Origins, bottlenecks, and present-day diversity: Patterns of morphospace occupation in marine bivalves

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It has long been known that species should not be distributed randomly in morphospace (a multidimensional trait space), even under simple models of evolution. However, recent studies suggest that position in morphospace can affect aspects of evolution such as the durations of clades and the species richness of their constituent taxa. Here we investigate the dynamics of morphospace occupancy in living and fossil marine bivalves using shell size and aspect ratio, two functionally important traits. Multiple lines of evidence indicate that the center of a family's morphospace today represents a location where taxonomic diversity is maximized, apparently owing to lower extinction rates. Within individual bivalve families, species with narrow geographic ranges are distributed throughout the morphospace but widespread species, which are generally expected to be extinction resistant, tend to be concentrated near the center. The morphospace centers of most species-rich families today (defined as the median value for all species in the family) tend to be close to the positions of the family founders, further suggesting an association between position in morphospace and net diversification rates. However, trajectories of individual subclades (genera) are inconsistent with the center of morphospace being an evolutionary attractor.

KEY WORDS: Clade age, disparity, extinction, geographic range, species diversity.

Empirical studies frequently detect complex patterns of occupancy when species are arrayed in a morphospace (a multidimensional space constructed using morphological traits). For example, passerine bird species are more concentrated toward the center of the overall passerine morphospace than expected from a normal distribution, and species-poor clades tend to occupy the periphery of that space, suggesting that "average" or unexceptional morphological types might be associated with the accumulation of greater taxonomic diversity (Ricklefs 2005, 2012). Such patterns are not simply artifacts created by the position of the most diverse single group (subtaxon) within a focal clade, but involve clustering of multiple diverse subtaxa in morphospace. Across large taxonomic groups, some evidence suggests that morphospace occupancy is also nonrandom relative to taxon durations, as geologically long-lived lineages tend to occupy "average" morphologies more often than expected by chance (Liow 2007; but see contrary results

in McGowan 2007). Mechanisms behind these patterns remain poorly understood, but testing alternative hypotheses, particularly for clades with a long evolutionary history, requires assessments of the stability of a clade's position in morphospace, which can be difficult given the pitfalls of reconstructing ancestral character states (Losos 2011). Here we combine fossil data in conjunction with information about living species to investigate macroevolutionary dynamics underlying morphospace occupancy in a large clade of marine invertebrates.

Many macroevolutionary studies of morphology assume the center (e.g., the point representing the median of each dimension) of the morphospace to be stable through time, as might be expected from a simple (unbounded) diffusion process (e.g., reviewed in Finarelli and Flynn 2006). With simple diffusion, present-day morphospace occupancy should approximate a normal distribution, with the founder of the clade positioned at the

center (median). If the positions of clade members (e.g., genera within a family) tend to be stable through time, and priority effects in the central space tend to exclude younger lineages (Liow 2007) or if there is some sequence to character-state evolution, then members at the periphery of the morphospace should be of later origin than those at the center. In contrast, diversification in a bounded morphospace, or in the context of an active trend, will create more complex patterns of how taxon ages are distributed across the morphospace (Foote 1994, 1997; Roy and Foote 1997; McShea 2000; Wagner 2000, 2010). Furthermore, if the clade is old enough to have weathered a major extinction event, then selective extinction, or even a severe random culling, could shift the clade's morphospace center and the distribution of taxon ages within the morphospace (see Dommergues et al. 1996; Korn et al. 2013). How such historical processes have shaped the deployments of living taxa in morphospace remains poorly explored.

