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1 **Macroevolutionary consequences of profound climate change on niche evolution in**
2 **marine molluscs over the past three million years**

3
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31 **Summary**

32 In order to predict the fate of biodiversity in a rapidly changing world, we must first
33 understand how species adapt to new environmental conditions. The long-term
34 evolutionary dynamics of species' physiological tolerances to differing climatic regimes
35 remains obscure. Here, we unite palaeontological and neontological data to analyse
36 whether species' environmental tolerances remain stable across three million years of
37 profound climatic changes using ten phylogenetically, ecologically, and developmentally
38 diverse mollusc species from the Atlantic and Gulf Coastal Plains, USA. We additionally
39 investigate whether these species' upper and lower thermal tolerances are constrained
40 across this interval. We find that these species' environmental preferences are stable
41 across the duration of their lifetimes, even when faced with significant environmental
42 perturbations. The results suggest that species will respond to current and future warming
43 by altering distributions to track suitable habitat, or, if the pace of change is too rapid, by
44 going extinct. Our findings also support methods that project species' present-day
45 environmental requirements to future climatic landscapes to assess conservation risks.

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48
49
50

Keywords Atlantic Coastal Plain | conservation palaeobiology | fundamental niche | macroevolution | mid-Pliocene Warm Period | Mollusca

51 **1. Introduction**

52 Earth's climate is rapidly changing, altering all facets of our planet at an
53 unprecedented rate, from the biosphere, to the hydrosphere, to the atmosphere. Given
54 these changes, debate exists as to whether species can adapt their physiological tolerances,
55 or niches, to altered environmental conditions [1-4]. Determining whether species' niches
56 evolve or remain stable in the face of environmental change is important for
57 implementing proper conservation measures, mitigating threats posed to biodiversity [5-
58 7], and for shedding light on macroevolutionary dynamics [8-11].

59 Here, we unite palaeontological and neontological data [12] to test niche stability
60 across three million years of environmental changes using ten phylogenetically,
61 ecologically, and developmentally diverse bivalve and gastropod species from the
62 Atlantic and Gulf Coastal Plains, USA, and surrounding region (electronic supplementary
63 material, table S1). Species' niches were quantified using ecological niche modelling [13]
64 for three time periods from the Pliocene—recent: the mid-Pliocene Warm Period
65 (mPWP; ~3.264–3.025 Ma); the Eemian Last Interglacial (LIG; ~130–123 Ka); and the
66 present-day interval (PI). We test whether these species' niches changed across both long
67 (Pliocene to Eemian; millions of years) and short (Eemian to present-day; thousands of
68 years) time scales. We additionally investigate whether these species' upper and lower
69 thermal tolerances changed across millions of years. Recent research suggests that
70 tolerances to heat are largely conserved within terrestrial species, but that tolerances to
71 cold are more variable [14]. This asymmetry is thought to diminish in the marine realm,

72 where ectotherms are limited by both cold and warm conditions due to decreased aerobic
73 capacity [15]. This study is the first to incorporate both modern and fossil data across
74 millions of years to understand ecological and evolutionary responses of species to
75 changes in their environment, though see [16-18] for analyses in deep time.

76 Theoretical [19, 20] and empirical studies have both supported [21, 22] and
77 questioned [16, 23, 24] niche stability. The debate has even continued at the genetic level,
78 where recent research indicates that genetic reshuffling in *Drosophila* species can occur
79 in response to climate change [25, 26]. Whether these genetic changes translate into
80 evolution of actual physiological tolerances, however, remains unclear. The context in
81 which niche evolution is considered is important with respect to whether change occurred
82 in actual physiological tolerances (i.e., the fundamental niche; FN), or whether change
83 occurred because of differences in resource utilization or underlying environmental
84 structure (i.e., changes in the realized niche; RN). Studies may incorrectly indicate niche
85 evolution if the environmental conditions that are available to a species are not taken into
86 account [4, 27, 28].

87 The aforementioned studies have contributed much to our understanding of how
88 species' environmental tolerances evolve, but questions about the relative dominance of
89 niche evolution *versus* stability remain, particularly since most studies lack a temporal
90 component that would allow for analysis of change across the entire duration of a
91 species' lifetime, which may span millions of years [8].

92 The region encompassing and surrounding the Atlantic and Gulf Coastal Plains is
93 ideal for elucidating the coevolution of species' niches and the environment. Not only has
94 it experienced profound environmental changes associated with the closure of the Central
95 American Seaway beginning in the Pliocene [29], but these environmental changes have

96 been linked to patterns of extinction, species turnover, and ecological change [30, 31].
97 The mPWP is considered a climatic analogue for conditions expected at the end of this
98 century and can contribute information on how target species may fare under future
99 climate scenarios [32]. Results such as those presented here are vital for proper mitigation
100 of the risks posed by current and future climate changes to Earth's biodiversity [7, 33].

