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

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Summary

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

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

1. Introduction

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

Here, we unite palaeontological and neontological data [12] to test niche stability across three million years of environmental changes using ten phylogenetically, ecologically, and developmentally diverse bivalve and gastropod species from the Atlantic and Gulf Coastal Plains, USA, and surrounding region (electronic supplementary material, table S1). Species' niches were quantified using ecological niche modelling [13] for three time periods from the Pliocene—recent: the mid-Pliocene Warm Period (mPWP; ~3.264–3.025 Ma); the Eemian Last Interglacial (LIG; ~130–123 Ka); and the present-day interval (PI). We test whether these species' niches changed across both long (Pliocene to Eemian; millions of years) and short (Eemian to present-day; thousands of years) time scales. We additionally investigate whether these species' upper and lower thermal tolerances changed across millions of years. Recent research suggests that tolerances to heat are largely conserved within terrestrial species, but that tolerances to cold are more variable [14]. This asymmetry is thought to diminish in the marine realm, where ectotherms are limited by both cold and warm conditions due to decreased aerobic capacity [15]. This study is the first to incorporate both modern and fossil data across millions of years to understand ecological and evolutionary responses of species to changes in their environment, though see [16-18] for analyses in deep time.

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

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

The region encompassing and surrounding the Atlantic and Gulf Coastal Plains is ideal for elucidating the coevolution of species' niches and the environment. Not only has it experienced profound environmental changes associated with the closure of the Central American Seaway beginning in the Pliocene [29], but these environmental changes have been linked to patterns of extinction, species turnover, and ecological change [30, 31]. The mPWP is considered a climatic analogue for conditions expected at the end of this century and can contribute information on how target species may fare under future climate scenarios [32]. Results such as those presented here are vital for proper mitigation of the risks posed by current and future climate changes to Earth's biodiversity [7, 33].

2. Materials and methods

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

(a) Taxa

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

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

(b) Distributional data

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

Fossil. We considered fossil distributional data from mPWP (~3.264–3.025 Ma) and LIG (~130–123 Ka) strata of the Atlantic and Gulf Coastal Plains, USA, and surrounding region. To ensure distributional data were derived from geologic units of similar ages to our periods of interest, we generated a stratigraphic database for all Pliocene–recent geologic units of the Atlantic Coastal Plain (electronic supplementary material, dataset S1). Correlations and unit ages were determined by extensive literature survey and use of various stratigraphic databases, resulting in ten viable formations for the Pliocene and 16 for the LIG. The formations from which occurrence data were derived are documented in dataset S1.

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

(c) Environmental data

Environmental data were derived from the coupled atmosphere-ocean HadCM3 global climate model (GCM) [42, 43] for three time slices: mPWP (~3.264–3.025 Ma), LIG (~130–123 Ka), and PI (considering the pre-industrial interval from ~1850–1890). Ideally, we would use an ensemble-modelling approach that considered multiple GCMs [44]; however, model output for the LIG was available to us only from HadCM3 and consisted of variations of temperature and salinity parameters. This GCM has been successfully used in a variety of Quaternary and pre-Quaternary modelling studies [45-47]. Boundary conditions for the LIG were from [46] and [48]. Here, atmospheric gas concentrations were derived from ice core records [49-51], and orbital parameters were from Berger and Loutre [52]. The mPWP GCM used the alternate PRISM3D PlioMIP dataset [53], and the pre-industrial experiment was equivalent to [54]. All GCM experiments were run for 500 model years, and environmental parameters were averaged from the final 30 years of each experiment at 1.25 x 1.25° resolution (~140 x 140 km at the equator). Where ocean data were unavailable (i.e., sites presenting macrofossil data, but where the GCM indicated land), we used an inverse-distance weighted algorithm to extrapolate model data.

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

(d) Modelling algorithm

To approximate niche parameters for these species, we generated ENMs using Maxent v.3.3.3 [58] (figure 1 and electronic supplementary material, figures S4-5). Maxent finds suitable environmental combinations for species under a null expectation that suitability is proportional to availability. Thus, Maxent minimized the relative entropy of observed environments relative to those in the background [59]. We enabled only quadratic features to simulate realistic bell-shaped response curves that are known from physiological experiments of plants and animals [60-62]. We calibrated models within a region bounded by the Americas and 34°W longitude, and 48°N and 44°S latitude (figure 1). We sought the union of the area sampled by researchers and most likely accessible to the species across spatial and temporal dimensions [13, 63, 64]. We used all spatially-explicit data points for each species/time slice, running 100 bootstrap replicates with a ten per cent random test percentage. The mean value of the suitability grids was used to threshold to binary predictions [65, 66].

