RESEARCH PAPER

Do past climate states influence diversity dynamics and the present-day latitudinal diversity gradient?

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ABSTRACT

Aim To identify the role of climate variations over geological time in shaping present-day diversity patterns, particularly the latitudinal diversity gradient (LDG; the decrease of taxonomic diversity from low towards high latitudes), using marine bivalves as a model system.

Location World-wide.

Methods We use the fossil record of extant and extinct bivalve taxa and information on global palaeoclimate states to evaluate how the climate state at the beginning of the evolutionary history of individual families influenced (a) their diversification dynamics through subsequent climate changes and (b) their present-day LDG. For (a), we estimated per-family genus origination and extinction rates during the last cool interval in the late Cenozoic and overall genus origination and extinction rates since the early Palaeozoic. For (b), we compared LDG slopes and oldest fossil occurrences of extant families with palaeoclimate data. We also tested whether such dynamics vary with life habits.

Results Families that originated in warm intervals tend to have higher extinction rates in the (cool) late Cenozoic and occasionally in other cool intervals. However, in contrast to the results of Romdal *et al.* (*Global Ecology and Biogeography*, 2013, **22**, 344–350), present-day LDG slopes do not vary with the climate state at the time of family origination, regardless of the palaeoclimatic scheme used. Infaunal living families have marginally higher origination rates in the late Cenozoic, but their LDG slopes do not differ significantly from the epifaunal families. In contrast, feeding habit appears to affect family LDG slopes, but not late Cenozoic diversification rates.

Main conclusion For marine bivalves, ancestral climate state appears to influence subsequent diversification dynamics with clades originating in warm intervals showing higher extinction rates during intervals of global cooling, but ancestral climate has no detectable influence on present-day LDGs.

Keywords
Biodiversity, bivalve, diversification, extinction, origination, palaeoclimate.

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INTRODUCTION

Large-scale variations in global climate during the geological past are known to have affected biodiversity dynamics across a wide range of spatial, temporal and taxonomic scales (Jackson & Williams, 2004; Erwin, 2009; Figueirido *et al.*, 2012; Mayhew *et al.*, 2012); present-day biodiversity patterns such as the latitudinal diversity gradient (LDG) are also likely to have been influenced by those past changes (Hawkins *et al.*, 2007; Powell, 2007; Davies *et al.*, 2011; Condamine *et al.*, 2012; Romdal *et al.*, 2013). Hypotheses on the role of climate in shaping LDG patterns mostly involve associations between climate and evolutionary rates (Currie *et al.*, 2004; Gillooly *et al.*, 2005; Jablonski *et al.*, 2006; Wright *et al.*, 2006; Mittelbach *et al.*, 2007; Erwin, 2009) and niche conservatism (Wiens & Donoghue, 2004; Wiens & Graham, 2005; Condamine *et al.*, 2012). The latter

suggests that the prevailing climate at the origin of a lineage (i.e. the ancestral climate niche) strongly affects its subsequent distribution and diversification. However, empirical analyses of the influence of ancestral climate niche on present-day species distributions and diversity gradients show mixed results, with some studies supporting the hypothesis (e.g. Wiens *et al.*, 2006; Hawkins *et al.*, 2007; Romdal *et al.*, 2013) while others do not (e.g. Colinvaux & De Oliveira, 2001; Kissling *et al.*, 2010; Leprieur *et al.*, 2011; Sandel *et al.*, 2011). Such differences could reflect the confounding effects of other abiotic and biotic factors (for reviews see Erwin, 2009; Condamine *et al.*, 2013) or among-study differences in temporal scale. Studies strongly supporting niche conservatism largely involve Cenozoic time-scales [i.e. at most the last 65 million years (Myr)] whereas the imprint of global climate states further back in time [e.g. the Cretaceous greenhouse climate (Skelton, 2003) and the late Palaeozoic ice-house (Montañez & Poulsen, 2013)] on the modern LDG remains poorly explored (but see Powell, 2007).

One attempt to bridge this gap, using a wide range of marine and terrestrial taxa over the past 630 Myr, suggested that the ancestral climate state, even back in the Palaeozoic or Mesozoic, could influence the slope of the present-day LDG for a lineage, a pattern attributed to niche conservatism (Romdal *et al.*, 2013). The idea that deep-time ancestral conditions can shape present-day LDGs despite subsequent extinction events and diversifications is surprising, particularly because global climate changes have driven independent range expansions and contractions of species and higher taxa in response to multiple warming and cooling cycles. Thus, further testing of this hypothesis using explicit estimates of diversification rates of geologically long-lived lineages is needed.

Spatial and temporal variations in diversification rate have emerged as an essential factor in shaping the modern-day LDG (Jablonski, 1993; Jablonski *et al.*, 2006, 2013; McKenna & Farrell, 2006; Mittelbach *et al.*, 2007; Condamine *et al.*, 2012). In general, the LDG is likely to be less steep in a warm world lacking polar ice and showing a broader extent of tropical conditions; a milder temperature gradient is also likely to accelerate diversification at mid latitudes and promote poleward expansion of existing taxa (Allen *et al.*, 2006; Gillman *et al.*, 2009; Archibald *et al.*, 2010). In contrast, global cooling should reduce origination rates, increase extinction rates, especially at higher latitudes, and induce range contraction to the tropics to generate a steeper LDG; reduced geographic range sizes may also increase extinction rates in the tropics (Weir & Schluter, 2007; Clapham *et al.*, 2009).

