely influenced niche change from the Maastrichtian
343 to the modern. Poor predictive performance of the terrestrial ecotype forward and backward
344 ENM projections suggest that climate drivers of the modern and Maastrichtian niche differ
345 significantly and/or that the climatic tolerances of terrestrial testudines may have undergone

346 greater evolutionary change than in their aquatic counterparts. Adaptation to shifting aquatic
347 environments during the Late Cretaceous could have played a key role in the success of
348 freshwater testudines compared to terrestrial relatives that occupied more homogeneous
349 habitats during this interval (34). While observations of niche expansion may relate to
350 evolution or adaptation in response to shifting abiotic conditions, it is important to
351 acknowledge that changes in biotic interactions and accessibility to suitable habitat can also
352 result in niche instability over time (66).

353 The retention of vertebrate ectotherm climate niche traits has primarily been tested over much
354 shorter geological time scales, such as the most recent glacial (60). For example, species
355 richness patterns of European reptiles and amphibians suggest niche stability between the
356 Last Glacial Maximum and present day (67) and phylogenetic niche conservatism has been
357 shown to influence the community structure of emydid turtle lineages in eastern North
358 America (64). Due to the complex nature of climatic niches it has been suggested that some
359 climate variables are subject to greater niche conservatism than others (68,69). Araújo et al.
360 (70) showed that tolerance to temperature maxima is largely conserved across lineages,
361 while temperature minima varies between and within species. This is due to the definitive
362 physiological limits posed by high temperatures whereas the evolution of cold temperature
363 tolerance may be more frequent and implies that ectotherm ranges are likely to be more
364 sensitive to climate cooling rather than warming (7,71). Niche stability results observed in
365 some testudine groups support these findings and indicate that warmer stable climates may
366 not necessarily be deleterious for testudines, in particular terrestrial testudinoids which
367 display the highest thermal optima of the clade (59). However, the ability of ectotherms to
368 track the current rate of climate change via large-scale migration remains controversial (72).

369

370 ***Phylogenetic perspectives on niche change***

371 The differences in niche stability between testudine groups appear to be under phylogenetic
372 control. Trionychia is the most ancient cryptodire lineage (originating >145 Ma), but this clade
373 did not dominate northern continental species assemblages until the Late Cretaceous (73).
374 Trionychidae originated in the late Albian (~113.0–100.5 Ma: 78) and by the Maastrichtian its
375 distribution had likely expanded to occupy a significant range of suitable climates. By contrast,
376 Americhelydia (the larger clade including Chelydridae) underwent a rapid radiation during the
377 Late Cretaceous, with the oldest chelydrid fossil recorded in the Albian (~ 113 – 100.5 Ma)

378 or Cenomanian (100.5 – 93.9 Ma) (75) but with clade diversification and geographic
379 expansion occurring mainly in the Neogene (76). More recently evolving families may have
380 expanded into climate spaces that differ from their Cretaceous relatives or ecotypes as they
381 underwent diversification (74) and could account for lower climate niche stability for
382 Chelydridae. Modern terrestrial testudinoids diversified after the K/Pg boundary (66.0 Ma),
383 during pronounced Paleogene warm periods (Late Paleocene Thermal Maximum and the
384 Early Eocene Climatic Optimum) (77). Maastrichtian terrestrial ecotype occurrences are of
385 the herbivorous, tortoise-like Nanhsiungchelyidae, a sister clade to the Trionychidae that is
386 not closely related to living Testudinidae; low environmental and geographic niche overlap
387 (and non-significant niche similarity) in this group strongly suggests that these early tortoise-
388 like nanhsiungchelyids had different climate tolerances from living terrestrial turtles and from
389 contemporaneous Cretaceous taxa that were predominantly omnivorous or carnivorous (34).
390 Consequently, variables other than temperature and precipitation may also have been
391 important for delimiting geographic distributions (i.e., biome type and gross primary
392 productivity) and could be tested using paleovegetation models.

