

## LETTER

# Differential niche dynamics among major marine invertebrate clades

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### Abstract

The degree to which organisms retain their environmental preferences is of utmost importance in predicting their fate in a world of rapid climate change. Notably, marine invertebrates frequently show strong affinities for either carbonate or terrigenous clastic environments. This affinity is due to characteristics of the sediments as well as correlated environmental factors. We assessed the conservatism of substrate affinities of marine invertebrates over geological timescales, and found that niche conservatism is prevalent in the oceans, and largely determined by the strength of initial habitat preference. There is substantial variation in niche conservatism among major clades with corals and sponges being among the most conservative. Time-series analysis suggests that niche conservatism is enhanced during times of elevated nutrient flux, whereas niche evolution tends to occur after mass extinctions. Niche evolution is not necessarily elevated in genera exhibiting higher turnover in species composition.

### Keywords

Carbonate environments, climate change, niche conservatism, species turnover, substrate affinity, terrigenous clastic environments.

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## INTRODUCTION

Niche conservatism, or the tendency for a taxon's niche to remain stable over time, potentially influences numerous aspects of ecology and evolution, including patterns of species richness, geographic range size, character divergence, community assembly, ecosystem function and food webs, species invasion potential and species response to climate change (reviewed in Pearman *et al.* 2008; Wiens *et al.* 2010). For example, niche conservatism can limit species invasion potential to areas similar to their native range, making it possible to predict what areas may be sensitive to the introduction of exotic species (Peterson 2003). When species with strong niche conservatism experience new conditions outside their range of tolerance, they must either migrate or face extinction; thus in the face of global climate change, species with strong niche conservatism are less likely to be able to adapt (Holt 1990). Changes in morphology and life-history may also be closely linked to traits habitat shifts during the course of evolution (Tokuda *et al.* 2010).

Previous studies on niche conservatism have focused almost exclusively on terrestrial systems (Wiens & Graham 2005; Pearman *et al.* 2008; Losos 2008; Wake *et al.* 2009 [and rest of special issue]; Peterson 2011). For example, only 2 of almost 40 empirical studies reviewed by Pearman *et al.* (2008), and 1 of 76 reviewed by Peterson (2011), focused on marine organisms. In fact, most data on niche conservatism in marine systems has come from the fossil record. Some of this work documents niche differentiation along depth gradients. Ando

*et al.* (2010) documented the reordering of depth associations within planktonic foraminifera species during the Early-Mid Cretaceous. Holland & Zaffos (2011) found that Late Ordovician benthic marine invertebrate genera were strongly conserved in where they were most abundant along a bathymetric gradient, but not conserved in the bathymetric range from which each was sampled. Stigall and colleagues found that within Late Ordovician brachiopods, niche conservatism dominated during periods of gradual sea level change but niche evolution occurred during periods of more rapid environmental change and species invasion into the region (summarised in Stigall 2012). Other work has documented asymmetric latitudinal shifts, particularly in marine bivalves: genera originating in tropical habitats more frequently expanded their ranges into higher latitude regions while maintaining a tropical presence (Jablonski *et al.* 2006). Jablonski *et al.* (2013) suggest that range expansion within bivalve genera occurred via constituent species which occupy a larger latitudinal range than most of their congeners, but it remains unclear when niche evolution occurred. Niche evolution may have occurred as genera expanded into higher latitudes, or genera may have shifted their latitudinal range during warming events (habitat tracking), with only those able to adapt as temperatures cooled again retaining a presence in higher latitudes. Nonetheless, these studies raise doubts that niche conservatism in marine clades is as pronounced as inferred from correlations between species richness and speciation rates (Allen & Gillooly 2006) or from work on terrestrial clades (Peterson 2011).

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Here, we assess the frequency of niche conservatism in marine clades, by calculating changes in habitat preferences within marine invertebrate genera throughout the entire Phanerozoic. We focus specifically on preference for marine habitats characterised by either calcium carbonate or terrigenous (clastic) substrates. The reason we focus on substrate is fourfold.

First, marine invertebrates are known to be physically and physiologically sensitive to differences in these two substrates. Boring, encrusting and attached sessile organisms are often highly sensitive to mineral composition (e.g. Bavestrello *et al.* 2000) and organisms have evolved a variety of adaptive strategies for attachment to carbonate vs. clastic substrates (Bromley & Heinberg 2006). Larval recruitment is influenced by mineralogy and associated sediment characteristics (e.g. Cerrano *et al.* 1999). Organisms may also have effective substrate preferences because their food sources and feeding strategies vary among substrate types (Bromley & Heinberg 2006), or through competition with substrate-sensitive taxa (e.g. Schiaparelli & Cattaneo-Vietti 1999).

Second, although it may be argued that substrate is only one aspect of a taxon's niche, it is in fact representative of a variety of environmental variables. Carbonate environments are typically confined to lower latitudes (Kiessling *et al.* 2003). They are also relatively nutrient limited compared to clastic environments (Wood 1993) and many taxa are sensitive to such differences. For example, coral reefs suffer under influxes of nutrients (Hallock & Schlager 1986), whereas the scarcity of bivalves in carbonate habitats is often explained by the nutrient deficiency of carbonate sediments (Eliuk 1998). Pelagic organisms may show a preference for one 'substrate' compared to the other because they are sensitive to nutrient input and climate. Although the data to determine nutrient levels on a collection-by-collection basis is not yet available, we were able to compare time series of environmental proxies for global nutrient input and remobilisation with faunal-level changes in habitat affinity. If nutrient levels are a driving force in determining taxon affinities for carbonate vs. clastic habitats, changes in habitat affinity should be associated with changes in nutrient levels.