Here, we investigate the role of past climate in shaping present-day LDGs by tracking temporal diversification dynamics through the *c.* 500-Myr history of shelf-depth marine bivalves. Bivalves have become a model system for the analysis of large-scale spatial and temporal patterns: they have a rich and heavily sampled fossil record and their present-day diversity patterns are well characterized (Jablonski *et al.*, 2006, 2013; Krug *et al.*, 2009; Bieler *et al.*, 2013). Specifically, we investigate whether and how global climate state affects the historical and present-day diversity patterns in this group by testing four

hypotheses. Distinguishing between the influence of climate state at the time of clade origination (in our case, a bivalve family) and that of climate states in subsequent intervals in the clade's history, we hypothesize that (1) bivalves as a group show higher per-genus diversification rates (higher origination and/or lower extinction rates) during warm intervals than during cool intervals, and (2) families that originated in warm intervals (hereafter warm-origin families) are more sensitive to climate change than those that originated in cool intervals (hereafter cool-origin families). These hypotheses stem from the significant positive relation between diversity and sea-surface temperature observed in bivalves today (e.g. Roy *et al.*, 2000) and the potential responses to climate changes discussed above.

To evaluate the effect of climate state at clade origin on present-day LDGs, as proposed by Romdal *et al.* (2013), we further test the hypothesis that (3) warm-origin bivalve families tend to show steeper LDGs today than cool-origin families. Romdal *et al.* (2013) suggested that warm-origin families might be less adapted to the relatively cool climate today than cool-origin families, and thus might have suffered range contractions and extinctions from higher latitudes. Therefore, we also hypothesize that (4) warm-origin families should show higher extinction rates in the late Cenozoic cool interval than cool-origin families. Finally, because previous work found different LDGs in bivalves with different life habits (Roy *et al.*, 2000), we partition our bivalve data by living position and food source in order to evaluate whether palaeoclimate has had different effects in different functional groups.

METHODS

Marine bivalve database

We focused on shallow-water (recorded from depths ≤ 200 m) bivalves as a model system (see Appendix S1 in Supporting Information regarding exclusion of deep-sea fauna). The fossil occurrences of individual taxa were obtained from an extensive stratigraphic dataset containing the first and last appearances of 1363 extinct bivalve genera plus the first geological record of 89% of the living genera (*n* = 869); most of the genera excluded from these data are exclusively deep-sea genera or belong to a few families with small body sizes (≤ 1 cm) and poor preservation potential (Valentine *et al.*, 2006). For details of the database, data compilation and standardization procedures, and excluded taxa see Krug *et al.* (2009) and Jablonski *et al.* (2013).

Palaeoclimate and diversification dynamics

As is common in palaeontological studies, we assumed the first known fossil appearance of the oldest genus in a family to be the time of origin of that family, and categorized the climatic condition at that time according to the simplified palaeoclimatic scheme used by Romdal *et al.* (2013) to facilitate comparisons with their results. Cool intervals were characterized by extensive continental glaciation, bracketed by times of global cooling before and deglaciation after, of varying durations; warm inter-

vals were characterized by further global warming; and a 'hot' interval was characterized by the warmest conditions (Romdal *et al.*, 2013). The only prolonged hot interval occurred *c.* 135–48 million years ago (Ma; Early Cretaceous to Early Eocene), bracketed by *c.* 10-Myr warm intervals. Thus, while the ages of families that originated in warm intervals can range from 481.5 to 39 Myr, and those originating in cool intervals range from 348 to 2.7 Myr, the families that originated in the hot interval are all necessarily relatively young. To avoid potential confounding effects of family age on diversification dynamics (reviewed in Cornell, 2013), which is beyond the scope of this study, we treated the hot interval and its adjacent warm intervals as a single warm interval in all analyses involving diversification dynamics (e.g. origination and extinction rates; see below). We retained the hot interval as a separate category in the analysis of present-day LDG slopes.

Although the first-order climatic history of the Earth is generally viewed as an alternation between 'greenhouse' and 'icehouse' conditions (respectively punctuated by 'hothouse' states and glaciations at one or both poles; e.g. Zachos *et al.*, 2008; Kidder & Worsley, 2010; NRC, 2011), smaller-amplitude, shorter-term fluctuations in global climate certainly occurred during each of the six intervals used in our analyses. Sampling limitations and problems of temporal resolution at global scales disallow large-scale analyses below the level of geological stages, most of which have durations of around 5 Myr. As a preliminary test of the robustness of our results, we repeated our analyses using a more recent and more highly resolved climate scheme, which includes the most marked of the short-lived cool intervals, and shifts the greenhouse–icehouse transitions slightly (NRC, 2011). We identified the palaeoclimate state in each geological stage included in our dataset based on Fig. 1.2 in NRC (2011) (and its primary sources). Because this scheme only included two very brief hot intervals (of *c.* 2 Myr), we treated the hot state as warm. Similarly, cool and cold states are combined as cool climates to afford a resolution that is compatible with the fossil data. Other brief intervals that lasted less than a full geological stage (e.g. brief 'cool snaps' during the Late Cretaceous) were also excluded due to insufficient resolution in the macrofossil record.