393 The climate niche stability observed in some testudine groups has implications for the use of
394 turtles as paleotemperature proxies in validation studies of GCM simulations of high-latitude
395 warmth in the geological record (13,58). While it suggests that long-established families that
396 range through from the Mesozoic to today are indeed highly useful for such comparisons,
397 caution should be applied when using fossils that represent testudine lineages originating or
398 diversifying close to the paleoclimate interval of focus.

399 The use of an ENM and ordination framework has enabled us to quantify modern and
400 Maastrichtian testudine niches, and test for niche stability in a fundamentally different global
401 climate to present day, providing novel insights into the group's biogeographic responses
402 under climatic conditions that were warmer and wetter than modern. These methods have
403 excellent potential for application to other vertebrate groups with fossil records exhibiting high
404 preservation potential and good geographical coverage, enabling comparisons between the
405 niche dynamics of other ectotherm and endotherm taxa, with those of extant relatives, over
406 extended geological timescales. Here, we applied one type of GCM as this was the only
407 appropriate climate model at the time of analysis, and we encourage future comparisons
408 between multiple ENMs that use multiple GCM outputs (i.e., an ensemble approach), as
409 these new GCMs become available for the Cretaceous. It is important to reiterate that our
410 findings assess long-term niche dynamics occurring over lengthy time scales and hundreds

411 of generations. Rates of climate change over the next century are projected to be more rapid
412 and show greater magnitudes than has been experienced over millions of years of
413 evolutionary history (1). In concert with neo-ecological studies, our findings provide an
414 important long-term perspective on testudine niche occupancy and climate. Given the current
415 uncertainty regarding ectotherm migration or dispersal capacity and their long generation
416 times (7), the potential for testudines to acclimatize or adapt undoubtedly poses significant
417 future challenges for conservation management strategies.

418 **Conclusions**

419 Our results indicate that the retention of climate niche characteristics over evolutionary
420 timescales varies among testudines. Temperature is the primary driver of modelled modern
421 and Maastrichtian distributions at the global scale, but precipitation-related variables also play
422 a significant role in delimiting freshwater turtle ranges. Niche change between the
423 Maastrichtian and modern appears to reflect turtle phylogenetic relationships; longer-
424 established groups show greater climate niche stability, whereas groups evolving closer to
425 the Late Cretaceous display niche expansion and highlight that diversification within the clade
426 likely led to the occupation of novel climate space.

427

428 **Author contributions**

429 P.M.B, D.N.S. and P.J.V conceived the study. P.J.V., D.B.N., P.A.H. and P.M.B contributed
430 data. A.M.W., P.A.H., D.N.S., P.J.V. and D.B.N. analysed the data and A.M.W. and D.N.S
431 wrote the manuscript, with contributions from other authors.

432

433 **Competing interests**

434 We have no competing interests.

435

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443 Finally, we offer our sincere thanks to all of the people who enter data into the PBDB.

444 Climate variables used in ENM and ordination analyses for the modern and Maastrichtian are
445 available at: <http://www.bridge.bris.ac.uk/resources/simulations>. Paleogeography of the
446 Maastrichtian continental configurations was calculated by Robertson, CGG Services (UK)
447 Limited. Maastrichtian turtle palaeorotations are based on the GETECH Plc. plate model and
448 methodologies of Markwick and Valdes (2004); Markwick (2007). Modern turtle occurrence
449 data are available at: <http://emys.geo.orst.edu/>. Maastrichtian turtle occurrence data are
450 archived on the PANGAEA data repository portal (http://pangaea.de/*awaiting DOI*).

451

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658

659

660 **Author Contributions**

661 P.M.B, D.N.S. and P.J.V conceived the study. P.J.V., D.B.N., P. A.H. and P.M.B contributed
662 data. A.M.W., P.A.H., D.N.S., P.J.V., D.B.N. and P.M.B. analysed the data and A.M.W. and
663 D.N.S wrote the manuscript, with contributions from other authors.