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

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

(e) Model verification

Two model validation methods were used, depending on the prevalence of distributional records (electronic supplementary material, table S2). For species/time slices with <25 points, we assessed statistical significance using a jackknife procedure under a least training presence threshold [41]. This method, however, may produce over-optimistic estimates of predictive power for sample sizes >25, and these species/time slices were tested using partial Receiver Operating Characteristic analyses [71].

(f) Niche comparisons

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

For each of the ten species, we compared observed niches across the three different time periods (mPWP, LIG, and PI). Comparisons were made in two directions [28, 35]; e.g., comparing the mPWP to the LIG, and the LIG to the mPWP, since it is possible for two niches to be more similar than expected based on the environment available for one time slice, but less similar than expected based on the environment available for the other. If the observed value fell outside the null distribution to the high end, niches were more similar than expected by chance, whereas if the observed value fell outside the null distribution to the lower end, niches were more different than expected by chance. Observed values that fell within the null distribution did not allow for discrimination of similarity or differences based on the environment available to the entities in question. We performed similarity tests using (1) a PCA applied to all six environmental variables; (2) a PCA applied to the three most important environmental variables; (3) raw average bottom temperature and maximum surface temperature in two-dimensional environmental space; (4) maximum surface temperature only; (5) minimum surface temperature only; and (6) ENMTools on projections of ecological niche models. The first five sets of tests compare niches in environmental space, with the first three multi-dimensional in nature, whereas the sixth compares niches in geographic space. Each of these tests resulted in 60 comparisons (i.e., 10 species x three time slices x two directions), for a total of 360. Details of the comparisons are provided below.

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

We tested for similarity using a principal component analysis (PCA) (1) applied to all six environmental parameters, and (2) when niche dimensionality was reduced to three variables, including surface coverages for maximum salinity, maximum temperature, and minimum temperature. These variables were retained because they explained the most variance in the dataset [57, 74, 75]. Analyses performed with this reduced set of variables are potentially more informative, as over-parameterization can constrict niche estimates and lead to approximations closer to the RN [13]. PCA analyses were calibrated on environments of both time slices (setting project equal to false). We used both the PCA-occ and PCA-env functions; the former calibrates the PCA based only on the distributional data, whereas the latter uses data from the entire environmental space of the two study systems. The results were equivalent, and thus we present only those from PCA-env. A bin size of 100 was used to characterize the environment, running 1,000 replicates for similarity tests. Since prevalence of distributional data varies through time, we generated input data from ENMs outside of the framework of [28], subsampling one point per pixel in binary predictions such that comparisons were unbiased with regard to the quantity of input data. Doing so ensures that we capture all of the environments that a species finds suitable, rather than the portion that happened to be occupied most frequently.

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

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

3. Results

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

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

(a) Environmental comparisons

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

Comparisons considering all six environmental variables indicate niches are statistically similar for most species and time slices (46 of 60 comparisons) (electronic supplementary material, table S3). When niche dimensionality was reduced to the most important variables, nine species show statistically similar niches for all comparisons, with the exception of one or two inconclusive tests for *Crepidula fornicata*, *Dinocardium* *robustum*, *Lucina pensylvanica*, and *Neverita duplicata* (49 of 60 comparisons; figure 2 and table 1). *Bulla occidentalis* is the only species with non-significant tests across multiple time slices. This species does not have any readily identifiable traits—such as larval strategy or feeding ecology—that would predispose it to occupying new environments relative to the other species that we studied. Niches also show stability when raw variables are considered. Seven of the ten species have statistically similar niches across all time comparisons (42 of 60 comparisons; electronic supplementary material, table S3). Two other species, *Oliva sayana* and *Crassostrea virginica*, have statistically similar niches with the exception of one and two inconclusive tests, respectively. Quantifying niche similarity for *B. occidentalis* proved more difficult, as three of six niche comparisons are non-significant (but not statistically different).

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

(b) Geographic comparisons

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

4. Discussion

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

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

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

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

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

(b) Macroevolutionary implications of stable niches

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

Niche stability also provides a potential mechanism for the morphological stasis observed within species over millions of years [8]. More specifically, niche stability requires species to track preferred habitats as the environment changes, thereby continuously joining and separating populations on scales less than 10,000 years or so. In this framework, any localized phenotypic adaptation is unlikely to be fixed across an entire species, such that no overall net changes are observed for the species as a whole [8].