To evaluate the impact of palaeoclimatic state on bivalve diversification dynamics through their evolutionary history, we calculated the bivalve per-genus origination rate ($\hat{p}$) and extinction rate ($\hat{q}$) in each geological stage since the Early Ordovician, using only those genera with stratigraphic ranges that cross at least one stage boundary, following Foote (2000) (Fig. S1a shows the number of boundary crossers per stage in warm or cool climate states). The per-genus rate is calculated as the log ratio of the number of genera crossing only one boundary (lower boundary for extinction and upper boundary for origination) to the number of genera crossing both boundaries, divided by the duration of the stage in Myr (Foote, 2000).

Our aim is to distinguish the role of climate state at the time of family origination (ancestral climate) from the effect of climate conditions during the later history of the family (subsequent climate). Therefore, we divided all bivalve genera (in both extant and extinct families) into warm-origin and cool-origin categories, according to the climate state of their family's origination. Note that because our focus is on testing whether the ancestral climate state of a *family* affects the diversification rates of genera in that family (i.e. conservatism at the family level), some genera categorized as having a warm origin based on the family origin may, in fact, have originated in a cool interval, and vice versa. For each geological stage, we calculated the genus-level origination and extinction rates for all bivalves and for the warm-origin and cool-origin groups separately. We then compared the per-genus origination and extinction rates (for all bivalves, the warm-origin group and the cool-origin group, respectively) between adjacent climate intervals using Wilcoxon tests to evaluate the null hypothesis of equal medians, which is insensitive to outliers (e.g. mass extinction events). Because evolutionary and biogeographic dynamics may differ from 'background' processes during and immediately after mass extinctions, we also repeated the analyses excluding the geological stages associated with the Big Five mass extinctions and their recovery intervals (see Foote, 2010).

Palaeoclimate at origin and present-day LDG

We quantified latitudinal diversity gradients using an existing database that currently includes *c.* 54,000 georeferenced occurrences of 5726 taxonomically standardized living species (Jablonski *et al.*, 2013, downloaded 16 March 2013). We then tested for an association between the initial climate state and the slope of the present-day LDG for each bivalve family. For all families that today contain 10 or more living species, we summed the number of species occurring at each degree of latitude, excluding latitudinal bins outside the overall geographic range of the family. We then fitted an ordinary linear regression model to the number of species per degree of latitude separately in the Northern and Southern Hemisphere and used the estimated slope as a measure of the family's LDG slope. We compared the species–LDG slopes among families that originated in different palaeoclimatic intervals using two standard tests that do not require normality assumptions for categorical predictors: Kruskal–Wallis rank-sum tests to evaluate the null hypothesis of identical distributions of LDG slopes among all family groups and Wilcoxon tests to evaluate the null hypothesis of equal medians in LDG slopes between two family groups. Slopes are not sensitive to coarser latitudinal binning schemes. Because our origination and extinction data are at the genus level, we also applied this method to families with 10 or more living genera to estimate genus-level LDG slopes. Because initial analyses showed consistent patterns between the two sets of analyses (see Results), but fewer families can be included in analyses of genus LDGs, we focus here on species-level LDGs. To further assess the sensitivity of our results to preservation potential, temporal sampling variation and the palaeoclimate model, we performed three sensitivity tests and found that results were qualitatively the same as the original analyses (see Appendix S1 for methods and results).

To evaluate whether the palaeoclimatic state at the time of origination of a family influenced its diversification dynamics during the last cool interval of the late Cenozoic (c. 37 Ma to present), we estimated the per-genus origination rate ($\hat{p}$) and extinction rate ($\hat{q}$) during this interval for all extant bivalve families (using only boundary-crossing genera) following Foote (2000) and Roy et al. (2009), and compared those rates among families originating in warm versus cool intervals using Wilcoxon rank-sum tests.

Influence of bivalve life habit

Finally, because bivalves with different life habits are known to differ in their LDGs, the effects of past climate states might vary among families that differ in major life habits. We categorized all extant families in our data set by living position – infaunal or epifaunal (the latter including semi-infaunal, as in Kowalewski et al., 2006), unless a family contained large proportions of both infaunal and epifaunal genera, in which case the family was classified as 'both'. We further categorized families by feeding habit – suspension feeders, non-suspension feeders or both. Non-suspension feeders comprise deposit feeders and several low-diversity or taxonomically restricted categories including carnivores, chemosymbiotic species and photosymbiotic species. We compared the numbers of infaunal versus epifaunal families, and suspension versus non-suspension feeding families, that first appeared in different climate states using Pearson's chi-squared tests. We further compared the LDG slopes and the per-genus origination and extinction rates during the last cool interval in the Cenozoic among families with different living positions and feeding habits, using Kruskal–Wallis tests for three-level comparisons and Wilcoxon tests for two-level comparisons.

All analyses were conducted in R 2.15.2 (R Development Core Team, 2012). The violin plots were generated using the R package vioplot 0.2 (Adler, 2005).

RESULTS

When all bivalves were analysed together, per-genus origination or extinction rates did not differ significantly between all the warm intervals and all the cool intervals (origination rate, $W = 1007.5$, $P = 0.442$; extinction rate, $W = 919$, $P = 0.997$) or between adjacent warm and cool climatic intervals (Figs S2 & S3, Table S1). The sole exception was the elevated extinction rate (and thus low net diversification rate) during the brief Late Jurassic cool interval. Comparisons of origination, extinction and net diversification rates between successive climatic states suggest that families originating during warm intervals ($n = 107$) tend to have significantly higher genus extinction rates in cool intervals than in warm intervals, whereas families originating during cool intervals ($n = 33$) tend to show stochastically constant rates regardless of climatic conditions (Figs 1 & 2, Table S1). These patterns are qualitatively the same when the first appearance of a family was assumed to be one geological stage earlier than indicated in fossil record, or when we repeated the analysis using the more recent palaeoclimate scheme (NRC, 2011) (Figs S4 & S5). The results are also qualitatively the same when the geological stages associated with the big five mass extinctions and subsequent recoveries were excluded from the analyses (Figs 2 & S5).