In this study, we examine morphospace occupancy of individual families of marine bivalves in relation to founder position, species diversity, geological age, and extinction risk. Bivalves have a rich and well-sampled fossil record and their present-day diversity is well characterized (Valentine 1989; Foote and Sepkoski 1999; Jablonski et al. 2006; Krug et al. 2009; Bieler et al. 2013; Jablonski et al. 2013), which allows us to compare the present-day distributions of taxa in morphospace to their ancestral conditions. We first define the center of a simple morphospace separately for each bivalve family based on the distribution of extant species in that space, and examine the composition of the suite of species in central versus peripheral zones of family morphospace to test the following hypotheses. Compared with the expectations from a uniform distribution (1) a higher proportion of species at the periphery are from species-poor genera; and (2) a higher proportion of peripheral species belong to young genera. To investigate the link between morphospace occupancy and extinction as a possible mechanism underlying hypotheses (1) and (2), we use geographic range size as an indicator of extinction risk (Jablonski 1987, 2008; Harnik et al. 2012b). Specifically, we test the hypothesis that (3) geographically widespread species are more concentrated near the center than expected by chance, leaving the geographically restricted species mostly at the periphery (species-level data still are too heterogeneous globally to directly quantify extinction rates). We then explore large-scale temporal dynamics by testing whether the morphospace occupied by each bivalve family has remained stable since its origin. Fossil data are not yet available to track the full evolutionary trajectory of individual bivalve families in morphospace (owing to slow progress in phylogenetic analysis and taxonomic revision), and so we place the oldest fossil member of each extant family in that family's present-day morphospace to test the null hypothesis that (4) in bivalve families, the distance between the founder and center of present-day morphology is independent of extant species diversity.

Methods
BIVALVE DATABASE
Maximum shell length (anterior–posterior distance) and height (dorsal–ventral distance) of 5289 extant bivalve species (recorded from depths ≤ 200 m) were compiled from the literature (for more information about data compilation, see Berke et al. 2013). The bivalve fauna of the deep sea is a distinct evolutionary and biogeographic unit compared to the continental shelf fauna (Valentine et al. 2006; Rex and Etter 2010) and is omitted from this study. We have not compiled morphological data for exclusively deep-sea taxa (about 1200 described species), but the proportion of species restricted to >200 m depth within a family (data from Huber 2010; augmented by Mikkelsen 2011; Janssen and Krylova 2014; Taylor et al. 2014 and other sources) does not correlate with the distance between founder species and the morphospace center of extant shelf-depth species (see below) in the family (raw distance: $\rho = -0.02$, $P = 0.91$; standardized distance: $\rho = -0.16$, $P = 0.235$), indicating that our results are not sensitive to our focus on shelf-depth taxa.

The geological ages of individual taxa were obtained from a stratigraphic dataset containing the first and last appearances for 2196 extinct bivalve genera and the oldest geological record of 86% of the extant genera ($N = 866$); most of the genera excluded from these data are exclusively deep sea or belong to a few families with small body sizes (≤ 1 cm) and poor preservation potential (Valentine et al. 2006). For more details of the database, data compilation and revision procedures, and the excluded taxa, see Jablonski et al. (2013) and Berke et al. (2013). Sampling and taxonomic revision of both extant and fossil bivalves are ongoing, however, so these data should be taken as a reflection of current knowledge in an active field.

BIVALVE MORPHOSPACE
We used the size and aspect ratio (hereafter shape) of shells to construct a two-dimensional morphospace as the focus of our investigation. Bivalve shell size and shape are associated with a wide range of physiological, functional, and ecological aspects of the bivalves, from resistance to predators to burrowing speed and depth (e.g., Stanley 1970, 1975; Kondo 1987; Leonard-Pingel and Jackson 2013). Shell size and shape were quantified as:

$$\text{Size} = \sqrt{\text{Length} \times \text{Height}};$$
$$\text{Shape} = \frac{\text{Length}}{\text{Height}}.$$

The size and shape data for all bivalve species were log-transformed (base 2) and then rescaled to have the same grand

mean (0) and variance (1) for both variables, thereby weighing them equally. Although shell length and height are highly correlated ($R^2 = 0.89$, $P < 0.001$ after log-transformation), little covariation in size and shape can be explained by a linear model ($R^2 = 0.004$, $P < 0.001$). Size and shape, respectively, are so highly correlated with the first and second principal components from the length and height data that we simply used the size and shape axes for our analyses (size to first principal component: $R^2 = 1$, $P < 0.001$; shape to second principal component: $R^2 = 1$, $P < 0.001$). Because different analyses might require different diversity thresholds, we specify the sample sizes and data exclusion criteria in the Results section or the captions for individual tables and figures.