Third, there is considerable evidence that substrate preference has contributed to long-term diversity dynamics of marine invertebrates (e.g. Foote 2006; Kiessling *et al.* 2010). Recent work has also shown a positive correlation between nutrient availability and rates of origination and overall marine biodiversity (Cárdenas & Harries 2010; Hannisdal & Peters 2011). This suggests that evolution of niches characterised by carbonate and clastic habitats play an important role in macroevolution. As the availability of different habitats changes over time, a taxon's capacity to survive may depend on its ability to exploit or adapt to new environmental variables, specifically those associated with a different substrate. For example, changes in ecological dominance of clades during the Ordovician have been associated with increased terrigenous content of marine sediments coupled with shifts in substrate affinity (Miller & Connolly 2001). Niche breadth is also associated with species duration, with generalists having greater longevity than specialists (Kammer *et al.* 1997; Liow 2007; Heim & Peters 2011) and lower rates of turnover and extinction risk (Baumiller 1993; Harnik *et al.* 2012). Thus, there may be a

long-term adaptive advantage to having weak substrate preferences or the ability to shift habitats through time.

Fourth, identification of these two habitats is straightforward and consistent throughout the fossil record. In contrast, the latitudinal extent of the tropics is likely to have shifted through time with changes in global temperature and ocean circulation, complicating interpretations of latitudinal range shifts over long timescales. Similarly, shifts in the location of the thermocline and changes in ocean stratification complicate interpretation of bathymetric shifts over long timescales.

Contrary to our expectations, we found that niche conservatism to carbonate or clastic habitats was common throughout the fossil record. However, niche conservatism varied among taxonomic groups and depended on how strong taxa were in their initial habitat preferences. We found that niche conservatism has been at its highest over the last 100 million years, and that Earth history has been punctuated by periods where niche conservatism was low, notably following mass extinctions. We found a negative association between global nutrient flux and global changes in habitat affinity, with a moderately low effect size for all marine invertebrates. This association appears to be driven by stronger associations within particular ecological or taxonomic groups.

A long standing question has been the frequency with which speciation is associated with the breakdown of niche conservatism and ecological innovation. Some authors have suggested that niche shifts within higher taxa reflect differential rates of origination and extinction (Jablonski *et al.* 2006; Holland & Zaffos 2011). A recent review of niche stability in primarily terrestrial organisms, however, found little to no niche differentiation during speciation (Peterson 2011). We also find little support for an association between species turnover and changes in habitat affinity within genera, suggesting a large role for ecological adaptation within species.

## MATERIALS AND METHODS

### Occurrence data

Habitat affinity was estimated using genus occurrences downloaded from the Paleobiology Database ([www.paleobiodb.org](http://www.paleobiodb.org)) on 19 June 2013 using the following protocol: (1) Multiple occurrences of a genus within a collection were lumped. (2) Subgenera were not treated as genera; only the genus name was used. (3) Generically indeterminate occurrences were disregarded but specifically indeterminate occurrences were included if they were assigned to genera. (4) Informal genus names and genus names qualified by 'aff.', '?', 'cf.', or quotation marks were disregarded. We estimated habitat affinity at the genus level because genera are more taxonomically stable and more robust against sampling artefacts relative to species-level data. Collection data were downloaded separately and used to calculate the number of collections sampled from each habitat, including those from which taxa were absent.

Occurrences and collections were assigned to one of 80 time intervals corresponding to geological stages from the early Cambrian through the Pleistocene, and to either carbonate or clastic habitats using the lithology of the rock from which collections were made (Table S1). In total, 338,730 occurrences

of 20357 genera could be assigned to a time interval and habitat (54% to carbonate habitats and 46% to clastic habitats). Taxonomically, the data set is dominated by gastropods, bivalves, corals and brachiopods (Table S2).

### Estimating habitat affinity

In order to estimate habitat affinity, we used the method developed by Simpson & Harnik (2009), which makes affinity assignments using Bayesian inference. The method explicitly separates the biological null hypothesis that a taxon has no affinity from the expected distribution of occurrences given the differential sampling of habitats. The null hypothesis is that a taxon is equally likely to prefer either of the two habitats ( $H_1$  or  $H_2$ ); in other words, that the prior probability  $P(H_1) = P(H_2) = 0.5$ . Following Bayes' theorem, the probability that a taxon prefers habitat 1 given the proportion of collections sampled from habitat 1 is equal to the prior probability times the compatibility of the observed data with the null hypothesis (the likelihood), over the evidence,  $E$ :

$$P(H_1|E) = P(H_1) * P(E|H_1) / P(E),$$

where  $P(E) = P(E|H_1) * P(H_1) + P(E|H_2) * P(H_2)$ .  $P(E|H_1)$  is given by the binomial probability of sampling the observed number of occurrences from habitat 1, with a probability of success equal to the proportion of all collections sampled from habitat 1.

Posterior probabilities that a taxon has an affinity for habitat 1 compared with habitat 2 range from 0 to 1. While taxa may be assigned to a habitat affinity based on an arbitrary threshold such as  $P(H_1|E) > 0.9$ , this is not actually necessary and results in a reduction of information. Instead, we treated the posterior probability values as measures of degree. For example, we interpreted a taxon with a posterior probability of 0.9 for habitat 1 as having a stronger preference for that habitat than another taxon with a posterior probability of 0.7. Because the calculation of posterior probabilities is sensitive to large differences in the frequency of collections from each habitat, we always calculated the posterior probability for the more frequently sampled habitat, and then for each calculation where the more frequently sampled habitat was a clastic substrate, subtracted the resulting posterior probability from 1. After doing this, all results lie on the same scale where a posterior probability of 0 indicates a strong affinity for clastic habitats and a posterior probability of 1 indicates a strong affinity for carbonate habitats. Habitat affinities were calculated per interval for all genera with at least three occurrences (the minimum required for probability calculations) in a given interval. A higher threshold for occurrence counts did not alter our basic results.

We assessed changes in habitat affinity by calculating the differences in probability values between adjacent time intervals within each genus, i.e. the posterior probability of Taxon X in time  $t + 1$  minus the posterior probability of Taxon X in time  $t$ . This yields a distribution of values ranging from  $-1$  to  $1$ , where a value above 0 indicates a shift towards carbonates, below 0 a shift towards clastics, and 0 indicates no change in habitat affinity. The magnitude of the difference indicates the degree of shifting that occurred within a genus across two time intervals, with smaller values indicating higher levels of conservatism in habitat affinity, i.e. greater niche conservatism.