The present-day latitudinal diversity gradient varied among 58 bivalve families containing 10 or more living species (Table S2; see Appendix S1 for a summary of the results). However, families that originated in different climate states (cool, $n = 7$; warm, $n = 27$; hot, $n = 24$) did not differ in their LDG slopes (Northern Hemisphere, $H = 3.045$, $P = 0.218$; Southern Hemisphere, $H = 0.607$, $P = 0.738$; Fig. 3), their poleward latitudinal extent (Northern Hemisphere, $H = 0.638$, $P = 0.727$; Southern Hemisphere, $H = 1.327$, $P = 0.515$), the median poleward extent of their constituent genera (Northern Hemisphere, $H = 3.749$, $P = 0.153$; Southern Hemisphere, $H = 1.461$, $P = 0.482$) or their genus-level LDG slopes (Northern Hemisphere, $H = 2.297$, $P = 0.317$; Southern Hemisphere, $H = 1.017$, $P = 0.601$). Wilcoxon rank-sum tests also found no significant difference in LDG slopes between families that originated during different climate states (Table S3). Compared to families that originated during cool climate states, warm-origin families had significantly higher extinction rates during the late Cenozoic cool interval ($W = 1100$, $P = 0.003$) but similar origination rates ($W = 578.5$, $P = 0.068$; Figs. 4).

The ratios of infaunal to epifaunal families that first appeared in different climate states did not differ from random ($\chi^2 = 3.901$ $P = 0.142$; Table S4), nor did the ratios of suspension versus non-suspension families that originated in different climate states ($\chi^2 = 1.354$, $P = 0.508$; Table S4). No difference in present-day species LDGs was detected between infaunal and epifaunal families (Northern Hemisphere, $W = 204$, $P = 0.374$; Southern Hemisphere, $W = 273$, $P = 0.463$; Fig. S6). In contrast, suspension feeding families showed significantly steeper LDG slopes than non-suspension feeding families in the Northern Hemisphere ($W = 96$, $P = 0.024$) but not in the Southern Hemisphere ($W = 214$, $P = 0.105$; Fig. S7). During the late Cenozoic cool interval, extant infaunal families had marginally higher genus origination rates than epifaunal families ($W = 772$, $P = 0.077$), and similar extinction rates ($W = 593.5$, $P = 0.856$; Fig. S8). However, suspension and non-suspension feeding families did not differ significantly in their late Cenozoic per-genus origination rates ($W = 503$, $P = 0.608$) or extinction rates ($W = 309$, $P = 0.139$).