(c) Potential caveats

Although our analyses are quantitatively robust, our study is not without limitations. First, our models may approximate the existing or realized niche, rather than the FN [91], because FNs are difficult to characterize without detailed physiological studies [13, 14]. With that said, niche estimates were calculated from environmental preferences that were averaged over a period of time, which may broaden estimates such that real physiological limits are captured [57]. The recovered pattern of niche stability is even more robust if we studied RNs, since change is expected to occur over time in RN parameters owing to differences in resource utilization or underlying environmental structure [4, 13, 27]. Second, estimates of present-day and past niches may not be equivalent and thus incomparable. This, however, is of less concern here since we documented niche stability rather than niche evolution. Third, we acknowledge that recognition of 'species'—especially in the fossil record—is sometimes contentious, and while these species are diagnosably distinct throughout their duration, they may not constitute single evolutionary lineages. Our results, however, are even more robust if we studied aggregated collections of closely-related lineages, since we would expect more change in niche parameters at speciation. We support conservatism of niches across speciation events if the entities in question represent closely-related species complexes. Fourth, we analysed data from warm time periods, as distributional data do not exist for glacial periods (e.g., the last glacial maximum; ~21 Ka). Therefore, our analyses may have missed rapid (but reversible) niche evolution that occurred in response to these colder conditions. Although possible, the scenario is unlikely because of the rate at which niche evolution would have had to occur, and because of the paucity of evidence for niche adaptation both in the fossil record [82] and in experimental studies [14]. Moreover, environmental conditions at the mPWP, LIG, and PI differ to a significant degree, such that we are still able to discern whether species adapted to new conditions or tracked stable climate envelopes. Finally, and related to this issue, because palaeoclimate models were only available for certain key temporal intervals, we could not capture the entire temporal history of these species in the context of an ENM framework. We did, however, examine changes across both long (mPWP to LIG) and short (LIG to PI) time scales.

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Data accessibility

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

References

1. Pearman P.B., Guisan A., Broennimann O., Randin C.F. 2008 Niche dynamics in space and time. *Trends Ecol Evol* **23**, 149–158.
2. Lavergne S., Mouquet N., Thuiller W., Ronce O. 2010 Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. *Annu Rev Ecol Evol Syst* **41**, 321–350.
3. Hoffmann A.A., Sgrò C.M. 2011 Climate change and evolutionary adaptation. *Nature* **470**, 479–485.
4. Guisan A., Petitpierre B., Broennimann O., Daehler C., Kueffer C. 2014 Unifying niche shift studies: insights from biological invasions. *Trends Ecol Evol* **29**, 260–269.
5. Pereira H.M., Leadley P.W., Proença V., Alkemade R., Scharlemann J.P.W., Fernandez-Manjarrés J.F., Araújo M.B., Balvanera P., Biggs R., Cheung W.W.L., et al. 2010 Scenarios for global biodiversity in the 21st Century. *Science* **330**, 1496–1501.
6. Dawson T.P., Jackson S.T., House J.I., Prentice I.C., Mace G.M. 2011 Beyond predictions: biodiversity conservation in a changing climate. *Science* **332**, 53–58.
7. Moritz C., Agudo R. 2013 The future of species under climate change: resilience or decline? *Science* **341**, 504–508.
8. Eldredge N., Thompson J.N., Brakefield P.M., Gavrilets S., Jablonski D., Jackson J.B.C., Lenski R.E., Lieberman B.S., McPeek M.A., Miller W.I. 2005 The dynamics of evolutionary stasis. *Paleobiology* **31**, 133–145.
9. Romdal T., Araújo M.B., Rahbek C. 2013 Life on a tropical planet: niche conservatism explains the global diversity gradient. *Glob Ecol Biogeogr* **22**, 344–350.
10. Jablonski D., Belanger C.L., Berke S.K., Huang S., Krug A.Z., Roy K., Tomasovych A., Valentine J.W. 2013 Out of the tropics, but how? Fossils, bridge species, and thermal ranges in the dynamics of the marine latitudinal diversity gradient. *Proc Natl Acad Sci* **110**, 10487–10494.
11. Vermeij G.J. 1991 When biotas meet: understanding biotic interchange. *Science* **253**, 1099–1104.
12. Fritz S.A., Schnitzler J., Eronen J.T., Hof C., Böhning-Gaese K., Graham C.H. 2013 Diversity in time and space: wanted dead and alive. *TREE* **28**, 509–516.

13. Peterson A.T., Soberón J., Pearson R.G., Anderson R.P., Martínez-Meyer E., Nakamura M., Araújo M.B. 2011 *Ecological Niches and Geographic Distributions*. Princeton, Princeton University Press.

14. Araújo M.B., Ferri-Yanez F., Bozinovic F., Marquet P.A., Valladares F., Chown S.L. 2013 Heat freezes niche evolution. *Ecol Lett* **16**, 1206–1219. (doi:10.1111/ele.12155).

15. Sunday J.M., Bates A.E., Dulvy N.K. 2011 Global analysis of thermal tolerance and latitude in ectotherms. *Proc R Soc B* **278**, 1823–1830.