PRESENT-DAY MORPHOSPACE OCCUPANCY

To investigate morphospace occupancy in relation to species diversity, lineage age, and extinction risk, we categorized species as central or peripheral according to their positions in the overall morphospace occupied by their specific families. Molecular data have largely supported families as monophyletic clades, and thus as meaningful analytical units (Taylor et al. 2007; Giribet 2008; Bieler et al. 2014). Here, we defined the center of a morphospace as the point representing the median of each morphological trait (i.e., size and shape). Because families span different ranges in size and shape, we standardized the differences between each species (S) and the median of its family (M) by the total range in the family (R), for both size and shape (preliminary analyses using variances for standardization yielded qualitatively same patterns). We calculated the overall morphodeviation (D_{morpho}, based on Euclidean distance) of a species as below:

$$D_{morpho} = \sqrt{\left(\frac{Size_S - Size_M}{Size_R}\right)^2 + \left(\frac{Shape_S - Shape_M}{Shape_R}\right)^2}.$$

Extant species with morphological data were divided into the central and peripheral groups, separated at the 50th percentile of D_{morpho}, with lower values treated as central. Because not all combinations of size and shape are biologically possible due to functional constraints, the morphospace is not fully occupied. The simple two-fold partition of the morphospace is insensitive to the details of potential morphospace occupation, including the sparse occupation of the corners in each panel of Figure 1 (discussed further below).

To compare the species assemblages in the central versus peripheral zones of the morphospace, species were also categorized by the total richness (hereafter diversity) of the genus they belong to, age of the genus (based on first appearance of a genus in fossil record; see Krug and Jablonski 2012; Jablonski et al. 2013), and the species' geographic range size (as in Jablonski et al. 2013). For each variable, we used the 50th percentile of all bivalve species

within each family as a cutoff value. Therefore, approximately 50% of the species in our dataset are in each of the following categories: species in species-rich genera (hereafter RG species) versus species-poor genera (hereafter PG species), species in geologically old genera (hereafter OG species) versus young genera (hereafter YG species), and widely distributed species (hereafter WD species) versus narrowly distributed species (hereafter ND species). Because some species have values precisely equal to the 50th percentiles, some of the categories do not have exactly 50% of all extant species; we minimized this effect by assigning species falling precisely on the cutoff values to the smaller assemblage. The numbers of central versus peripheral species in each category were compared using a Chi-square test to test the null hypothesis of random distribution of species among categories.

Our initial analyses of species distribution in family morphospace found complex patterns that are difficult to capture using standard statistical tests for categorical variables: overall, PG species and ND species occurred throughout the morphospace, but RG species and WD species tend to be concentrated near the center (see more in Discussion). To test the sensitivity of the results to definitions of center and periphery, we further varied the cutoffs of central versus peripheral species using 10–90th percentiles of D_{morpho} (illustrated in Fig. 1), and bootstrapped the whole dataset to generate confidence intervals (5–95th percentiles based on bootstrapped data) for comparisons of the proportions of species from different categories. We also compared the observed compositions to a null distribution generated by randomly sampling the same number of species as the central and peripheral species, 1000 times at each cutoff. We calculated the P value as the proportion of random samples producing either higher or lower values than our empirical data.