Because the Paleobiology Database is an ongoing enterprise, geographic and taxonomic coverage varies through time, and sampling noise may be substantial. In order to determine whether our results were biologically meaningful, we assigned habitat randomly to each genus occurrence and recalculated the change in habitat affinity within each genus per time interval. This was repeated 1000 times and then treated as a null distribution against which to compare the empirical results.

Uneven sampling may also influence the calculation of the affinity estimate itself. During any given time interval, two genera with the same proportion of occurrences in carbonates vs. clastics but different total numbers will have similar but not identical posterior probabilities, and thus different habitat affinities. As a result, a genus could show a change in affinity simply because there was a change in the number of occurrences of that genus. Such changes could result because of real changes in geographic range or abundance, but may also reflect uneven sampling. Worse, changes in affinity might be spuriously associated with large changes in diversity. In order to test this, we also measured affinity as the difference between observed and expected frequency of occurrence in each environmental setting, such that

$$\text{Affinity} = \text{CA}_{\text{gen}} / (\text{CA}_{\text{gen}} + \text{CL}_{\text{gen}}) - \text{CA}_{\text{coll}} / (\text{CA}_{\text{coll}} + \text{CL}_{\text{coll}})$$

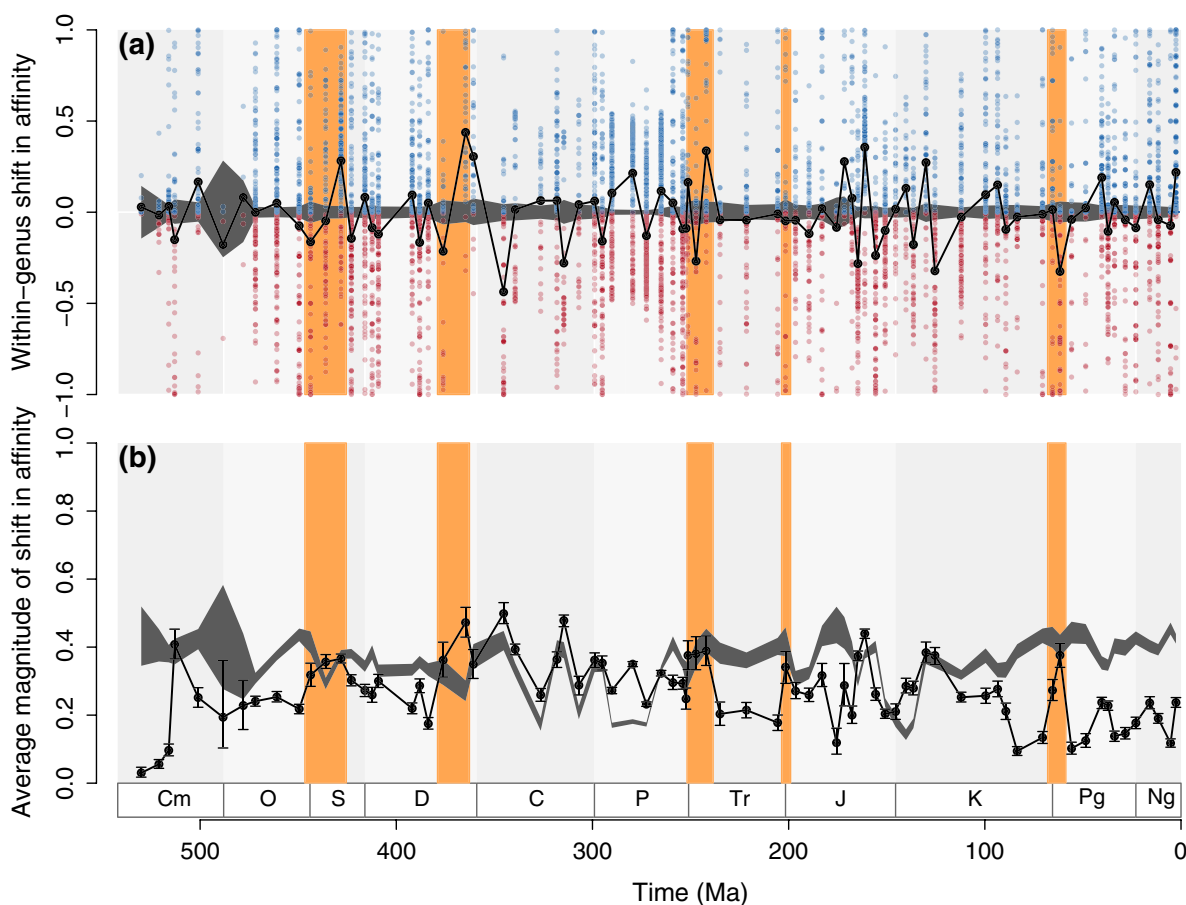
where  $\text{CA}$  = number of generic occurrences (gen) or collections (coll) from carbonates and  $\text{CL}$  = number of generic occurrences or collections from clastics. Results were qualitatively the same, even at mass extinction events (Fig. S1, compare with Fig. 1 discussed below). We chose to retain the results from the Bayesian method for the remaining analyses because they are easier to interpret.

### Environmental proxy data and time-series analysis

We used the following stable isotope data as proxies for global nutrient flux:  $^{87}\text{Sr}/^{86}\text{Sr}$ , a proxy for nutrient input from weathering of continental rocks; and  $\delta^{34}\text{S}$ , a proxy for nutrient input from recycling of organic material in ocean sediments, or nutrient remobilisation (Cárdenas & Harries 2010). Stable isotope data was obtained from Prokoph *et al.* (2008) and averaged within each of the 80 time intervals. Both series were linearly detrended, power transformed using the Yeo-Johnson transformation to stabilise variance, and mean standardised. Because conservation of substrate affinity shows an increasing trend through time (see Results), mean change in affinity was also detrended. To test for cross-correlations in our time-series data, we applied generalised differencing, transforming each value in each time series by  $\Delta x = x_t - r_A(x_{t-1})$ , where  $x_t$  is the original value and  $r_A$  is the lag 1 autocorrelation of the respective time series (McKinney & Oyen 1989).