16. Stigall A.L. 2012 Using ecological niche modelling to evaluate niche stability in deep time. *J Biogeogr* **39**, 772–781.

17. Stigall A.L. 2014 When and how do species achieve niche stability over long time scales? *Ecography*. (doi:10.1111/ecog.00719).

18. Malizia R.W., Stigall A.L. 2011 Niche stability in Late Ordovician articulated brachiopod species before, during, and after the Richmondian invasion. *Palaeogeogr Palaeoclimatol Palaeoecol* **311**, 154–170.

19. Holt R.D. 1996 Adaptive evolution in source-sink environments: direct and indirect effects of density-dependence on niche evolution. *Oikos* **75**, 182–192.

20. Kawecki T.J. 1995 Demography of source-sink populations and the evolution of ecological niches. *Evol Ecol* **9**, 38–44.

21. Martínez-Meyer E., Peterson A.T. 2006 Conservatism of ecological niche characteristics in North American plant species over the Pleistocene-to-Recent transition. *J Biogeogr* **33**, 1779–1789.

22. Strubble D., Broennimann O., Chiron F., Matthysen E. 2013 Niche conservatism in non-native birds in Europe: niche unfilling rather than niche expansion. *Glob Ecol Biogeogr* **22**, 962–970.

23. Broennimann O., Treier U.A., Müller-Schärer H., Thuiller W., Peterson A.T., Guisan A. 2007 Evidence of climatic niche shift during biological invasion. *Ecol Lett* **10**, 701–709.

24. Rödder D., Lötters S. 2009 Niche shift versus niche conservatism? Climatic characteristics of the native and invasive ranges of the Mediterranean house gecko (*Hemidactylus turcicus*). *Glob Ecol Biogeogr* **18**, 674–687.

25. Umina P.A., Weeks A.R., Kearney M.R., McKechnie S.W., Hoffmann A.A. 2005 A rapid shift in a classic clinal pattern in *Drosophila* reflecting climate change. *Science* **308**, 691–693.

26. Balanyá J., Oller J.M., Huey R.B., Gilchrist G.W., Serra L. 2006 Global genetic change tracks global warming in *Drosophila subobscura*. *Science* **313**, 1773–1775.

27. Araújo M.B., Peterson A.T. 2012 Uses and misuses of bioclimatic envelope modeling. *Ecology* **93**, 1527–1539.

28. Broennimann O., Fitzpatrick M.C., Pearman P.B., Petitpierre B., Pellissier L., Yoccoz N.G., Thuiller W., Fortin M.-J., Randin C., Zimmermann N.E., et al. 2012 Measuring ecological niche overlap from occurrence and spatial environmental data. *Glob Ecol Biogeogr* **21**, 481–497.

29. Cronin T.M. 1988 Evolution of marine climates of the U.S. Atlantic Coast during the past four million years. *Phil Trans R Soc B* **318**, 661–678.

30. Todd J.A., Jackson J.B.C., Johnson K.G., Fortunato H.M., Heitz A., Alvarez M., Jung P. 2002 The ecology of extinction: molluscan feeding and faunal turnover in the Caribbean Neogene. *Proc R Soc B* **269**, 571–577.

31. Vermeij G.J. 2009 One-way traffic in the western Atlantic: causes and consequences of Miocene to early Pleistocene molluscan invasions in Florida and the Caribbean. *Paleobiology* **31**, 624–642.

32. Robinson M.M., Dowsett H.J. 2008 Pliocene role in assessing future climate impacts. *EOS, Trans Am Geo Un* **89**, 501–502.

33. Warren R., VanDerWal J., Price J., Welbergen J.A., Atkinson I., Ramirez-Villegas J., Osborn T.J., Jarvis A., Shoo L.P., Williams S.E., et al. 2013 Quantifying the benefit of early climate change mitigation in avoiding biodiversity loss. *Nature Clim Change* **3**, 678–682.

34. Warren D.L., Glor R.E., Turelli M. 2008 Environmental niche equivalency versus conservatism: Quantitative approaches to niche evolution. *Evolution* **62**, 2868–2883.

35. Warren D.L., Glor R.E., Turelli M. 2010 ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography* **33**, 607–611.

36. Saupe E.E., Hendricks J.R., Townsend A.T., Lieberman B.S. 2014 Climate change and marine molluscs of the western North Atlantic: future prospects and perils. *J Biogeogr* **41**, 1352–1366.

37. Graham C.H., Elith J., Hijmans R.J., Guisan A., Peterson A.T., Loiselle B.A., Group T.N.P.S.D.W. 2008 The influence of spatial errors in species occurrence data used in distribution models. *J Appl Ecol* **45**, 239–247.