FOUNDER POSITIONS IN MORPHOSPACE

To investigate the deviation of the present-day centers from the initial morphology of bivalve families, we compiled length and height data from the literature and calculated sizes and shapes of the oldest known fossil species (hereafter founders) for extant bivalve families (Table S1). In the few cases where multiple species appeared in the first geological stage (usually ~5 Myr long) or substage (usually ~2 Myr long) of a family's evolutionary history, we used the median size and shape of those species to quantify the deviation of present-day mode from the founder. We scaled the size and shape data of family founders to the same distributions of the raw size and shape data of living species (see above). We then quantified the raw and standardized (using the same method for quantifying D_{morpho} of living species) Euclidean distances between the founder and present-day center (i.e., median; hereafter F-M distance) for each family, and tested its relation with species diversity and family age using Spearman's rank-order tests.
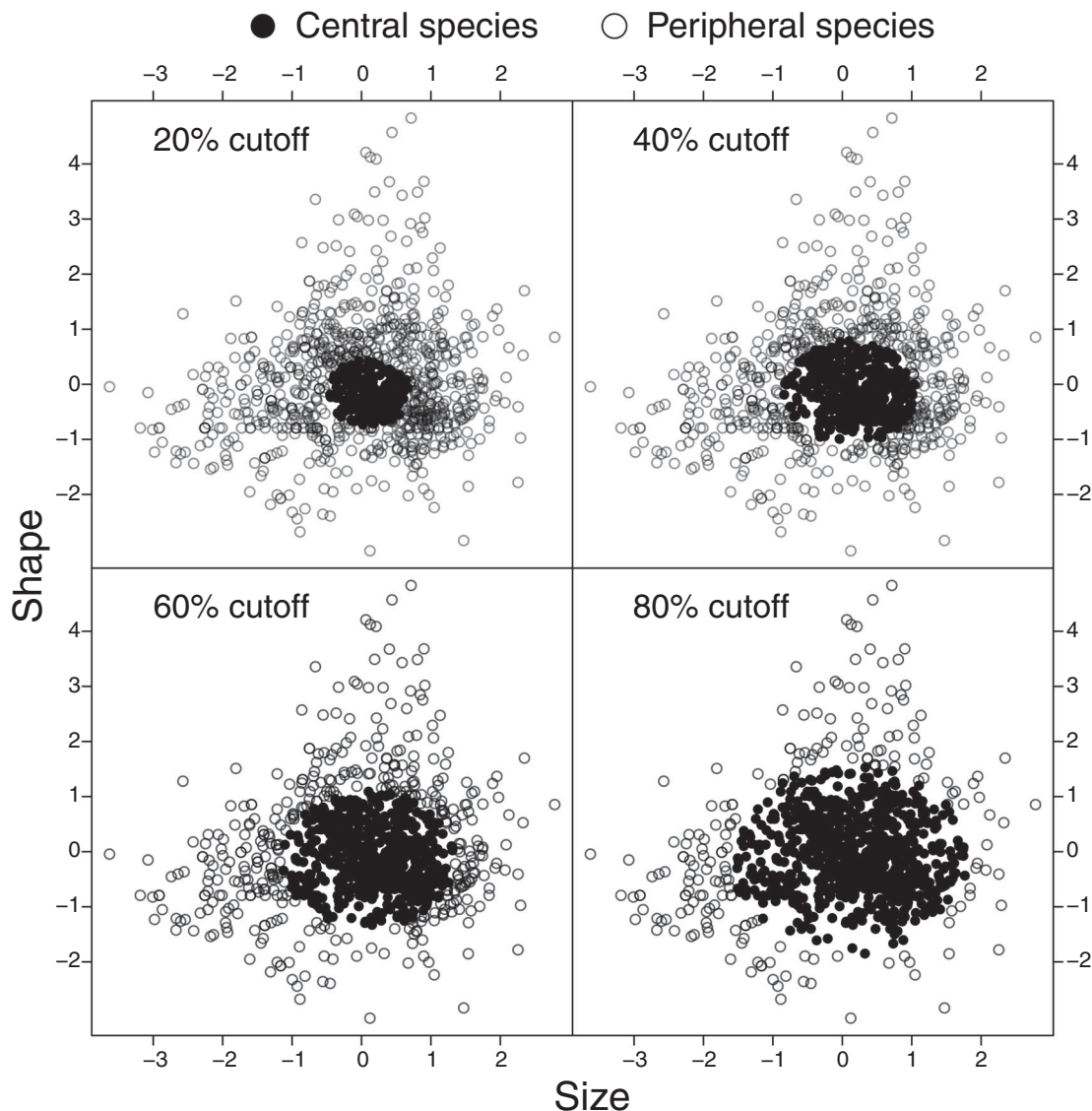
Figure 1. Conceptual diagram illustrating the use of different cutoffs for central (solid) versus peripheral (open) species. Size and shape data were randomly drawn from the data ($N = 1000$).