### Estimating latitudinal range shifts

In order to determine if habitat shifting occurred in concert with geographic relocation, we estimated latitudinal range shifts by comparing the means of all paleolatitudes at which a genus has been sampled in two consecutive time intervals. Paleocoordinates were derived from Scotese's models of continental drift



**Figure 1** (a) Within-genus shifts in habitat affinity through time. Red = shift away from affinity for carbonates; blue = shift away from affinity for clastics. Black line = mean. Gray polygons = averages of 1000 permutations of randomly assigned habitats. (b) Change in habitat affinity based only on the magnitude of the shift (i.e. the absolute value of the change in habitat affinity). Error bars are standard errors. Time axis is in millions of years ago (Ma). Cm = Cambrian; O = Ordovician; S = Silurian; D = Devonian; C = Carboniferous; P = Permian; Tr = Triassic; J = Jurassic; K = Cretaceous; Pg = Paleogene; Ng = Neogene. Orange rectangles = major mass extinctions and subsequent recovery intervals. Data points are plotted on the boundary between the two time intervals under comparison (e.g. point on K-Pg boundary represents shift in habitat affinity over the end-Cretaceous mass extinction).

and rotation through time, provided as part of the standard download protocol from the Paleobiology Database. Plate tectonic rotations are constrained by a combination of paleomagnetic measurements of rocks and magnetic sea floor anomaly data (Scotese 2004). Latitudinal range shifts were standardised for plate tectonic movement and uneven sampling by subtracting the mean latitudinal shift of all occurrences.

#### Estimating species turnover

Species occurrence data was downloaded from the Paleobiology Database on 06 July 2013 using the same protocol outlined above for generic occurrences but excluding specifically indeterminate occurrences and those qualified by 'aff.', '?', 'cf.', or quotation marks. We marked each species as 'present' or 'absent' within each time interval. Then we estimated similarity of species composition within each genus for each pair of adjacent time intervals using the Jaccard distance. A Jaccard distance close to one indicates high turnover in species composition within the genus between the two intervals.

#### Possible phylogenetic autocorrelation

Some analyses herein include comparisons among data points that are potentially phylogenetically non-independent (e.g. the association between change in habitat affinity and amount of species turnover within genera). Although no phylogenetic hypothesis comprising marine invertebrates through time is currently available, we were able to account for phylogenetic relatedness by including taxonomic assignment as a random effect in a linear mixed-effect model and comparing the resulting effect sizes with the output from a linear model that excluded taxonomy (Pinheiro & Bates 2000). Although models including taxonomy were better supported by AIC, effect sizes were marginally decreased and did not alter the interpretation of the results (Table S3). Therefore, we report simple Spearman rank correlations to indicate effect sizes between pairs of variables where the strength of association was of interest. We did not attempt to factor in turnover for the time-series analyses because changes in habitat affinity are assessed at the whole-faunal level. Instead we assessed the strength of the association between series for taxonomic subsets.

### Possible lithification bias

Aragonitic fossils are more likely to dissolve after burial than calcite fossils (e.g. Wright *et al.* 2003). Although it appears that the effect of this bias is neither as severe as originally predicted (Bush & Bambach 2004) nor responsible for changes in diversity through time (Kidwell 2005), the preferential dissolution of aragonite makes aragonitic taxa less likely to be sampled, decreasing the possibility of including them in the analysis (i.e. no affinity would be calculated for them). For the purposes of this study, this would only bias the results if aragonite dissolution occurred more frequently in one specific habitat.

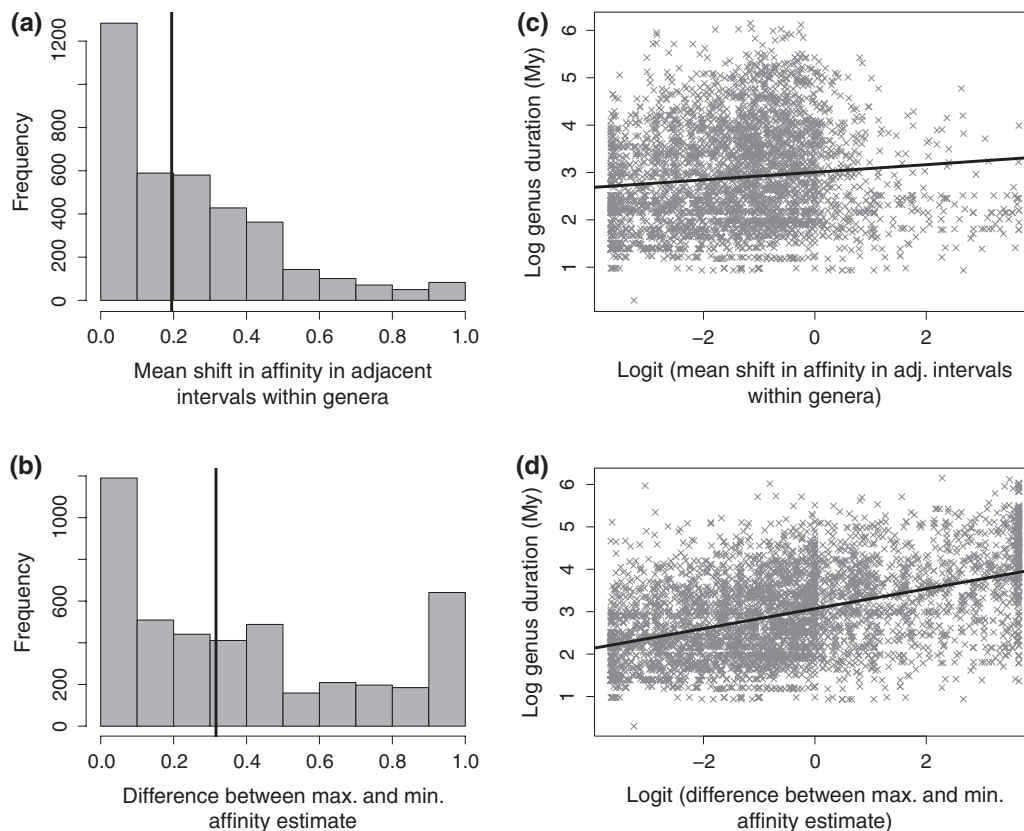
Although we cannot investigate the effect of preferential aragonite dissolution directly, aragonite dissolution is more common in lithified sediments than unlithified sediments (Hendy 2009). Lithification can also bias the recovery of specimens from samples in other ways. For example, small or fragile specimens may be destroyed during compaction, and those that survive are more likely to be overlooked or destroyed during specimen sampling and preparation if they are from lithified rocks (Kowalewski *et al.* 2006; Sessa *et al.* 2009). Unlithified collections also preserve small organisms with higher taxonomic resolution (Sessa *et al.* 2009). Thus, it is possible that small taxa that occur equally in carbonate and clastic habitats will appear to have an affinity for clastic habitats simply because they are not sampled