38. Royle J.A., Chandler R.B., Yackulic C., Nichols J.D. 2012 Likelihood analysis of species occurrence probability from presence-only data for modelling species distributions. *Methods Ecol Evol* **3**, 545–554.

39. Yackulic C.B., Chandler R., Zipkin E.F., Royle J.A., Nichols J.D., Campbell Grant E.H., Veran S. 2013 Presence-only modelling using MAXENT: when can we trust the inferences? *Methods Ecol Evol* **4**, 236–243.

40. Hernandez P.A., Graham C.H., Master L.L., Albert D.L. 2006 The effect of sample size and species characteristics on performance of different distribution modeling methods. *Ecography* **29**, 773–785.

41. Pearson R.G., Raxworthy C.J., Nakamura M., Peterson A.T. 2007 Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *J Biogeogr* **34**, 102–117.

42. Gordon C., Cooper C., Senior C.A., Banks H., Gregory J.M., Johns T.C., Mitchell J.F.B., Wood R.A. 2000 The simulation of SST, sea ice extents and ocean heat transports in a version of the Hadley Centre coupled model without flux adjustments. *ClDy* **16**, 147–168.

43. Pope V.D., Gallani M.L., Rowntree P.R., Stratton R.A. 2000 The impact of new physical parameterizations in the Hadley Centre Climate model: HadAM3. *ClDy* **16**, 123–146.

44. Fordham D.A., Wigley T.M.L., Watts M.J., Brook B.W. 2012 Strengthening forecasts of climate change impacts with multi-ensemble averaged projections using MAGICC/SCENGEN 5.3. *Ecography* **45**, 4–8.

45. Eriksson A., Betti L., Friend A.D., Lycett S.J., Singarayer J.S., von Cramon-Taubadel N., Valdes P.J., Balloux F., Manica A. 2012 Late Pleistocene climate change and the global expansion of anatomically modern humans. *Proc NatlAcad Sci* **109**, 16089–16094.

46. Singarayer J.S., Valdes P.J. 2010 High-latitude climate sensitivity to ice-sheet forcing over the last 120 kyr. *Quat Sci Rev* **29**, 43–55.

47. Haywood A.M., Ridgwell A., Lunt D.J., Hill D.J., Pound M.J., Dowsett H.J., Dolan A.M., Francis J.E., Williams M. 2011 Are there pre-Quaternary geological analogues for a future greenhouse gas-induced global warming? *Phil Trans R Soc A* **369**, 933–956.

48. Singarayer J.S., Valdes P.J., Friedlingstein P., Nelson S., Beerling D.J. 2011 Late Holocene methane rise caused by orbitally controlled increase in tropical sources. *Nature* **470**, 82–85.

49. Petit J.R., Jouzel J., Raynaud D., Barkov N.I., Barnola J.-M., Basile I., Bender M., Chappellaz J., Davis J., Delaygue G., et al. 1999 Climate and atmospheric history of the past 420,000 years from the Vostok Ice Core, Antarctica. *Nature* **399**, 429–436.

50. Loulergue L., Schilt A., Spahni R., Masson-Delmotte V., Blunier T., Lemieux B., Barnola J.-M., Raynaud D., Stocker T.F., Chappellaz J. 2008 Orbital and millennial-scale features of atmospheric CH_4 over the past 800,000 years. *Nature* **453**, 383–386.

51. Spahni R., Chappellaz J., Stocker T.F., Loulergue L., Hausammann G., Kawamura K., Fluckiger J., Schwander J., Raynaud D., Masson-Delmotte V., et al. 2005 Atmospheric methane and nitrous oxide of the Late Pleistocene from Antarctic ice cores. *Science* **310**, 1317–1321.

52. Berger A., Loutre M.F. 1991 Insolation values for the climate of the last 10 million years. *Quat Sci Rev* **10**, 297–317.

53. Haywood A.M., Dowsett H.J., Robinson M.M., Stoll D.K., Dolan A.M., Lunt D.J., Otto-Bliesner B., Chandler M.A. 2011 Pliocene Model Intercomparison Project (PlioMIP): experimental design and boundary conditions (Experiment 2). *Geoscientific Model Development* **4**, 571–577.

54. Braconnot P., Otto-Bliesner B., Harrison S., Joussaume S., Peterchmitt J.-Y., Abe-Ouchi A., Crucifix M., Driesschaert E., Fichefet T., Hewitt C.D., et al. 2007 Results of PMIP2 coupled simulations of the Mid-Holocene and Last Glacial Maximum – Part 1: experiments and large-scale features. *CliPa* **3**, 261–277.

55. Tomašových A., Kidwell S.M. 2009 Preservation of spatial and environmental gradients by death assemblages. *Paleobiology* **35**, 119–145.