DISCUSSION

While ancestral climate niches might affect the nature of present-day LDGs in relatively young taxa (Wiens & Donoghue, 2004), our analyses suggest that the effects of niche conservatism are not evident in geologically old lineages, presumably because the signal fades with time. More generally, because climate can influence biodiversity dynamics both directly and indirectly, understanding the specific role of climate in shaping past diversity dynamics remains a challenge (Erwin, 2009). Our analyses of two key components of diversity dynamics, origination and
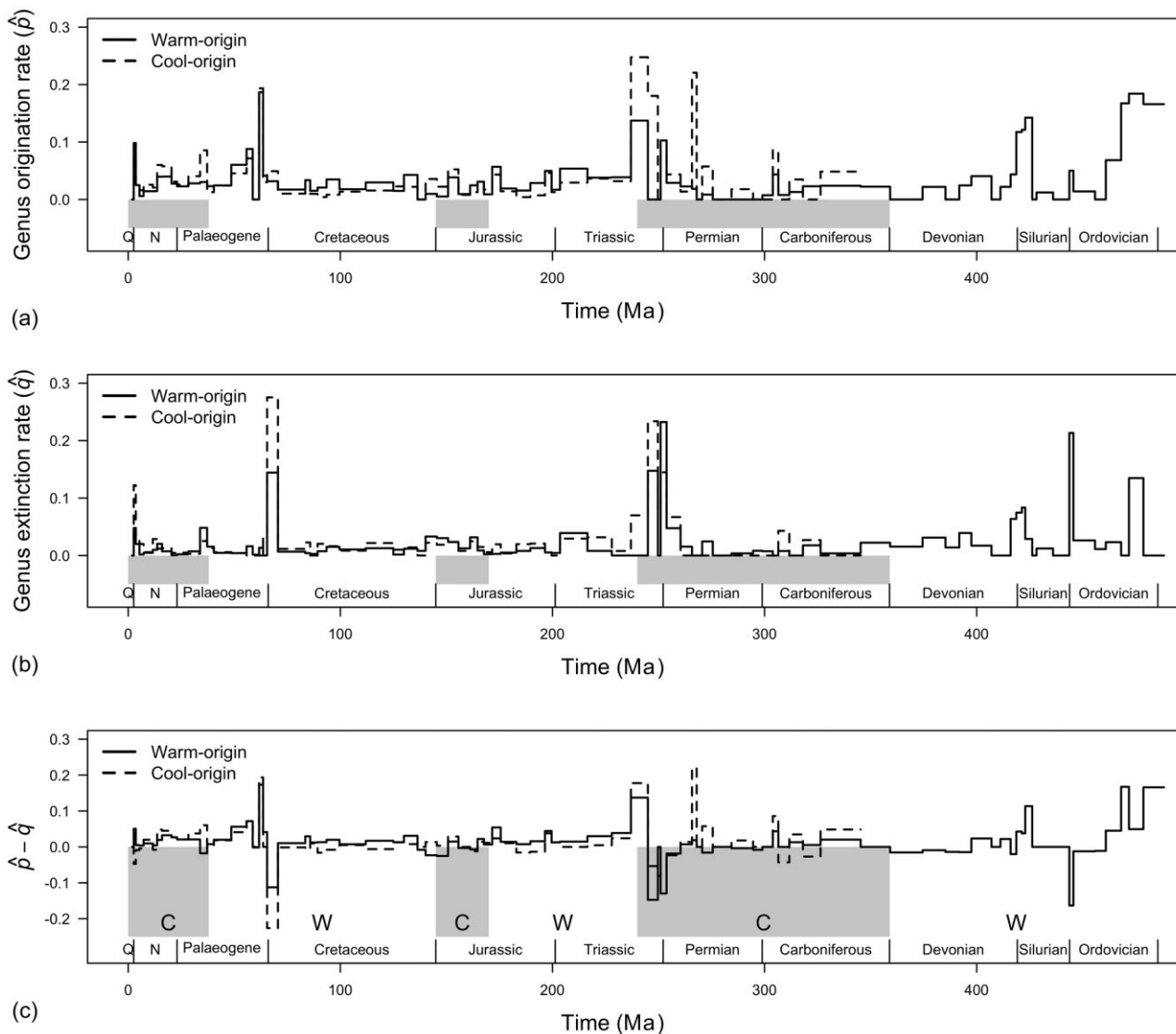
Figure 1 Bivalve per-genus rates of (a) origination ($\hat{p}$), (b) extinction ($\hat{q}$) and (c) net diversification ($\hat{p} - \hat{q}$), for warm-origin and cool-origin groups in each geological stage. Palaeoclimate states (following Romdal *et al.*, 2013; see Fig. S4 for results using an alternative scheme) are indicated by the bar below 0.0, with grey shading indicating the cool intervals, and by letters in (c), with C indicating cool climate state and W indicating warm climate state. The first bivalves to originate in a cool climate state appear at *c.* 350 Ma.

extinction (the third component being spatial shifts, which are not considered here), detected occasional differences in per-genus extinction rates between adjacent cool and warm climates over geological time, mainly due to rate variations in the genera belonging to warm-origin families. We also detected a significant difference in genus-level extinction rates during the late Cenozoic cool interval among families that originated in different climate states. Consistent with previous studies, we found support for a link between Cenozoic origination rates and living position, with higher origination rates in infaunal families (Crame, 2000), and an association between present-day LDG slope and feeding habit, with steeper LDG slopes in suspension feeding families (Roy *et al.*, 2000). However, none of these correlations produced any apparent association between the

climate state at time of origination of a bivalve family and its present-day LDG.

Our results do support the idea that changes in global climate over geological time have had a long-term influence on diversity dynamics in other ways. Bivalve families that originated in warm intervals appear to experience higher extinction rates in the late Cenozoic cool interval, but at most the net result was a set of present-day LDG slopes similar to those of the cool-origin families. Further analyses of Eocene or Middle Miocene LDGs are needed to determine whether warm-origin and cool-origin families had different gradients prior to late Cenozoic cooling. Our results also indicate that overall family origination rates do not vary with climate states in general, at least at the temporal resolution used here (Fig. 5). The modest increase in overall
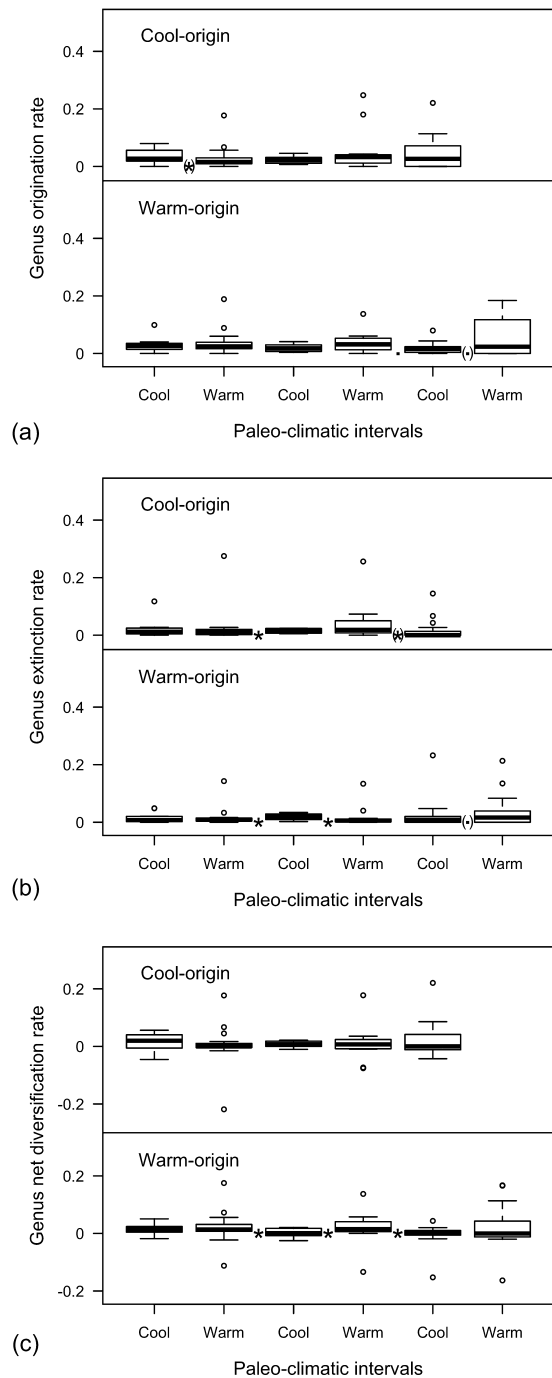
(a)