from lithified carbonates, an effect similar to aragonite dissolution. In order to explore how lithification may have biased the results, we removed occurrences sampled from poorly lithified and unlithified sediments and compared the results.

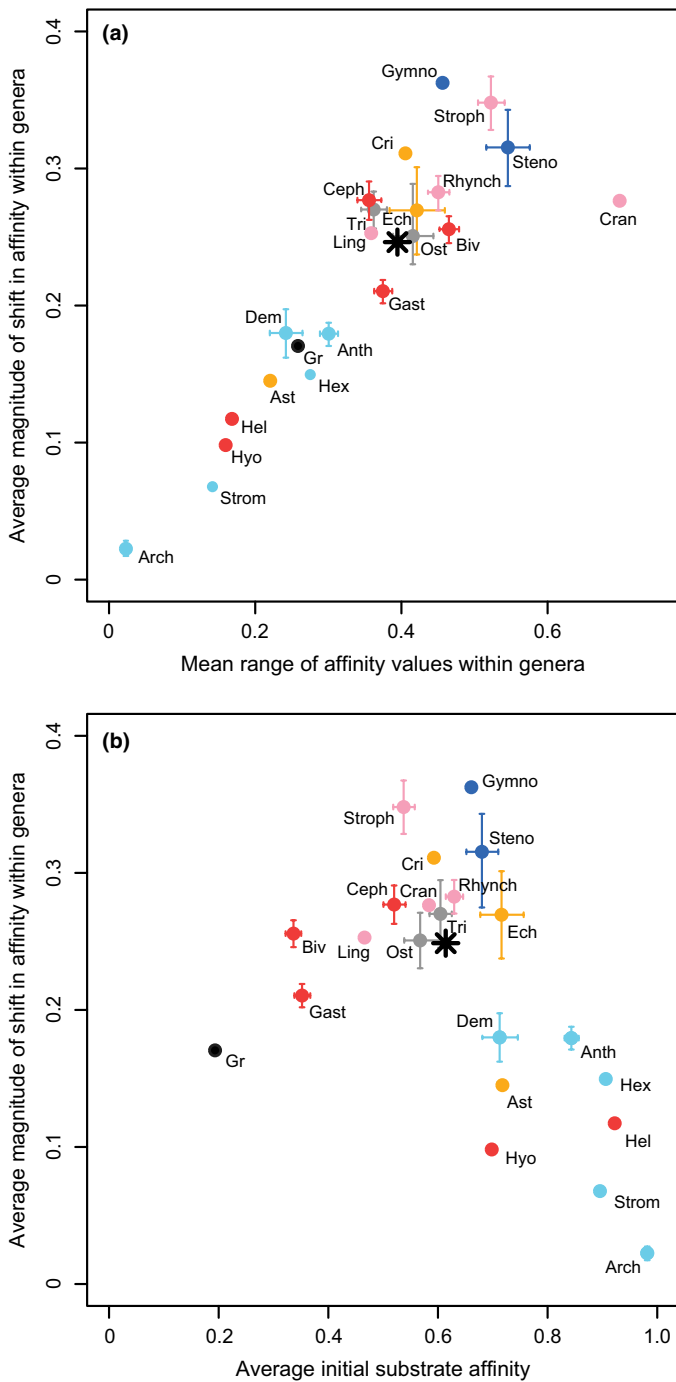
### RESULTS

The distribution of changes in habitat affinity within genera varies over time and is frequently much more than expected if habitat were assigned randomly (Fig. 1a). With random assignments, the distribution of changes is symmetrical around 0 but has a high standard deviation (Fig. S2). In contrast, the empirical results show many intervals with asymmetric distributions and a greater-than-expected shift towards either carbonates or clastic substrates. Deviations from zero largely reflect directionality of habitat shifting, and changes in habitat affinity are often dominated by shifts towards a particular environment, even though the average shift across the entire Phanerozoic is 0.

The magnitude of change in habitat affinity is significantly lower than expected if habitats were assigned randomly (Fig. 1b, Mann–Whitney  $U$ -test = 4803,  $P < 0.0001$ , median shift = 0.26, median shift if habitat assigned randomly = 0.38). The magnitude of change in habitat affinity is also low within genera over their durations (Fig. 2a, median