56. Buckley L.B., Hurlbert A.H., Jetz W. 2012 Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Glob Ecol Biogeogr* **9**, 873–885.

57. Sunday J.M., Bates A.E., Dulvy N.K. 2012 Thermal tolerance and the global redistribution of animals. *Nature Clim Change* **2**, 686–690.

58. Phillips S.J., Anderson R.P., Schapire R.E. 2006 Maximum entropy modeling of species geographic distributions. *Ecol Modell* **190**, 231–259.

59. Elith J., Phillips S.J., Hastie T., Dudik M., Chee Y.E., Yates C.J. 2011 A statistical explanation of MaxEnt for ecologists. *Divers Distrib* **17**, 43–57.

60. Austin M.P., Nicholls A.O., Doherty M.D., Meyers J.A. 1994 Determining species response functions to an environmental gradient by means of a beta-function. *J Veg Sci* **5**, 215-228.

61. Angilletta M. 2009 *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford, Oxford University Press.

62. Hooper H.L., Connon R., Callaghan A., Fryer G., Yarwood-Buchanan S., Biggs J., Maund S.J., Hutchinson T.H., Sibly R.M. 2008 The ecological niche of *Daphnia magna* characterized using population growth rate. *Ecology* **89**, 1015–1022.

63. Phillips S.J., Dudík M., Elith J., Graham C.H., Lehmann A., Leathwick J., Ferrier S. 2009 Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecol Appl* **19**, 181–197.

64. VanDerWal J., Shoo L.P., Graham C., Williams S.E. 2009 Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? *Ecol Modell* **220**, 589–594.

65. Liu C., Berry P.M., Dawson T.P., Pearson R.G. 2005 Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* **28**, 385–393.

66. Freeman E.A., Moisen G.G. 2008 A comparison of the performance of threshold criteria for binary classification in terms of predicted prevalence and kappa. *Ecol Modell* **217**, 48–58.

67. Dudík M., Schapire R.E., Phillips S.J. 2005 Correcting sample selection bias in maximum entropy density estimation. In *Adv Neural Inf Process Syst* (pp. 323–330, The MIT Press.

68. Svenning J.-C., Fløjgaard C., Marske K.A., Nógues-Bravo D., Normand S. 2011 Applications of species distribution modeling to paleobiology. *Quat Sci Rev* **30**, 2930–2947.

69. Kearney M.R., Simpson S.J., Raubenheimer D., Kooijman S.A.L.M. 2013 Balancing heat, water and nutrients under environmental change: a thermodynamic framework. *Funct Ecol* **27**, 950–966.

70. Kearney M.R., Wintle B.A., Porter W.P. 2010 Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conserv Lett* **3**, 203–213.

71. Peterson A.T., Papeş M., Soberón J. 2008 Rethinking receiver operating characteristic analysis. *Ecol Modell* **213**, 63–72.

72. Schoener T.W. 1968 *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* **49**, 704–726.

73. Hof C., Rahbek C., Araújo M.B. 2010 Phylogenetic signals in the climatic niches of the world's amphibians. *Ecography* **33**, 242–250.

74. Tewksbury J.J., Huey R.B., Deutsch C.A. 2008 Putting the heat on tropical animals. *Science* **320**, 1296–1297.

75. Tunnell J.W., Andrews J., Barrera N.C., Moretzsohn F. 2010 *Encyclopedia of Texas Seashells: Identification, Ecology, Distribution & History*. College Station, Texas A&M University Press.

76. Owens H.L., Campbell L.P., Dornak L.L., Saupe E.E., Barve N., Soberón J., Ingenloff K., Lira-Noriega A., Hensz C.M., Myers C.E., et al. 2013 Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. *Ecol Modell* **263**, 10–18.

77. Bijma J., Pörtner H.-O., Yesson C., Rogers A.D. 2013 Climate change and the oceans – what does the future hold? *Mar Pollut Bull* **74**, 495–505.

78. Zu Ermgassen P.S.E., Spalding M.D., Blake B., Coen L.D., Dumbauld B., Geiger S., Grabowski J.H., Grizzle R., Luckenbach M., McGraw K., et al. 2012 Historical ecology with real numbers: past and present extent and biomass of an imperilled estuarine habitat. *Proc R Soc B* **279**, 3393–3400.

79. Willis K.J., MacDonald G.M. 2011 Long-term ecological records and their relevance to climate change predictions for a warmer world. *Annu Rev Ecol Evol Syst* **42**, 267–287.

80. Trakhtenbrot A., Nathan R., Perry G., Richardson D.M. 2005 The importance of long-distance dispersal in biodiversity conservation. *Divers Distrib* **11**, 173–181.