101

102 **2. Materials and methods**

103 In order to test for within-lineage niche stability, we used ecological niche
104 modelling (ENM), a correlative process whereby known occurrences of species are
105 associated with environmental parameters to characterize a species' environmental
106 requirements [13]. Models of species' abiotic niche parameters were constructed for each
107 of three temporal intervals—the mPWP, LIG, and PI—using taxon occurrence data and
108 environmental parameters unique to each time slice. The resulting niche estimates were
109 compared through time to statistically assess similarity using both environmental and
110 geographic approaches [28, 34, 35]. In both approaches, an observed similarity metric is
111 computed and compared to a simulated null distribution. Details of our methodology are
112 outlined below.

113

114 **(a) Taxa**

115 We selected ten species that occur in both the modern and fossil (from ~3.1 Ma to
116 recent) records of the Atlantic and Gulf Coastal Plains, USA, and surrounding region
117 (Table 1). Species were chosen because they have diverse phylogenetic positions, varied
118 ecological habits and larval developmental modes, and abundant distributional data
119 available from fossil and modern localities (electronic supplementary material, table S1).

120 We used morphological criteria to identify target species, as each taxon is readily
121 diagnosable. All evidence suggests that these lineages represent species that have distinct
122 evolutionary trajectories, a supposition supported by the fact that many invertebrate
123 species have durations greater than three million years [8]. Consequently, we studied
124 within-lineage rather than across-lineage niche evolution, although see the Discussion
125 section for potential caveats.

126

127 **(b) Distributional data**

128 *Present day.* Presence-only distributional data were derived from [36] (electronic
129 supplementary material, table S1 and figures S1-3). Only records with spatial uncertainty
130 <15 km were retained, ensuring that they were matched correctly with corresponding
131 environmental data of a coarser spatial resolution (i.e., 1.25 x 1.25°) [37]. We
132 subsampled distributional data to leave one record per environmental pixel to account for
133 sampling biases in R.15.2 (R Core Team, 2012), which resulted in 20–58 unique
134 occurrences per species (electronic supplementary material, table S1). This process did
135 not affect the resultant overall distribution of the species, but rather prevented certain
136 localities with multiple records from being unduly weighted in the niche modelling
137 analyses [38, 39].

138 *Fossil.* We considered fossil distributional data from mPWP (~3.264–3.025 Ma)
139 and LIG (~130–123 Ka) strata of the Atlantic and Gulf Coastal Plains, USA, and
140 surrounding region. To ensure distributional data were derived from geologic units of
141 similar ages to our periods of interest, we generated a stratigraphic database for all
142 Pliocene–recent geologic units of the Atlantic Coastal Plain (electronic supplementary
143 material, dataset S1). Correlations and unit ages were determined by extensive literature

144 survey and use of various stratigraphic databases, resulting in ten viable formations for
145 the Pliocene and 16 for the LIG. The formations from which occurrence data were
146 derived are documented in dataset S1.

147 Distributional records were obtained from onsite investigations of collections to
148 ensure proper species identification, including the Florida Museum of Natural History,
149 Paleontological Research Institution, Virginia Museum of Natural History, Academy of
150 Natural Sciences of Drexel University, and Yale Peabody Museum. As with present-day
151 distributional data, we subsampled fossil distributional data to leave one record per
152 environmental pixel, resulting in six to 16 unique occurrences per species (electronic
153 supplementary material, table S1). At least six spatially-explicit distributional records
154 were used for model calibration for any given species/time period; studies have shown
155 this number to be statistically robust for extant species [40, 41].

156

157 **(c) Environmental data**

158 Environmental data were derived from the coupled atmosphere-ocean HadCM3
159 global climate model (GCM) [42, 43] for three time slices: mPWP (~3.264–3.025 Ma),
160 LIG (~130–123 Ka), and PI (considering the pre-industrial interval from ~1850–1890).
161 Ideally, we would use an ensemble-modelling approach that considered multiple GCMs
162 [44]; however, model output for the LIG was available to us only from HadCM3 and
163 consisted of variations of temperature and salinity parameters. This GCM has been
164 successfully used in a variety of Quaternary and pre-Quaternary modelling studies [45-
165 47]. Boundary conditions for the LIG were from [46] and [48]. Here, atmospheric gas
166 concentrations were derived from ice core records [49-51], and orbital parameters were
167 from Berger and Loutre [52]. The mPWP GCM used the alternate PRISM3D PlioMIP

168 dataset [53], and the pre-industrial experiment was equivalent to [54]. All GCM
169 experiments were run for 500 model years, and environmental parameters were averaged
170 from the final 30 years of each experiment at 1.25 x 1.25° resolution (~140 x 140 km at
171 the equator). Where ocean data were unavailable (i.e., sites presenting macrofossil data,
172 but where the GCM indicated land), we used an inverse-distance weighted algorithm to
173 extrapolate model data.