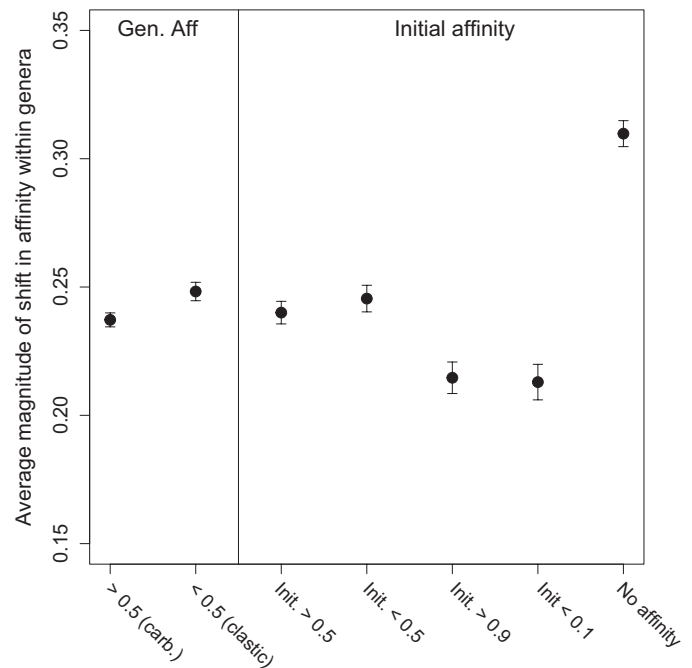
**Figure 2** Histograms showing the distribution of average magnitude of shift in habitat affinity within each genus (a), and the distribution of differences between the maximum and minimum affinity estimate (range) for each genus (b). Black lines show median values. (c) Relationship between logit-transformed mean in affinity estimates and log-transformed genus durations ( $\rho = 0.44$ ,  $P < 0.0001$ ). (d) Relationship between logit-transformed range in affinity estimates and log-transformed genus durations ( $\rho = 0.14$ ,  $P < 0.0001$ ). Logit transformation of proportions remapped to the interval 0.025–0.095 in order to retain affinity estimates of 0 and 1 after the transformation.



**Figure 3** (a) Comparison of average magnitude of shift in affinity within genera and average per-genus range in substrate affinity within major clades (classes). (b) Comparison of average magnitude of shift in affinity within genera and average per-genus initial affinity within clades. Error bars are standard errors for all clades with more than 50 genera. Pink = brachiopods: Cran = Craniata, Stroph = Strophomenata, Rhynch = Rhynchonellata, Ling = Lingulata. Blue = bryozoans: Steno = Stenolaemata; Gymno = Gymnolaemata. Red = mollusks: Biv = Bivalvia; Ceph = Cephalopoda; Gast = Gastropoda; Hel = Helcionelloida; Hyo = Hyolitha. Orange = Echinoderms: Ech = Echioidea; Ast = Astroidea; Cri = Crinoidea. Gray = Arthropods: Tri = Trilobita†; Ost = Ostracoda. Light blue = corals and sponges: Anth = Anthozoa; Dem = Demospongia; Hex = Hexactinellida; Strom = Stromatoporoidea†; Arch = archeocyathids†. Gr = Graptolithina† (macrozooplankton). Asterisk = all marine invertebrates. †extinct clade.

shift = 0.19). Similarly, the range in habitat affinity (the difference between the maximum habitat affinity estimate and the minimum habitat affinity estimate over a genus duration) is low (Fig. 2b, median = 0.32). The range of affinity estimates within a genus is positively correlated with its duration (Fig. 2d, Spearman's  $\rho = 0.44$ , d.f. = 3688,  $P < 0.0001$ ). However, the mean change between intervals is much less strongly correlated with duration (Fig. 2c,  $\rho = 0.14$ , d.f. = 3688,  $P < 0.0001$ ). Thus, long-lived taxa that acquire large ranges in substrate affinities do so through many small changes in affinity. Despite considerable fluctuations in average magnitude of niche shifting through time, niche conservatism has increased over the Phanerozoic ( $\rho = 0.23$ , d.f. = 77,  $P = 0.045$ ), especially since the Devonian ( $\rho = 0.58$ , d.f. = 54,  $P < 0.0001$ ).

Although marine invertebrates appear to be rather conservative in habitat affinities overall, some clades are much less conservative than others (Fig. 3a). In addition, clades where most genera show a strong initial affinity for clastic or carbonate habitats show more niche conservatism (Fig. 3b), as do the genera themselves (Fig. 4). In fact, the average habitat affinity within a genus is highly correlated with its initial affinity ( $\rho = 0.81$ , d.f. = 4428,  $P < 0.0001$ , for all genera



**Figure 4** Average magnitude of shift in affinity within genera for different ecological groups. '> 0.5 (carb.)' = genera with overall affinity for carbonate environments. '< 0.5 (clastic)' = genera with overall affinity for clastic environments. 'Init. > 0.5' = genera with initial affinity for carbonate environments. 'Init. < 0.5' = genera with initial affinity for clastic environments. 'Init. > 0.9' = genera with very strong initial affinity for carbonate environments. 'Init. < 0.1' = general with very strong initial affinity for clastic environments. 'No affinity' = genera with initial affinity between 0.25 and 0.75 (weak to no affinity). Note that axis ranges only from 0.15 to 0.35 (possible values range from 0 to 1). Error bars are standard errors.

where affinity estimates could be made for more than one time interval). Not surprisingly, corals and sponges are highly conservative, and predominantly confined to carbonate habitats. Bryozoans and brachiopods are the least conservative (Fig. 3b). Pelagic taxa (here represented by cephalopods) show lower niche conservatism. There is no difference between taxa that show an initial affinity for carbonate habitats and those that show an initial affinity for clastic habitats (Fig. 4).

Faunal-level changes in habitat affinity were negatively correlated with  $^{87}\text{Sr}/^{86}\text{Sr}$  (global nutrient input from land), and to a lesser extent  $\delta^{34}\text{S}$  (nutrient remobilisation) (Table 1). In particular, infaunal and sessile or facultatively mobile taxa show strong associations between habitat conservatism and both  $^{87}\text{Sr}/^{86}\text{Sr}$  and  $\delta^{34}\text{S}$ , as do taxonomic clades characterised by these ecologies (e.g. corals, crinoids and bivalves). There is no correlation between the degree of shifting in habitat affinity and mean latitudinal shifts between intervals ( $\rho = -0.002$ , d.f. = 77,  $P = 0.988$ ).

Although there is a significant positive correlation between species turnover and changes in habitat affinity, the effect size is low ( $\rho = 0.08$ , d.f. = 8846,  $P < 0.0001$ , Fig. 5), with the majority of taxa showing niche conservatism despite high species turnover rates. Given high species turnover, the odds that a genus will show a change in habitat affinity that is greater than the mean is not significantly different from 1 (Fisher exact test of contingency table shown in Fig. 5, odds ratio = 0.91, confidence interval = 0.81–1.02,  $P = 0.1211$ ).