81. Chen I.-C., Hill J.K., Ohlemüller R., Roy D.B., Thomas C.D. 2011 Rapid range shifts of species associated with high levels of climate warming. *Science* **333**, 1024–1026.

82. Hof C., Levinsky I., Araújo M.B., Rahbek C. 2011 Rethinking species' ability to cope with rapid climate change. *Glob Change Biol* **17**, 2987–2990.

83. Williams J.W., Jackson S.T. 2007 Novel climates, no-analog communities, and ecological surprises. *Front Ecol Environ* **5**, 475–482.

84. Fordham D.A., Mellin C., Russell B.D., Akçakaya R.H., Bradshaw C.J.A., Aiello-Lammens M.E., Caley J.M., Connell S.D., Mayfield S., Shepherd S.A., et al. 2013 Population dynamics can be more important than physiological limits for determining range shifts under climate change. *Glob Change Biol* **19**, 3224–3237.

85. IPCC. 2013 *Climate Change 2013: The Physical Science Basis.* Geneva, Intergovernmental Panel on Climate Change Secretariat.

86. Davis A.J., Jenkinson L.S., Lawton J.H., Shorrocks B., Wood S. 1998 Making mistakes when predicting shifts in species range in response to global warming. *Science* **391**, 783–786.

87. Kearney M., Shine R., Porter W.P. 2009 The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. *Proc Natl Acad Sci* **106**, 3835–3840.

88. van Dam J.A., Aziz H.A., Álvarez Sierra M.Á., Hilgen F.J., van den Hoek Ostende L.W., Lourens L.J., Mein P., van der Meulen A.J., Palaez-Campomanes P. 2006 Long-period astronomical forcing of mammal turnover. *Nature* **443**, 687–691.

89. Peterson A.T., Soberón J., Sanchez-Cordero V. 1999 Conservatism of ecological niches in evolutionary time. *Science* **285**, 1265–1267.

90. Kozak K.H., Wiens J.J. 2006 Does niche conservatism promote speciation? A case study in North American salamanders. *Evolution* **60**, 2604–2621.

91. Soberón J., Nakamura M. 2009 Niches and distributional areas: concepts, methods, and assumptions. *Proc Natl Acad Sci* **106**, 19644–19650.

Figure and Table Legends

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

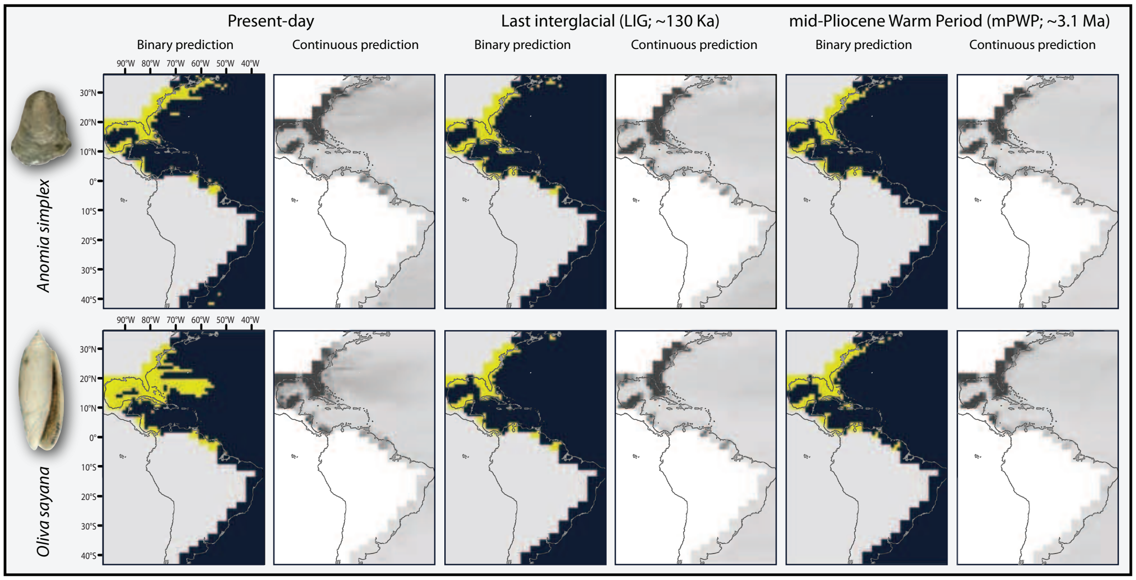

Figure 2 | Representative results from niche comparison analyses. Comparisons for *Anomia simplex* and *Oliva sayana* using a PCA on the three most important environmental variables: maximum and minimum surface temperature, and maximum surface salinity. Comparisons are shown for the Last Interglacial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