664

665 **Competing financial interests**

666 The authors declare no competing financial interests.

667

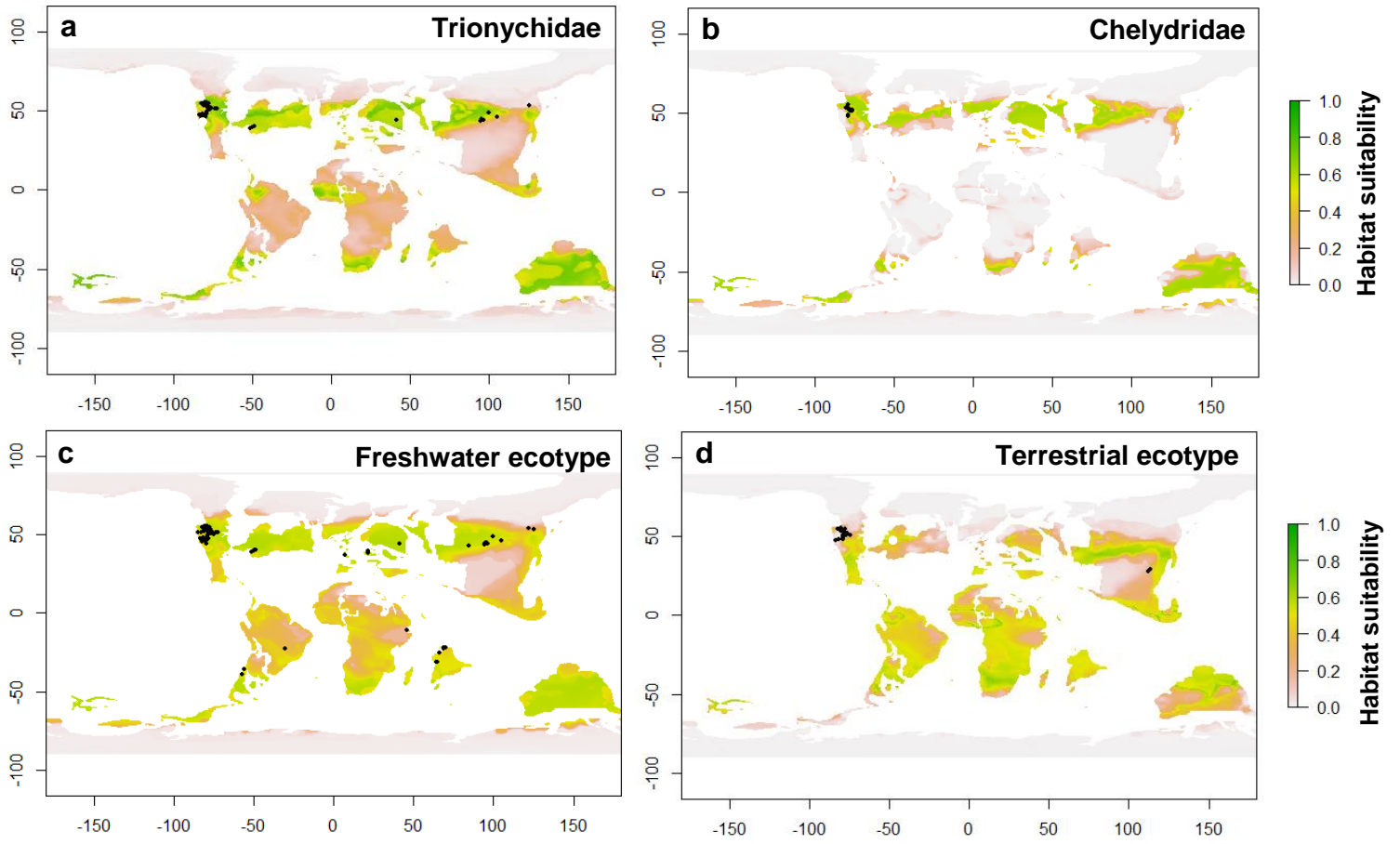
668 **Figure captions**

669 **Figure 1. Modern MaxEnt ENMs projected to Maastrichtian climate layers.** Maastrichtian
670 testudine fossil occurrences (●) overlay the maps of habitat suitability for Trionychidae (a),
671 Chelydridae (b), freshwater ecotype (c) and terrestrial ecotype (d). Geographically filtered
672 occurrences (1 per climate grid cell) are: Trionychidae: 60, Chelydridae: 19, freshwater ecotype: 111,
673 terrestrial ecotype: 27. The continents are in a paleoconfiguration, using a reconstruction following
674 the methodologies in 31.

675 **Figure 2. Testudine niche change between the Maastrichtian and the modern.** Niche change in
676 climate space is presented for Trionychidae (a), Chelydridae (b), freshwater ecotype (c) and terrestrial
677 ecotype (d). Environmental gradient 1 represents 52.88 % total variation and environmental gradient
678 2 represents 22.8 % (contribution of original climate variables are shown in SI 1 Figure 15). Solid
679 contour lines illustrate the full range (100%) of climate space in the two time slices and dashed lines
680 are 50%. A pooled-range approach was used (15), thus contour lines for the Maastrichtian (red) and
681 modern (green) are identical. Shading shows the density of modern species occurrences per grid cell
682 and the red arrow indicates the change in direction of the niche centre from the Maastrichtian to the
683 modern. Blue pixels show niche stability (climate conditions occupied in both time periods), red pixels
684 show niche expansion (climate conditions occupied in the modern only) and green pixels show niche
685 unfilling (climate conditions occupied in the Maastrichtian only).

686 **Figure 3. Availability of non-analogue climate space between the modern and Maastrichtian.**
687 Green = regions of similar climate variables (0 indicates maximum similarity), red = regions with at
688 least one variable outside of the univariate range (type 1 novelty). The more negative values the type
689 1 novelty, the less similar the climates are in these regions.