At the family level no phylogenetic structure is evident for extant diversity (Blomberg's $K = 0.567$, $P = 0.326$; see Blomberg and Garland 2002; Blomberg et al. 2003) or F-M distances ($K = 0.64$, $P = 0.387$), and a phylogenetic generalized least-square test of diversity and (raw or standardized) F-M distance did not find significant phylogenetic autocorrelation in the data ($\lambda = 0$ based on maximum likelihood; phylogeny of bivalve families from Roy et al. 2009). Therefore, we treated families as independent observations in the correlation tests.

All analyses were conducted in R 3.0.1 (R Development Core Team 2012), using the packages *ape* (Paradis et al. 2004), *caper* (Orme 2012), and *picante* (Kembel et al. 2010) for testing phylogenetic structure in the data, and *gplots* (Warnes et al. 2009) for plotting confidence intervals.

Results

PRESENT-DAY MORPHOSPACE OCCUPANCY

Our analyses of morphospace occupancy by extant bivalve species showed that the composition of central versus peripheral assemblages differs significantly ($P \leq 0.004$ for all three χ^2, Table 1), although not dramatically, from the chance expectation. In particular, the peripheral assemblage has slightly higher proportions of species from species-poor genera (47.5% PG species), species from young genera (43.4% YG species), and species that have narrow distribution (53.0% ND species) than the central assemblage (39.3%, 40.4%, and 46.9%, respectively).

These are rather subtle differences, so to test whether the periphery contains an unusual assemblage, we repeated the analysis using different cutoffs between central and peripheral species,

Table 1. Comparisons of numbers (and proportions in parentheses underneath the numbers) of species from species-rich genera (RG) versus species-poor genera (PG), species from old genera (OG) versus young genera (YG), and widely distributed (WD) versus narrowly distributed (ND) species, in the central versus peripheral zone of each family's morphospace.

	RG species	PG species	OG species	YG species	WD species	ND species	Total
Total	2509	2196	2789	2010	2530	2505	5061
	(56.6%)	(43.4%)	(58.1%)	(41.9%)	(50.5%)	(49.5%)	(4799[*])
Central	1536	995	1441	1059	1343	1188	2531
	(60.7%)	(39.3%)	(59.6%)	(40.4%)	(53.1%)	(46.9%)	(2417[*])
Periphery	1329	1201	1348	1167	1188	1342	2530
	(52.5%)	(47.5%)	(56.6%)	(43.4%)	(47.0%)	(53.0%)	(2382[*])
G test	$G = 34.3, P < 0.001$		$G = 8.3, P = 0.004$		$G = 19.0, P < 0.001$		

All partitions were based on 50th quantiles of all 5061 species (4813 species in the case of genus age by excluding genera lacking a fossil record). The distance between a species and its family's morphospace center is standardized by the range of its family's morphospace occupancy to allow global comparison. Only the 49 families each containing ≥10 species and three genera (a total of 5061 species) were included, to ensure statistically meaningful variations in D_{morpho} and other variables within a family.
*Number of species in center and periphery with data for genus age.