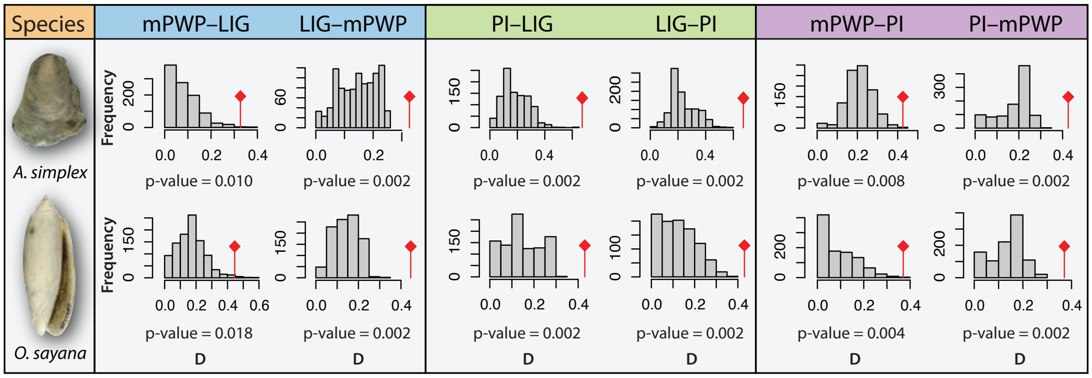

Table 1 | Comparisons of multi-dimensional niches and thermal tolerance limits. Bold values indicate non-significant results. All other comparisons are statistically more similar than expected given the environmental background of the variable in question. Note that it is possible for two niches to be more similar than expected based on the environment available for one time slice, but less similar than expected based on the environment available for the other. See electronic supplementary material, dataset S2, 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	*Anomia simplex*	0.01	0.00	0.00	0.00	0.01	0.00
	Crassostrea virginica	0.04	0.00	0.03	0.00	0.00	0.00
	Dinocardium robustum	0.01	0.00	0.00	0.02	**0.09**	0.00
	Lucina pensylvanica	**0.25**	0.01	0.00	0.00	0.03	0.03
	Mercenaria campechiensis	0.01	0.00	0.00	0.02	0.00	0.00
Gastropoda	*Bulla occidentalis*	**0.34**	**0.54**	**0.10**	**0.29**	**0.31**	**0.20**
	Crepidula fornicata	0.03	0.00	0.02	0.00	**0.29**	**0.58**
	Neverita duplicata	0.08	0.00	0.01	**0.44**	0.01	0.00
	Oliva sayana	0.02	0.00	0.00	0.00	0.00	0.00
	Terebra dislocata	0.02	0.00	0.00	0.01	0.00	0.00
Environmental comparison: maximum surface temperature							
Bivalvia	*Anomia simplex*	0.04	0.00	0.00	0.00	0.00	0.00
	Crassostrea virginica	0.00	0.00	0.00	0.02	0.01	0.00
	Dinocardium robustum	0.03	0.00	0.00	0.00	**0.09**	0.00
	Lucina pensylvanica	0.00	0.00	0.00	0.00	**0.81**	**0.42**
	Mercenaria campechiensis	0.01	0.00	0.00	0.03	0.00	0.00
Gastropoda	*Bulla occidentalis*	0.00	0.00	0.02	**0.60**	**0.96**	0.02
	Crepidula fornicata	0.00	0.00	0.00	0.00	0.01	0.00
	Neverita duplicata	0.01	0.00	0.00	**0.06**	0.00	0.00
	Oliva sayana	0.00	0.00	0.01	**0.15**	**0.54**	0.00
	Terebra dislocata	0.03	0.00	0.00	0.02	**0.43**	0.02
Environmental comparison: minimum surface temperature							
Bivalvia	*Anomia simplex*	**0.21**	0.00	0.00	0.00	0.00	0.00
	Crassostrea virginica	**0.91**	0.05	0.00	0.03	0.01	0.00
	Dinocardium robustum	**0.11**	0.00	0.00	0.00	0.00	0.00
	Lucina pensylvanica	**0.68**	0.00	0.00	0.00	**0.77**	**0.22**
	Mercenaria campechiensis	**0.82**	0.00	0.00	0.00	0.01	0.00
Gastropoda	*Bulla occidentalis*	**0.66**	0.00	**0.09**	0.10	**0.85**	**0.10**
	Crepidula fornicata	**0.17**	0.00	0.01	0.00	**0.44**	0.00
	Neverita duplicata	0.50	0.00	**0.05**	0.00	0.00	0.00
	Oliva sayana	**0.07**	0.00	0.03	0.00	**0.29**	0.00
	Terebra dislocata	**0.18**	0.00	0.00	0.00	0.05	0.00