174 Modelled monthly salinity and temperature outputs were converted to maximum,
175 minimum, and average yearly coverages for both surface and bottom conditions using
176 ArcGIS. From these 12 coverages, we eliminated variables that significantly co-varied
177 (assessed using the ‘cor’ function in R.15.2; R Core Team, 2012). Ultimately, two bottom
178 variables (yearly average salinity and temperature) and four surface variables (maximum
179 and minimum salinity, and maximum and minimum temperature) were retained. These
180 six variables were preserved because they did not significantly co-vary and are deemed
181 biologically important for marine ectotherms [55-57].

182

183 **(d) Modelling algorithm**

184 To approximate niche parameters for these species, we generated ENMs using
185 Maxent v.3.3.3 [58] (figure 1 and electronic supplementary material, figures S4-5).
186 Maxent finds suitable environmental combinations for species under a null expectation
187 that suitability is proportional to availability. Thus, Maxent minimized the relative
188 entropy of observed environments relative to those in the background [59]. We enabled
189 only quadratic features to simulate realistic bell-shaped response curves that are known
190 from physiological experiments of plants and animals [60-62]. We calibrated models
191 within a region bounded by the Americas and 34°W longitude, and 48°N and 44°S

192 latitude (figure 1). We sought the union of the area sampled by researchers and most
193 likely accessible to the species across spatial and temporal dimensions [13, 63, 64]. We
194 used all spatially-explicit data points for each species/time slice, running 100 bootstrap
195 replicates with a ten per cent random test percentage. The mean value of the suitability
196 grids was used to threshold to binary predictions [65, 66].

197 To correct for potential biases in fossil distributional data, we implemented what
198 is called a ‘bias file’ within Maxent for past modelling [67]. The bias file describes the
199 probability that an area was sampled; thus, regions with rock outcrop (i.e., areas where
200 species may actually be sampled) were weighted twice as heavily as regions without rock
201 outcrop. Maxent will then factor out this bias during the modelling process (see [67] for
202 details). This method essentially accounts for incomplete knowledge of species’
203 distributions *sensu* [68].

204 Although characterizing the entirety of a species’ FN is often difficult without
205 mechanistic studies [14], we study close approximations here, given that recent
206 biophysical approaches have determined that FNs can be represented by limited sets of
207 parameters such as temperature [69, 70]. This is particularly true for marine ectotherms,
208 which have been shown to closely match range limits within their thermal tolerances [15].
209 That being said, our estimates may reflect some quantity between the RN and the FN,
210 since our niche parameters are ultimately derived from the areas occupied by a species
211 [13, 14, 27].

212

213 **(e) Model verification**

214 Two model validation methods were used, depending on the prevalence of
215 distributional records (electronic supplementary material, table S2). For species/time

216 slices with <25 points, we assessed statistical significance using a jackknife procedure
217 under a least training presence threshold [41]. This method, however, may produce over-
218 optimistic estimates of predictive power for sample sizes >25, and these species/time
219 slices were tested using partial Receiver Operating Characteristic analyses [71].

220

221 **(f) Niche comparisons**

222 Characterizations of species' niches were compared through time using two
223 statistical approaches: a kernel smoothing script [28] and ENMTools [35]. Both
224 frameworks use randomization tests to compare observed similarity to that expected
225 under a null hypothesis. The null is rejected if models are more or less similar than
226 expected by chance, based on the environment within the geographical regions of interest.
227 Similarity is quantified using Schoener's D [72], with values ranging from 0 to 1, or more
228 to less similar, respectively.