When species richness is low, complete species turnover (a Jaccard distance of 1), or complete absence of species turnover (a Jaccard distance of 0), within a genus between adjacent time intervals is likely. Indeed, 72% of the comparisons with a Jaccard distance of 0 or 1 involve only one species in each time interval (either the same or different). As the minimum number of congeners in each adjacent intervals is increased, effect size gets smaller. Thus in speciose genera, shifts in habitat affinity are even less frequently associated with turnover in species composition.

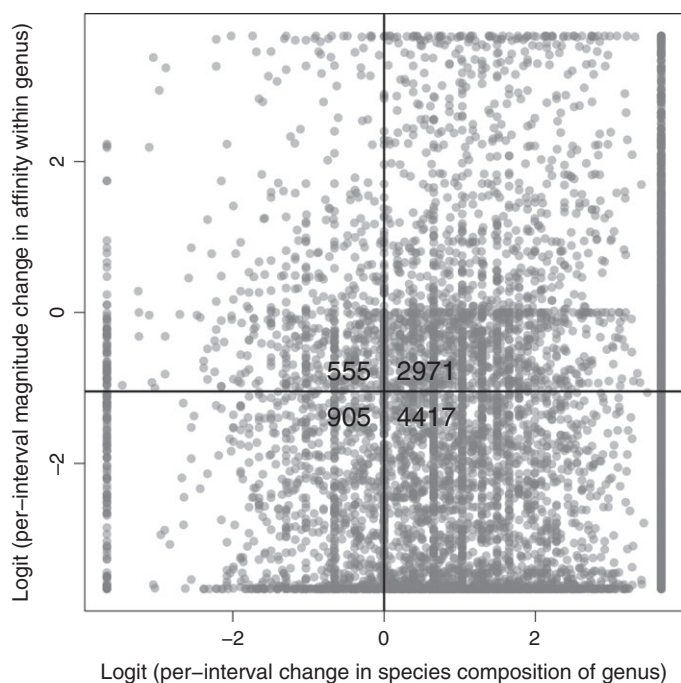
#### Possible lithification bias

Poorly lithified and unlithified sediments comprised 12% of the occurrences in the data set. Ninety-two percent of these were sampled from clastic sediments and largely consist of bivalve and gastropod occurrences (81%). These occurrences are also predominantly from the last 50 million years (73%) (Fig. S3). Because of this, excluding these occurrences had a systematic effect on the results, primarily by biasing estimates for young bivalves and gastropods towards weaker affinities for clastic habitats and stronger affinities for carbonate habitats. This artificially decreased the estimated niche conservatism in these clades, in particular because longer lived genera show larger shifts from clastic affinities to carbonate affinities. Other clades were not affected, and niche conservatism in marine invertebrates as a whole remained high. Thus, rather than uncovering a pattern otherwise obscured by differential

**Table 1** Correlations between nutrient proxies and average magnitude of shift in affinity within genera, for ecological groups and for major taxonomic clades.

	$^{87}\text{Sr}/^{86}\text{Sr}$			$\delta^{34}\text{S}$			N
	$\rho$	<i>P</i> -value	pFDR	$\rho$	<i>P</i> -value	pFDR	
ALL	-0.242	<b>0.0370</b>	0.0563	-0.229	<b>0.0741</b>	0.0907	79
Epifaunal benthic	-0.171	0.1427	0.1370	-0.159	0.2167	0.1857	79
Infaunal benthic	-0.394	<b>0.0006</b>	<b>0.0060</b>	-0.521	<b>&gt; 0.0001</b>	<b>0.0010</b>	77
All benthic	-0.266	<b>0.0266</b>	<b>0.0456</b>	-0.265	<b>0.0375</b>	0.0563	79
Pelagic	0.118	0.3261	0.2609	-0.094	0.4736	0.3343	73
Mobile	-0.180	0.1214	0.1306	-0.196	0.1275	0.1306	79
Stationary	-0.277	<b>0.0177</b>	<b>0.0456</b>	-0.365	<b>0.0043</b>	<b>0.0172</b>	77
FM	-0.238	<b>0.0414</b>	0.0584	-0.413	<b>0.0010</b>	<b>0.0060</b>	77
Stationary & FM	-0.267	<b>0.0211</b>	<b>0.0456</b>	-0.285	<b>0.0249</b>	<b>0.0456</b>	77
Gastropoda	0.039	0.7473	0.4484	-0.121	0.3585	0.2710	72
Bivalvia	-0.353	<b>0.0025</b>	<b>0.0120</b>	-0.420	<b>0.0010</b>	<b>0.0060</b>	73
Cephalopoda	0.189	0.1306	0.1306	-0.026	0.8475	0.4730	65
Rhynchonellata	0.031	0.8144	0.4730	0.079	0.5988	0.3992	59
Strophomenata	0.304	0.0970	0.1109	0.506	<b>0.0205</b>	<b>0.0456</b>	31
Lingulata	-0.061	0.7173	0.4460	-0.438	<b>0.0263</b>	<b>0.0456</b>	39
Anthozoa	-0.318	<b>0.0115</b>	<b>0.0345</b>	-0.266	<b>0.0498</b>	0.0664	63
Demospongiae	-0.076	0.7248	0.4460	-0.286	0.2345	0.1941	26
Stenolaemata	0.010	0.9548	0.5208	-0.275	0.1931	0.1782	33
Trilobita <sup>†</sup>	0.165	0.3726	0.2710	0.080	0.7243	0.4460	33
Ostracoda	-0.319	0.0756	0.0907	-0.115	0.5840	0.3992	32
Crinoidea	-0.529	<b>0.0061</b>	<b>0.0209</b>	-0.268	0.2159	0.1857	26
Echinoidea	-0.174	0.3640	0.2710	-0.043	0.8291	0.4730	29

*P*-values adjusted for multiple comparisons ('pFDR' = FDR-adjusted *P*-value using graphically sharpened method of Benjamini & Hochberg 2000). 'Mobile' includes actively and passively mobile genera; 'FM' = genera that are generally stationary but have the ability to move (i.e., 'facultatively mobile').  
<sup>†</sup>Extinct clade.