(b)

(c)

Figure 2 Bivalve per-genus (a) origination, (b) extinction and (c) net diversification rates, for warm-origin and cool-origin groups, in six palaeoclimate intervals from the most recent cool interval on the left to the first warm interval having a significant bivalve fauna, in the Early Ordovician, on the right. The solid black lines inside the boxes represent the medians, the top and bottom edges of the boxes represent 25–75% quantiles, and whiskers represent the range of the data excluding outliers (over twice the internal quantile). Specific statistics are given in Table S1. Significant differences between adjacent intervals are indicated by °$P < 0.1$ and *$P < 0.05$; significant differences detected after excluding stages associated with mass extinctions and the following recovery are indicated with parentheses.

extinction rate during the Late Jurassic cool interval should be viewed with caution, as the earliest Cretaceous is not as well sampled as the Late Jurassic, potentially inflating apparent Late Jurassic extinction (see Foote, 2003).

The elevated extinction rate of warm-origin families during cool intervals is not fully understood. Given that most late Cenozoic bivalve genera, and post-Palaeozoic invertebrate orders, preferentially originated in the tropics and subsequently expanded to temperate regions (Jablonski *et al.*, 2006, 2013; Kiessling *et al.*, 2010), it is likely that bivalve families also preferentially originated in the tropics, regardless of the prevailing global climate state. While a warm climate might allow clade originations across a broader latitudinal range than a cool climate, this initial distribution could be altered by subsequent climate cooling and regional or global extinction of species and genera within those clades. In any case, our results are consistent with taxonomically broader analyses showing that cooling episodes such as the Eocene–Oligocene and Pliocene–Pleistocene transitions have had larger effects than warm episodes such as the Palaeocene–Eocene thermal maximum and the Mid-Miocene climatic optimum (e.g. Foote, 2010; see also Powell, 2005). One point worth further evaluation is that cooler climates may lower sea levels and so might reduce palaeontological sampling at a global scale, which could shift originations into the succeeding warm interval. However, our sensitivity test did not show a strong pulse of originations immediately following the cold intervals, aside from confirmed intervals of recovery after mass extinctions, suggesting that this potential bias is not the primary signal in our data (see also Foote, 2003, 2010).

Our results for life habits show no clear connection between diversification dynamics in the late Cenozoic and present-day LDG patterns at the family level. Infaunal families showed marginally higher origination rates than epifaunal families in the late Cenozoic cool interval and the ratio of overall infaunal versus epifaunal bivalve diversity increases towards higher latitudes in the north-east Pacific (perhaps because such exposure becomes increasingly disadvantageous with increasing seasonality; Thorson, 1965; Roy *et al.*, 2000), but species-level LDG slopes are similar between families of the two groups. At the same time, although suspension feeders tend to have steeper LDG slopes in the Northern Hemisphere than non-suspension feeders (also consistent with previous results from the north-east Pacific, which show a monotonic diversity decline in suspension feeders alone; Roy *et al.*, 2000), we found no significant difference in late Cenozoic genus origination or extinction rates between suspension and non-suspension feeding families.