229 For each of the ten species, we compared observed niches across the three
230 different time periods (mPWP, LIG, and PI). Comparisons were made in two directions
231 [28, 35]; e.g., comparing the mPWP to the LIG, and the LIG to the mPWP, since it is
232 possible for two niches to be more similar than expected based on the environment
233 available for one time slice, but less similar than expected based on the environment
234 available for the other. If the observed value fell outside the null distribution to the high
235 end, niches were more similar than expected by chance, whereas if the observed value
236 fell outside the null distribution to the lower end, niches were more different than
237 expected by chance. Observed values that fell within the null distribution did not allow
238 for discrimination of similarity or differences based on the environment available to the
239 entities in question. We performed similarity tests using (1) a PCA applied to all six

240 environmental variables; (2) a PCA applied to the three most important environmental
241 variables; (3) raw average bottom temperature and maximum surface temperature in two-
242 dimensional environmental space; (4) maximum surface temperature only; (5) minimum
243 surface temperature only; and (6) ENMTools on projections of ecological niche models.
244 The first five sets of tests compare niches in environmental space, with the first three
245 multi-dimensional in nature, whereas the sixth compares niches in geographic space.
246 Each of these tests resulted in 60 comparisons (i.e., 10 species x three time slices x two
247 directions), for a total of 360. Details of the comparisons are provided below.

248 *Environmental comparisons.* We calculated metrics of niche overlap in gridded
249 environmental space using the methodology of [28]. Here, ordination techniques [73]
250 allow for direct comparison of species-environment relationships in environmental space
251 [27]. Observed densities for each region are corrected in light of the availability of
252 environmental space using kernel density functions (table 1 and electronic supplementary
253 material, table S3 and dataset S2). Niche overlap is measured along gradients of a
254 multivariate analysis, and statistical significance is assessed using the framework
255 described above.

256 We tested for similarity using a principal component analysis (PCA) (1) applied
257 to all six environmental parameters, and (2) when niche dimensionality was reduced to
258 three variables, including surface coverages for maximum salinity, maximum
259 temperature, and minimum temperature. These variables were retained because they
260 explained the most variance in the dataset [57, 74, 75]. Analyses performed with this
261 reduced set of variables are potentially more informative, as over-parameterization can
262 constrict niche estimates and lead to approximations closer to the RN [13]. PCA analyses
263 were calibrated on environments of both time slices (setting project equal to false). We

264 used both the PCA-occ and PCA-env functions; the former calibrates the PCA based only
265 on the distributional data, whereas the latter uses data from the entire environmental
266 space of the two study systems. The results were equivalent, and thus we present only
267 those from PCA-env. A bin size of 100 was used to characterize the environment,
268 running 1,000 replicates for similarity tests. Since prevalence of distributional data varies
269 through time, we generated input data from ENMs outside of the framework of [28],
270 subsampling one point per pixel in binary predictions such that comparisons were
271 unbiased with regard to the quantity of input data. Doing so ensures that we capture all of
272 the environments that a species finds suitable, rather than the portion that happened to be
273 occupied most frequently.

274 We also tested similarity in raw variables (table 1 and electronic supplementary
275 material, table S3 and dataset S2). We used the script of [28] to analyse each of the six
276 variables individually, and we modified the script to compare raw variables in two
277 dimensions, while still accounting for differences in availability of environments in a
278 given time period. We were interested in testing for evolution in overall temperature
279 parameters, and thus we assessed similarity using average bottom temperature and
280 maximum surface temperature.

281 ***Geographic projections.*** In addition to the comparisons made entirely in
282 environmental space, we used ENMTools [35] to compare the geographic projections of
283 niches. Null distributions consisted of 100 random models generated within Maxent, with
284 model parameters drawn from and constrained by the study system. To ensure accurate
285 response curves when projecting, we disabled clamping and enabled extrapolation within
286 Maxent [76].

287

288 **3. Results**

289 Model verification exercises suggest that models of species' niches are
290 statistically significant for each time slice ($P < 0.05$; see electronic supplementary material,
291 table S2). The niche model depictions are shown in figure 1 and electronic supplementary
292 material, figures S4-5.

293 Together, the suite of niche comparisons (360 in total) indicates these species'
294 environmental preferences are stable across millions of years. In 359 of 360 cases, we
295 found no evidence of niche dissimilarity across all comparisons. Indeed, of the ten
296 ecologically diverse species studied, nine show the opposite pattern: statistically similar
297 niches for the majority of the comparisons. Probabilistically, this result would be
298 obtained $< 1\%$ of the time, assuming equal likelihood for evolution *versus* stability of
299 niche attributes. We obtain evidence of niche similarity for tests on both principle
300 component analyses (PCAs) and raw variables. Moreover, minimum and maximum
301 temperature tolerances are generally conserved through time.

302

303 **(a) Environmental comparisons**

304 Comparisons on multi-dimensional niches indicate overwhelming signals of niche
305 stability across the time slices. Of these 180 comparisons, 149 indicate statistically
306 similar niches through time, and no comparison found evidence of niche dissimilarity.