from 10th to 90th percentiles (see a conceptual illustration in Fig. 1). The differences between the central versus peripheral assemblages tend to increase, in terms of species richness (i.e., position of RG vs. PG species) and geographic range size (WD vs. ND species), as our definition of the peripheral zone becomes more extreme (i.e., with more central species and fewer peripheral ones; Fig. 2). Thus, when only the most extreme 10% were considered peripheral species, 51.7% of them were from species-poor genera ($P < 0.001$, i.e., the observed value exceeds that seen in all of the simulated proportions). Although this difference appears marginal, 56.0% peripheral species under the same criterion also had small geographic ranges ($P < 0.001$), indicating higher extinction risk. The proportions of PG species differ significantly in the central versus peripheral assemblages (no overlap of confidence intervals based on bootstrapped data) for all cutoff values, but significant differences occur only at 30% and higher cutoffs for ND species (all with significant difference from randomly simulated data), and only at 40% and 50% for YG species (with no difference from randomly simulated data). When we used more extreme cutoffs for dividing central and peripheral assemblages, the proportions of YG species in the two assemblages appear to be similar, indicating little tendency of genus origination on the periphery. We illustrate these results with the most diverse family, Veneridae, in Figure 3.

FOUNDER POSITIONS IN MORPHOSPACE

Of the 57 families with good fossil-preservation potential (see above), morphological measurements of founder species, and more than one extant species (Table S1), 68% showed significant shifts in both size and shape relative to their founders, and an additional 21% shifted significantly along one of the two morphospace axes. Overall, 21 families did not shift significantly in

median size, 24 today have larger median sizes relative to the founders, and 12 have smaller medians than the founder. Significant shape changes were pervasive, but equally distributed between greater elongation and increased relative height (23 vs. 25 families, respectively). Of the 10 families that originated during the Cenozoic Era (i.e., after the end-Cretaceous mass extinction 66 Myr ago), five changed significantly relative to the size/shape medians of the founders, and increases in median size were more frequent than decreases. Nevertheless, for most families (86%), the founder is closer to the extant median than at least one extant species (Fig. S1).

Across the 57 families (as above), the magnitude of the morphological deviation from the founder is positively correlated with the age of the family ($\rho = 0.33$, $P = 0.012$). Although there is no significant correlation between such deviations and species diversity, the two variables show a triangular relationship, with species-rich families tending to deviate less from the founders than species-poor families (Fig. 4). This tendency becomes significant when we use standardized F-M distance ($\rho = -0.55$, $P < 0.001$; ordinary linear model with log-transformed variables: $R^2 = 0.35$, $P < 0.001$).