Combining fossil and present-day data we were able to separate the signature of the climate state at the time of family origination from the impact of climate states in subsequent time intervals. Our results suggest that the two have interactively influenced bivalve diversification dynamics, supporting the broad hypothesis that climate drives diversification rate variations across space (Wiens, 2007; Jansson & Davies, 2008; Svenning *et al.*, 2008) and through time (Finarelli & Badgley, 2010; Mayhew *et al.*, 2012; Condamine *et al.*, 2013; Cooper *et al.*, 2013). Specifically, the per-genus extinction rate of warm-
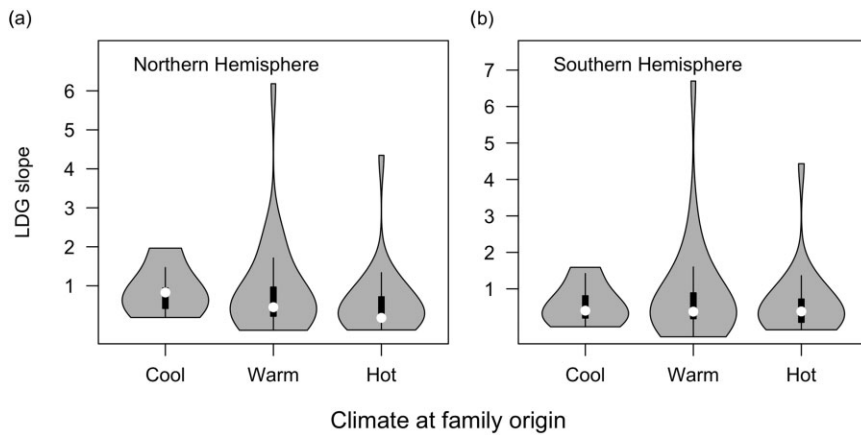
Figure 3 Estimated slopes of latitudinal diversity gradient (LDG), in the (a) Northern and (b) Southern Hemispheres, do not differ among families that originated in different palaeoclimatic intervals. The violin shape represents a smoothed probability distribution of the data (family LDG slopes in each category). White dots represent the medians, black bars represent 25–75% quantiles, and whiskers represent the range of the data excluding outliers.
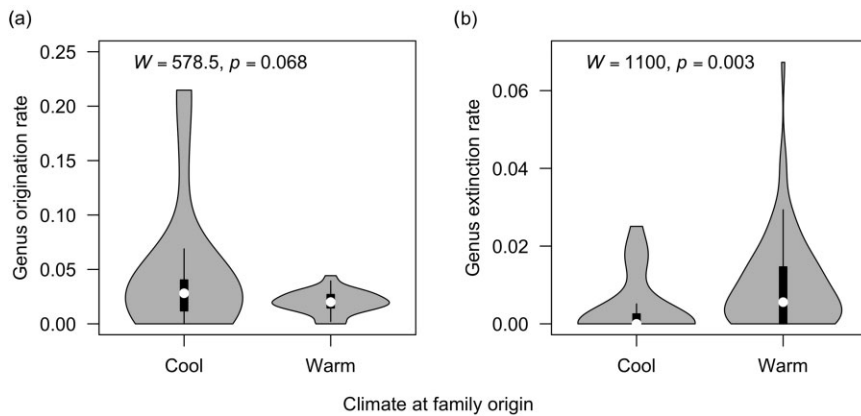

Figure 4 During the last cool interval in the Cenozoic, per-genus origination rates (a) do not differ among families that originated in different palaeoclimatic intervals but extinction rates (b) do. The violin shape represents a smoothed probability distribution of the data (origination and extinction rates in each category).

origin families appears to be sensitive to climate *change*, perhaps because the contraction of tropical regions during cooling intervals leaves some of the warm-origin taxa at high latitudes (which are tropical during the warm interval) at greater risk of extinction, and reduces the geographic ranges of tropical taxa, perhaps elevating extinction rates even there (Condamine *et al.*, 2012). Although we did not detect a strong association between climate state and genus origination rate, albeit with a few more rate shifts between climate states using the NRC (2011) climate scheme (Fig. S5), we cannot rule out that such effects might emerge given higher spatial and temporal resolution. For example, the Mid to Late Jurassic cool interval is relatively brief ($n = 6$ geological stages, *c.* 30 Myr), affording limited statistical power for detecting damped origination rates. Further detailed analyses of time series for extinctions in cold-temperate regions might also show stronger responses to warming and cooling episodes in comparison with warmer regions.

Palaeoclimate data and models are constantly evolving, and the scheme we used in this study, in order to allow direct comparison with Romdal *et al.*'s (2013) results, is not necessarily the most accurate. For example, many studies now suggest that the long cold interval starting in the Carboniferous ended in the Permian (i.e. before 250 Ma; e.g. Montañez & Poulsen, 2013). Shifting this climate-state boundary, i.e. shifting the Early Triassic from cool to warm added six warm-origin families and a
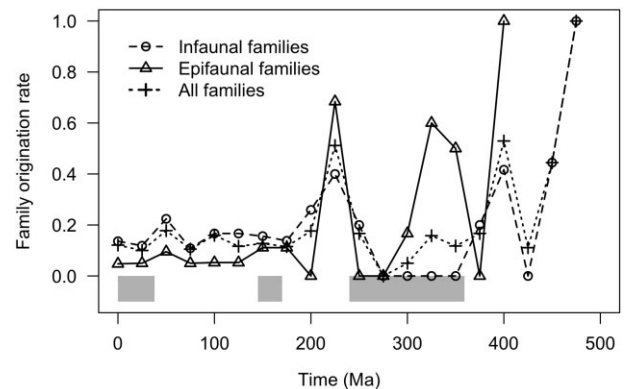

Figure 5 Infaunal (circles and dashed line), epifaunal (triangles and solid line) and all (crosses and dotted line) family origination rates in 25-Myr intervals throughout bivalve evolutionary history, calculated as the ratio of the number of families that originated in the interval to the total number of families that have been sampled for each life-habitat category in the interval (including those that originated during the interval). Calculation was based on families that crossed interval boundaries. The bar below 0 indicates palaeoclimate state, with grey indicating cool intervals and white indicating warm intervals. Both extant and extinct families are included. Families with a mixture of infaunal and epifaunal species are excluded in this analysis.

significantly higher genus origination rate in the Triassic warm interval than in the Permo-Carboniferous cool interval (Wilcox's $W = 51$, $P = 0.025$); but it had no effect on results regarding the present-day LDG (see Table S2). When we used a more recent climate scheme (summarized by NRC, 2011), only one of the extant families (but 20 extinct families) in our dataset originated in a cool interval, further supporting the result that the variation in present-day LDG slopes in marine bivalve families (Table S2) is not related to global climate conditions at the time of family origination (see Appendix S1 for more discussion on the climate models).