307 Comparisons considering all six environmental variables indicate niches are
308 statistically similar for most species and time slices (46 of 60 comparisons) (electronic
309 supplementary material, table S3). When niche dimensionality was reduced to the most
310 important variables, nine species show statistically similar niches for all comparisons,
311 with the exception of one or two inconclusive tests for *Crepidula fornicata*, *Dinocardium*

312 *robustum*, *Lucina pensylvanica*, and *Neverita duplicata* (49 of 60 comparisons; figure 2
313 and table 1). *Bulla occidentalis* is the only species with non-significant tests across
314 multiple time slices. This species does not have any readily identifiable traits—such as
315 larval strategy or feeding ecology—that would predispose it to occupying new
316 environments relative to the other species that we studied. Niches also show stability
317 when raw variables are considered. Seven of the ten species have statistically similar
318 niches across all time comparisons (42 of 60 comparisons; electronic supplementary
319 material, table S3). Two other species, *Oliva sayana* and *Crassostrea virginica*, have
320 statistically similar niches with the exception of one and two inconclusive tests,
321 respectively. Quantifying niche similarity for *B. occidentalis* proved more difficult, as
322 three of six niche comparisons are non-significant (but not statistically different).

323 Species seem to conserve their upper thermal tolerance limits, but results are less
324 conclusive for minimum temperature tolerances (table 1 and electronic supplementary
325 material, dataset S2). Across the suite of species, the majority of comparisons are
326 statistically similar with regard to maximum surface temperature, although five species
327 have one or two comparisons that are inconclusive (*B. occidentalis*, *D. robustum*, *L.*
328 *pensylvanica*, *N. duplicata*, *O. sayana*, and *Terebra dislocata*). Comparisons also indicate
329 statistical similarity with regard to minimum temperature tolerances. However, the
330 structure of this variable changes through time, making it difficult to quantify similarities
331 or differences. For example, all mPWP–LIG comparisons are inconclusive with the
332 exception of *N. duplicata*, as are at least half of the comparisons for *B. occidentalis* and *L.*
333 *pensylvanica*.

334

335 **(b) Geographic comparisons**

336 Results from comparisons of the geographic projections of niches mirror those
337 from the environmental comparisons. Niches are statistically similar for seven of the ten
338 species across all comparisons (42 of 60 comparisons; electronic supplementary material,
339 table S3 and dataset S2). *Crassostrea virginica* and *L. pensylvanica* have one comparison
340 that is inconclusive (LIG–mPWP and PI–mPWP, respectively), while the niche of *B.*
341 *occidentalis* is significantly dissimilar for the LIG–mPWP comparison and non-
342 significant for the PI–mPWP comparison.

343

344 **4. Discussion**

345 Our analyses find no support for niche evolution. Instead, we observe statistically
346 significant niche stability across three million years of considerable environmental
347 changes, from extreme warmth during the mPWP to glacial cycles during the Pleistocene
348 [29]. This is true for all of ten of the species analysed. Importantly, niche stability will
349 not be recovered within analyses for reasons other than similarity, whereas niche
350 differences can be obtained as a function of changing parameters of the RN [14].
351 Therefore, the lack of any net change suggests that species were either shifting their niche
352 preferences in response to oscillating climatic conditions at scales too rapid to be detected
353 by our analyses, or their preferences remained stable across this temporal interval. In
354 either case, overall niche stability has profound implications for understanding
355 conservation priorities and for elucidating macroevolutionary dynamics.

356

357 **(a) Implications for survival of taxa during times of change**

358 These results aid our understanding of how species may respond to climate
359 change on both long and short time scales. As climate continues to change, species that

360 are unable to adapt to new conditions face two futures: extinction or shifting distributions
361 to follow suitable areas. Already, both responses have been documented or predicted as a
362 result of current climate change. Marine and terrestrial species are forecast to experience
363 climate-driven extinctions into the 22nd century [77, 78]. Indeed, the niche stability we
364 have documented may doom many marine species to extinction over the next 100+ years,
365 particularly if they live at their thermal tolerance limits and are unable to alter their upper
366 thresholds [57]. The target species considered here are predicted to experience severe
367 distributional reductions by the end of this century when variables other than temperature
368 and salinity are considered, but wholesale extinction is unlikely [36]. This prediction is
369 supported by their survival in the Pliocene, albeit in geographically-reduced areas, when
370 conditions were purportedly similar to those expected at the end of this century [32].
371 These small areas of suitability—or refugia—are thought to have played an important
372 role in species' survival during past episodes of climate change [79].