**Figure 5** Per-interval change in species composition (measured using Jaccard distance) compared to per-interval magnitude change in habitat affinity within each genus. Gray lines delineate quadrants at Jaccard distance = 0.5 (indicating 50% species turnover) and magnitude of change = 0.26 (indicating the mean change across the Phanerozoic); each quadrant is labelled with the number of comparisons that fall within in it. Logit transformation of proportions remapped to the interval 0.025–0.095 in order to retain affinity estimates of 0 and 1 after the transformation.

lithification, this approach would bias our results by selectively removing collections from particular taxonomic groups and time intervals. For that reason, we conclude that results from the full data set are more reliable.

## DISCUSSION

Overall, marine invertebrate genera are more conservative in their preferences for habitats than expected by chance (Fig. 1b). The strength of niche conservatism varies substantially among clades (Fig. 3). In addition, there are more clades comprised of genera with strong initial affinities for carbonate than clastic environments, that is, a substantial proportion of genera in most clades had an affinity for carbonate environments after origination. This finding supports previous work that documented higher rates of origination in carbonate reef environments (Kiessling *et al.* 2010), predicting differences between carbonate and clastic environments in the number of taxa with strong initial affinities. Niche conservatism is greater in clades comprised of genera that show strong affinities for one habitat early in their duration. This implies that taxa that are more specialised early in their evolutionary history are either less likely to evolve more generalised affinities or do so at a slower rate (because the average shift per time interval is smaller). In contrast, taxa that initially show weak to no preference for a particular environment frequently become more specialised, and may do so over a relatively short time inter-

val. Both positive (e.g. Futuyma & Moreno 1988) and negative (e.g. Whitlock 1996) relationships between niche breadth and rate of niche evolution have been predicted based on theoretical considerations, but other empirical evidence also shows that rates are slower in specialist taxa (e.g. Fisher-Reid *et al.* 2012; Litsios *et al.* 2012).

The significant correlation between magnitude of shifts in habitat affinity and  $^{87}\text{Sr}/^{86}\text{Sr}$  and  $\delta^{34}\text{S}$  isotope curves suggests that nutrient flux is also an important driver of niche evolution in the oceans. In general, as nutrient input or remobilisation increases, niche conservatism increases as well, particularly in groups expected to be sensitive to local nutrient availability such as infaunal taxa and sessile taxa (Table 1). One interpretation of this result is that as nutrient remobilisation within sediments increases, some taxa show greater conservatism because they are increasingly less resource-limited (e.g. bivalves). On the other hand, as nutrient input from continental weathering and seafloor spreading increases, some taxa show greater conservatism because fewer nutrient-poor environments are available to them (e.g. corals). Nutrient loading has also influenced latitudinal and bathymetric diversity gradients in mollusks (Rex *et al.* 2005).

We did not find convincing support for the idea that changes in habitat affinity within genera are necessarily associated with species turnover, i.e. macroevolution (Fig. 5). This suggests a significant role for ecological microevolutionary response within species. Furthermore, the lack of correlation between shifts in habitat affinity and shifts in latitude indicate that adaptation to new substrate habitats does not necessarily occur during relocation. Rather, major niche shifts may occur as taxa respond to changing environmental conditions where they are, with relocation reflecting habitat tracking. If this is true, we would predict that large-scale range expansion in the ocean occurs via habitat tracking followed by in situ adaptation. This scenario also provides a mechanism for the out-of-the-tropics model which has been proposed to explain the latitudinal biodiversity gradient in bivalves (Jablonski *et al.* 2006, 2013). In this case, the expansion of tropical bivalve taxa into extratropical regions would have occurred predominantly during warming events, with only those able to adapt during subsequent cooling events retaining a presence at higher latitudes. This is consistent with the frequency at which genera expanded into extratropical areas after origination (Jablonski *et al.* 2013).

The average magnitude of change in habitat affinity increases across all mass extinction boundaries, and continues to increase for up to two more subsequent time intervals (Fig. 1b). There is also a lot of species turnover during these time intervals: 60% of the genera surviving these extinctions show complete turnover at the species level (Jaccard distance = 1). During the end-Permian and end-Cretaceous mass extinctions, the correlation between mean absolute change in affinity and turnover in species composition is comparatively high ( $\rho = 0.27$ ,  $P = 0.010$  and  $\rho = 0.25$ ,  $P = 0.011$  respectively). This indicates that during these intervals, there was more niche shifting driven by macroevolution than during background intervals. The recovery period after the Cretaceous is also remarkable for being directional: almost all shifts



are towards increasing affinity for clastic environments (Fig. 1a).

Although the increase across mass extinction boundaries is notable in its consistency, there are other periods when niche shifting is also high, in particular the Carboniferous, late Jurassic and early Cretaceous (Fig. 1b). During these time intervals, changes in the extent of carbonate and clastic environments are at their most divergent (Fig. S4): the Carboniferous is characterised by large fluctuations in the relative proportion of carbonate vs. clastic habitats, while the late Jurassic to middle Cretaceous is characterised by a dramatic expansion of clastic relative to carbonate environments. The low niche conservatism during these periods is likely due to major changes in the availability of each habitat relative to genus duration. In contrast to much of the previous Earth history, niche conservation has been high over the last 100 million years, with a brief interruption during the end-Cretaceous mass extinction.

Finally, many of the studies that have investigated the influence of substrate affinity on long-term diversity dynamics of marine invertebrates implicitly assumed that taxa are stable in their substrate preferences (e.g. Foote 2006; Kiessling *et al.* 2010). While the results of our study largely support this assumption, the degree to which genera are conservative is sensitive to clade membership, nutrient flux and initial habitat preferences.

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#### STATEMENT OF AUTHORSHIP

All authors designed research and contributed to implementation in R; MJH performed analyses and wrote the manuscript, incorporating revisions from co-authors.

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