Given our results, a logical next step would be to combine temporal origination and diversification data with the detailed spatial histories of these clades. For example, previous studies incorporating spatial variation in diversification dynamics showed that diversification rates tend to be higher in the tropics, and that latitudinal rate variations are a major determinant of the LDG in bivalves (Jablonski *et al.*, 2006, 2013) and many other taxa (McKenna & Farrell, 2006; Wiens, 2007; Condamine *et al.*, 2012; Smith *et al.*, 2012; but see Jansson *et al.*, 2013 for a different argument). However, whether warm-origin families have higher diversification rates than cool-origin families *in the tropics*, or cool-origin families have higher diversification rates than warm-origin families *in extratropical areas*, remains unknown. Unfortunately, bivalve distributions in the geological past are not yet sufficiently documented to address these questions. The data are also lacking for large-scale analyses of how climate state influences the geographic range dynamics of species and genera over longer geological time frames. Many marine and terrestrial species and genera demonstrably expand latitudinal ranges during warm intervals, and withdraw from higher latitudes during glacial times (Roy *et al.*, 1996; Hawkins *et al.*, 2007; Sandel *et al.*, 2011; Jablonski *et al.*, 2013), and such climate-driven range shifts could erase the effect of the ancestral climatic niche on long-term diversification dynamics.

Evolutionary and ecological events that occurred in a particular interval might be only distantly connected to global climate states, but could still drive the patterns observed here. For example, the apparent increase in predation intensity, known as the Mesozoic marine revolution (Vermeij, 1987; Harper, 2003), could have contributed to increased rates of origination of bivalve families during the post-Palaeozoic warm intervals, and perhaps promoted differential diversification dynamics related to the biological traits of clades (Vermeij, 1987; Ros *et al.*, 2011). Similarly, two major peaks in (extant and extinct) family origination rates for epifaunal bivalves, one in the Carboniferous cool interval and the other in the Early to Mid Triassic during a warm interval (Fig. 5), could arguably be responses to the Late Devonian and end Permian mass extinctions, respectively (see Foote, 2000, 2010). In fact, the recovery intervals following all of the 'big five' mass extinctions fall within warm intervals; the opportunities opened by the extinctions are likely to have had a major role in promoting diversification at those times (e.g. Foote, 2010, Krug & Jablonski, 2012), and are difficult to directly attribute to climate alone. However, we have no comparative data to determine whether recoveries would be less prolific if they occurred during cool intervals instead. The inception and progress of events such as the Mesozoic marine revolution and recovery from a mass extinction, however, may ultimately have been related to climate states and accompanying changes in the physical environment. A better understanding of how climate interacts with other biotic and abiotic forces to influence diversification dynamics will, again, require spatially explicit analyses at higher temporal resolution, using models that incorporate all the relevant parameters.

In summary, we evaluated the impact of past global climate states on bivalve diversification dynamics as a potential mechanism linking climatic history to present diversity patterns. Our results indicate that the initial climate state interacts with subsequent climate states to shape clade diversification, particularly differential extinction. At least in bivalves, underlying mechanisms might involve differences in life habit that evidently impose differential responses to climate states. However, these effects do not produce predictable variations in LDG slopes among bivalve families that originated during different global climate states; tropical niche conservatism, hypothesized to shape LDGs over Phanerozoic time-scales (Romdal *et al.*, 2013) is not supported by our results. To better understand whether (and how) the LDG patterns of clades respond to climate states, more detailed analyses of spatial patterns of diversification dynamics over time are needed. A further and more difficult step is to evaluate the role of biotic interactions, such as predation and competition, on diversification dynamics (Jablonski, 2008; Phillimore & Price, 2008; Rabosky, 2009; Schemske *et al.*, 2009; Ezard *et al.*, 2012) within a framework of climate change.

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Additional references may be found at the end of Appendix S1 at [http://onlinelibrary.wiley.com/doi/10.1111/geb.12153/suppinfo].

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Result and discussion supplements.
Figure S1 Genus-level diversity throughout the bivalve fossil record.
Figure S2 Per-genus origination, extinction and net diversification rates throughout the bivalve fossil record.
Figure S3 Per-genus origination, extinction and net diversification rates in different palaeoclimate intervals.
Figure S4 Bivalve per-genus rates of origination, extinction and net diversification, for warm-origin and cool-origin groups in each geological stage.
Figure S5 Bivalve per-genus origination, extinction and net diversification rates, for warm-origin and cool-origin groups, in six palaeoclimate intervals.
Figure S6 Latitudinal diversity gradient slopes in families with different living positions.
Figure S7 Latitudinal diversity gradient slopes in families with different feeding habits.
Figure S8 Per-genus origination, extinction and net diversification rates in families with different living positions.

Figure S9 Per-genus origination, extinction and net diversification rates in families with different living positions throughout the bivalve fossil record.
Table S1 Statistical comparisons of per-genus origination, extinction and net diversification rates between adjacent warm and cool intervals.
Table S2 Family age, present-day genus and species richness, and latitudinal diversity gradient slopes.
Table S3 Pair-wise comparisons of latitudinal diversity gradient slopes in families that originated from cool, warm and hot intervals.
Table S4 Numbers of extant warm-origin and cool-origin families with different living positions relative to substratum and feeding habits.

BIOSKETCHES

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