373 If species are able to keep pace with the changing environment, distributional
374 shifts, rather than extinctions, are expected [33]. Under this scenario, dispersal ability
375 becomes an important parameter predicting species' responses to climate change [80].
376 Present-day elevational, latitudinal, and bathymetric shifts [81] have already been
377 observed in response to current warming patterns, and, indeed, the fossil record provides
378 abundant evidence for habitat tracking during rapid Pleistocene climate cycles [82], often
379 creating non-analogous community assemblages [83]. The rate at which climate changes
380 also dictates whether species can track preferred environments, and future rates are
381 anticipated to exceed those experienced during the geologic intervals analysed within this
382 study [57, 84, 85]. In a rapidly changing world, species will most likely be forced to
383 move to suitable areas or face extinction, since it seems unlikely they will alter their

384 abiotic preferences on extremely short time scales if they are unable to do so on longer
385 time scales, as we demonstrated here.

386 Methodologically, niche stability provides support for ENM and species
387 distribution modelling (SDM) analyses that attempt to predict how species will respond
388 to altered climatic conditions [13]. In particular, our results may somewhat alleviate
389 concerns over inaccurate forecasts due to changing niches [1, 3]. Problems still remain,
390 however, in that ENM and SDM methods typically do not account for dispersal
391 limitations or altered biotic interactions [86], though see [84], nor do they consider that
392 species can alter their behaviour or microhabitat preferences to buffer against
393 environmental changes [2, 87].

394

395 **(b) Macroevolutionary implications of stable niches**

396 We show that large-scale parameters of species' niches, in this case temperature
397 and salinity, do not change for a phylogenetically and ecologically diverse set of marine
398 molluscs. Although species may modify their behaviour or resource utilization, the FN
399 places constraints on species' interactions with the environment, which potentially
400 governs speciation and extinction processes over long time scales [10, 88]. Some
401 researchers have suggested that niche stability may promote allopatric speciation [89, 90].
402 That is, environmental perturbations may separate two populations, with those
403 populations prevented from merging back together because of constraints imposed by the
404 FN, which will then eventually lead to diversification.

405 Niche stability also provides a potential mechanism for the morphological stasis
406 observed within species over millions of years [8]. More specifically, niche stability
407 requires species to track preferred habitats as the environment changes, thereby

408 continuously joining and separating populations on scales less than 10,000 years or so. In
409 this framework, any localized phenotypic adaptation is unlikely to be fixed across an
410 entire species, such that no overall net changes are observed for the species as a whole [8].

411

412 **(c) Potential caveats**

413 Although our analyses are quantitatively robust, our study is not without
414 limitations. First, our models may approximate the existing or realized niche, rather than
415 the FN [91], because FNs are difficult to characterize without detailed physiological
416 studies [13, 14]. With that said, niche estimates were calculated from environmental
417 preferences that were averaged over a period of time, which may broaden estimates such
418 that real physiological limits are captured [57]. The recovered pattern of niche stability is
419 even more robust if we studied RNs, since change is expected to occur over time in RN
420 parameters owing to differences in resource utilization or underlying environmental
421 structure [4, 13, 27]. Second, estimates of present-day and past niches may not be
422 equivalent and thus incomparable. This, however, is of less concern here since we
423 documented niche stability rather than niche evolution. Third, we acknowledge that
424 recognition of ‘species’—especially in the fossil record—is sometimes contentious, and
425 while these species are diagnosably distinct throughout their duration, they may not
426 constitute single evolutionary lineages. Our results, however, are even more robust if we
427 studied aggregated collections of closely-related lineages, since we would expect more
428 change in niche parameters at speciation. We support conservatism of niches across
429 speciation events if the entities in question represent closely-related species complexes.
430 Fourth, we analysed data from warm time periods, as distributional data do not exist for
431 glacial periods (e.g., the last glacial maximum; ~21 Ka). Therefore, our analyses may

432 have missed rapid (but reversible) niche evolution that occurred in response to these
433 colder conditions. Although possible, the scenario is unlikely because of the rate at which
434 niche evolution would have had to occur, and because of the paucity of evidence for
435 niche adaptation both in the fossil record [82] and in experimental studies [14]. Moreover,
436 environmental conditions at the mPWP, LIG, and PI differ to a significant degree, such
437 that we are still able to discern whether species adapted to new conditions or tracked
438 stable climate envelopes. Finally, and related to this issue, because palaeoclimate models
439 were only available for certain key temporal intervals, we could not capture the entire
440 temporal history of these species in the context of an ENM framework. We did, however,
441 examine changes across both long (mPWP to LIG) and short (LIG to PI) time scales.