Figure 1



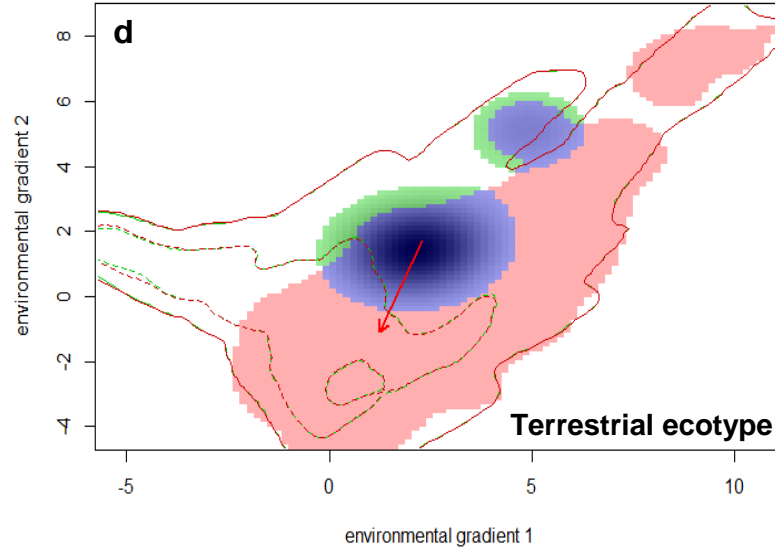
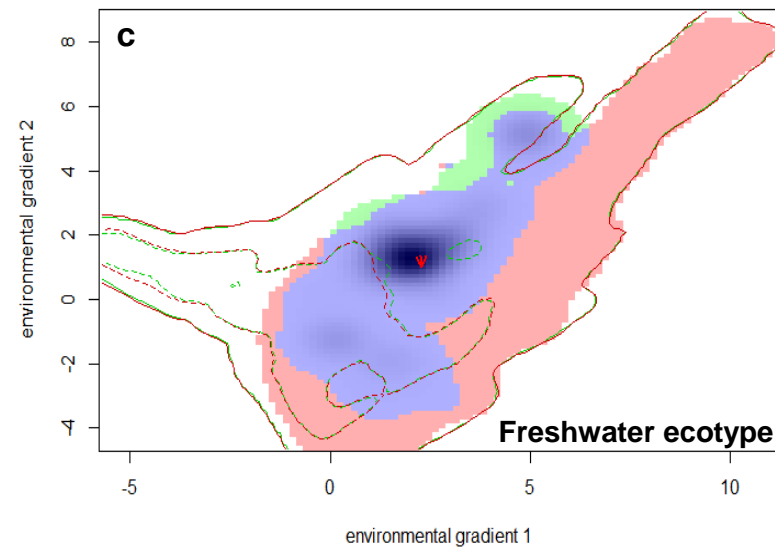
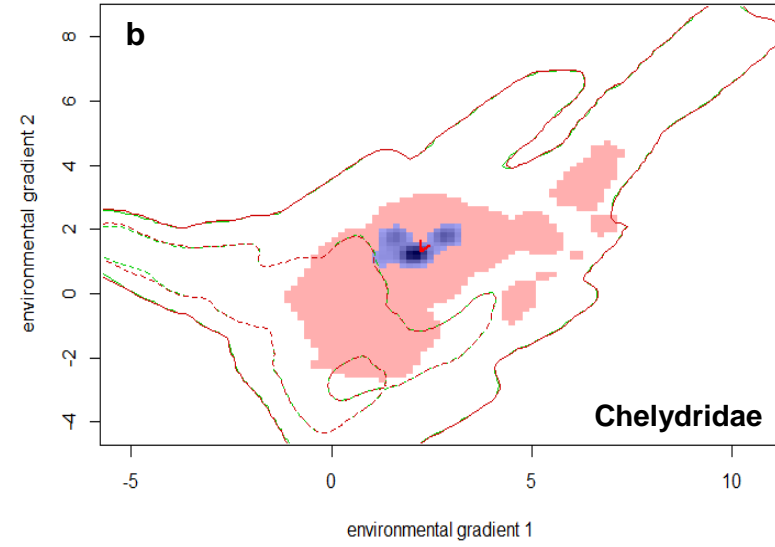
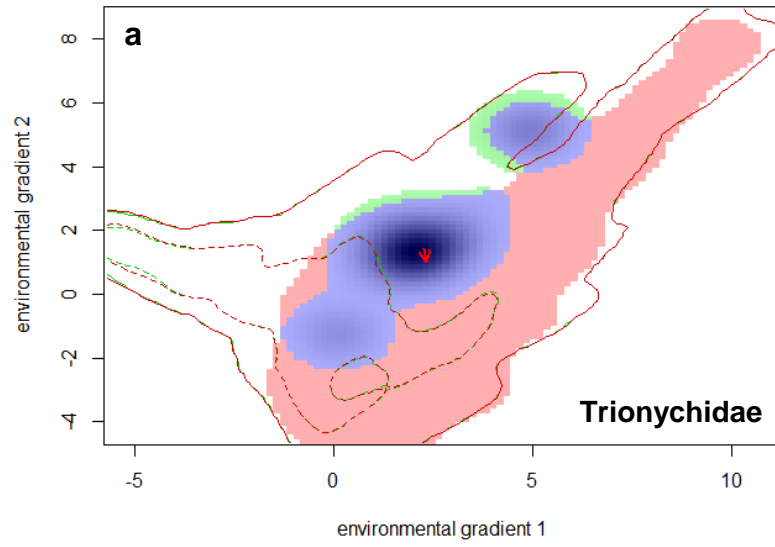


Figure 2

Figure 3