442

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467

468 **Data accessibility**

469 The stratigraphic database (dataset S1) and output from niche comparison tests (dataset
470 S2) are available in the electronic supplementary material. Climate and distributional data
471 are available on Dryad, doi: XXX.

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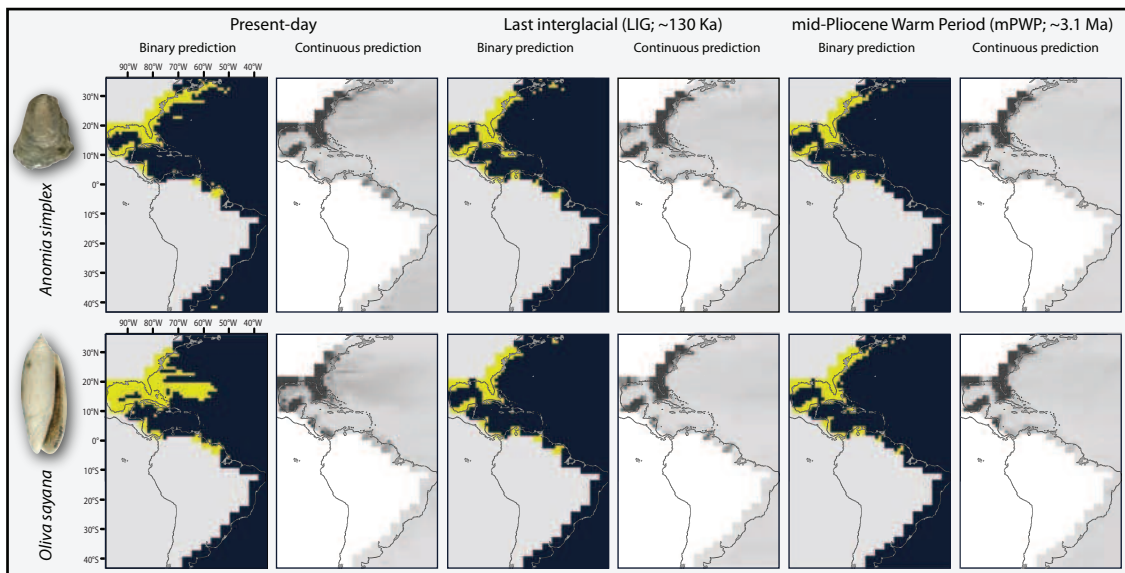
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727 **Figure and Table Legends**

728 **Figure 1 | Representative ecological niche models.** Model results for the present, Last
729 Interglacial, and mid-Pliocene Warm Period for two species: *Anomia simplex* and *Oliva*
730 *sayana*. Binary and continuous predictions are presented, with binary predictions
731 thresholded using the mean suitability value from the continuous output. For the binary
732 predictions, yellow=suitable and dark blue=unsuitable, whereas for the continuous
733 predictions, darker greys indicate higher suitability. All analyses were conducted within
734 the geographic extent shown. Note that the modelled shorelines do not match the
735 continental shorelines because of the nature of our GCM data and the need to capture the
736 higher sea levels characteristic of the mid-Pliocene Warm Period. See electronic
737 supplementary material, figures S4-5, for remaining species analysed.



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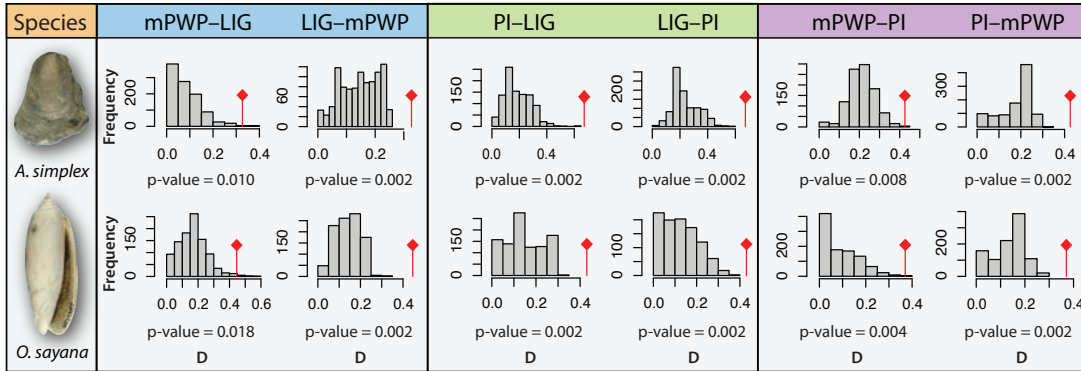
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748 **Figure 2 | Representative results from niche comparison analyses.** Comparisons for
 749 *Anomia simplex* and *Oliva sayana* using a PCA on the three most important
 750 environmental variables: maximum and minimum surface temperature, and maximum
 751 surface salinity. Comparisons are shown for the Last Interglacial (LIG, ~130 Ka), mid-
 752 Pliocene Warm Period (mPWP, ~3.1 Ma), and present-day (PI). The histograms show the
 753 null distribution of similarity values (D) drawn from the study area, with the observed
 754 similarity value in red. All comparisons indicate that niches are statistically more similar
 755 than expected given the environmental backgrounds. For other comparisons, see table 1
 756 and electronic supplementary material, table S3 and dataset S2.



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772 **Table 1 | Comparisons of multi-dimensional niches and thermal tolerance limits.**
 773 Bold values indicate non-significant results. All other comparisons are statistically more
 774 similar than expected given the environmental background of the variable in question.
 775 Note that it is possible for two niches to be more similar than expected based on the
 776 environment available for one time slice, but less similar than expected based on the
 777 environment available for the other. See electronic supplementary material, dataset S2,
 778 for graphical depictions of similarity tests

Species/Comparison	mPWP-LIG	LIG-mPWP	PI-LIG	LIG-PI	mPWP-PI	PI-mPWP	
Environmental comparison: p-values for tests using PCA on 3 most important variables							
Bivalvia	<i>Anomia simplex</i>	0.01	0.00	0.00	0.00	0.01	0.00
	<i>Crassostrea virginica</i>	0.04	0.00	0.03	0.00	0.00	0.00
	<i>Dinocardium robustum</i>	0.01	0.00	0.00	0.02	0.09	0.00
	<i>Lucina pensylvanica</i>	0.25	0.01	0.00	0.00	0.03	0.03
	<i>Mercenaria campechiensis</i>	0.01	0.00	0.00	0.02	0.00	0.00
Gastropoda	<i>Bulla occidentalis</i>	0.34	0.54	0.10	0.29	0.31	0.20
	<i>Crepidula fornicata</i>	0.03	0.00	0.02	0.00	0.29	0.58
	<i>Neverita duplicata</i>	0.08	0.00	0.01	0.44	0.01	0.00
	<i>Oliva sayana</i>	0.02	0.00	0.00	0.00	0.00	0.00
	<i>Terebra dislocata</i>	0.02	0.00	0.00	0.01	0.00	0.00
Environmental comparison: maximum surface temperature							
Bivalvia	<i>Anomia simplex</i>	0.04	0.00	0.00	0.00	0.00	0.00
	<i>Crassostrea virginica</i>	0.00	0.00	0.00	0.02	0.01	0.00
	<i>Dinocardium robustum</i>	0.03	0.00	0.00	0.00	0.09	0.00
	<i>Lucina pensylvanica</i>	0.00	0.00	0.00	0.00	0.81	0.42
	<i>Mercenaria campechiensis</i>	0.01	0.00	0.00	0.03	0.00	0.00
Gastropoda	<i>Bulla occidentalis</i>	0.00	0.00	0.02	0.60	0.96	0.02
	<i>Crepidula fornicata</i>	0.00	0.00	0.00	0.00	0.01	0.00
	<i>Neverita duplicata</i>	0.01	0.00	0.00	0.06	0.00	0.00
	<i>Oliva sayana</i>	0.00	0.00	0.01	0.15	0.54	0.00
	<i>Terebra dislocata</i>	0.03	0.00	0.00	0.02	0.43	0.02
Environmental comparison: minimum surface temperature							
Bivalvia	<i>Anomia simplex</i>	0.21	0.00	0.00	0.00	0.00	0.00
	<i>Crassostrea virginica</i>	0.91	0.05	0.00	0.03	0.01	0.00
	<i>Dinocardium robustum</i>	0.11	0.00	0.00	0.00	0.00	0.00
	<i>Lucina pensylvanica</i>	0.68	0.00	0.00	0.00	0.77	0.22
	<i>Mercenaria campechiensis</i>	0.82	0.00	0.00	0.00	0.01	0.00
Gastropoda	<i>Bulla occidentalis</i>	0.66	0.00	0.09	0.10	0.85	0.10
	<i>Crepidula fornicata</i>	0.17	0.00	0.01	0.00	0.44	0.00
	<i>Neverita duplicata</i>	0.50	0.00	0.05	0.00	0.00	0.00
	<i>Oliva sayana</i>	0.07	0.00	0.03	0.00	0.29	0.00
	<i>Terebra dislocata</i>	0.18	0.00	0.00	0.00	0.05	0.00

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