Discussion

Our analyses show complex patterns in present-day morphospace occupancy in bivalve families, relative to the evolutionary and biogeographic properties in those clades. Consistent with Liow's (2007) and Ricklefs' (2012) findings, the peripheral area of the bivalve morphospace is less likely to accumulate and maintain taxonomic diversity, as multiple high-diversity subtaxa tend to lie near the center of the morphospace. Peripheral species in bivalve morphospace are not only less likely to belong to species-rich
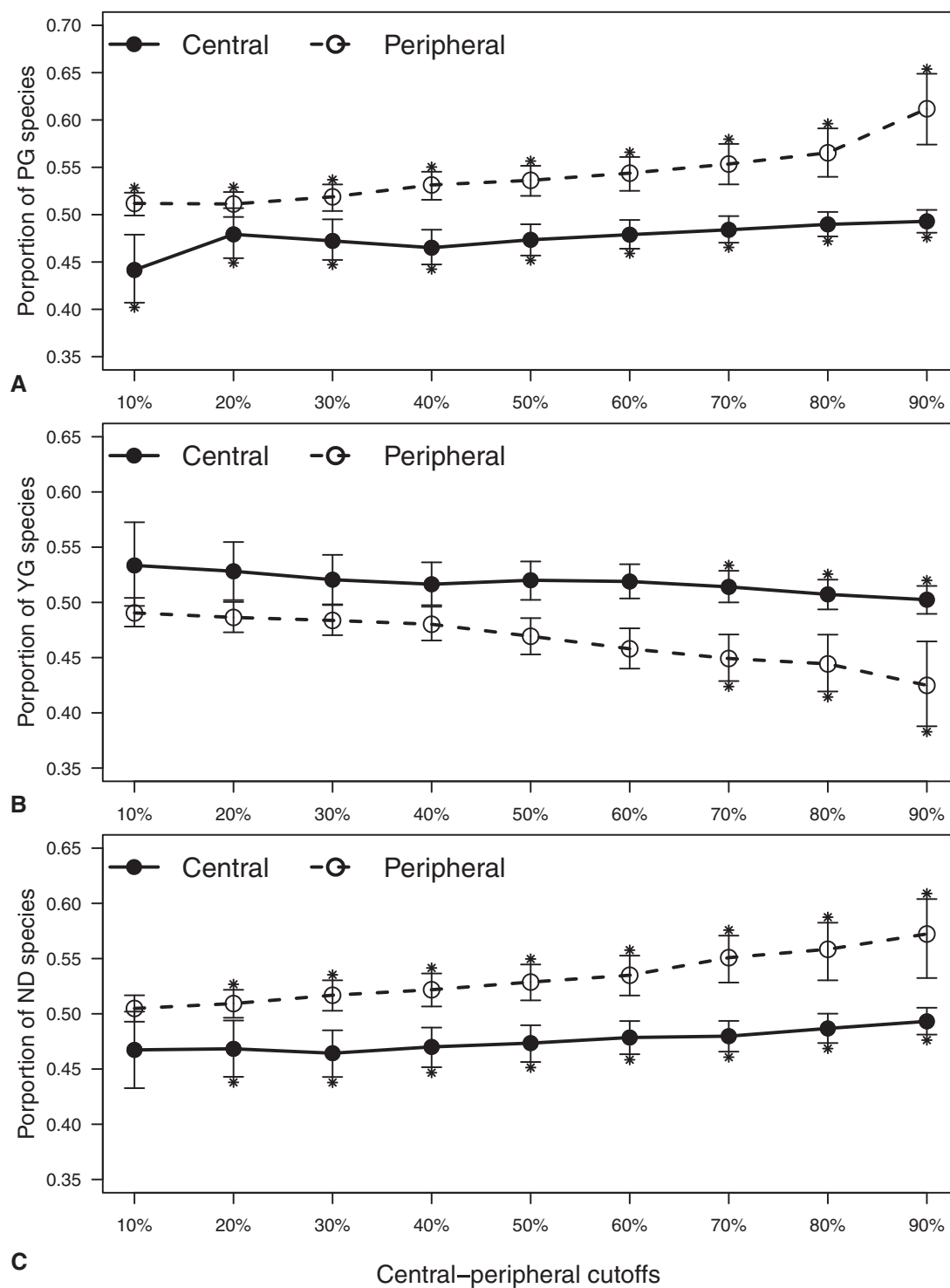
Figure 2. Proportions of central and peripheral species (A) from species-poor genera (PG species), (B) from young genera (YG species), and (C) with narrow distribution (ND species). PG species, YG species, and ND species were defined based on the 50th percentiles of all species of the same family. To test for sensitivity to the cutoffs, central versus peripheral species were iteratively defined using the 10–90th percentiles of all species' distances to their families' morphospace center (medians in size and shape). The error bars represent the 5th and 95th percentiles generated from bootstrapped data. Asterisk (∗) indicates the observed proportion is higher or lower than 95% of the random simulations (i.e., $P < 0.05$). We only included the 49 families that each contain at least 10 species and three genera (a total of 5061 species) to ensure statistically meaningful variations in D_{morpho} and other variables within a family.
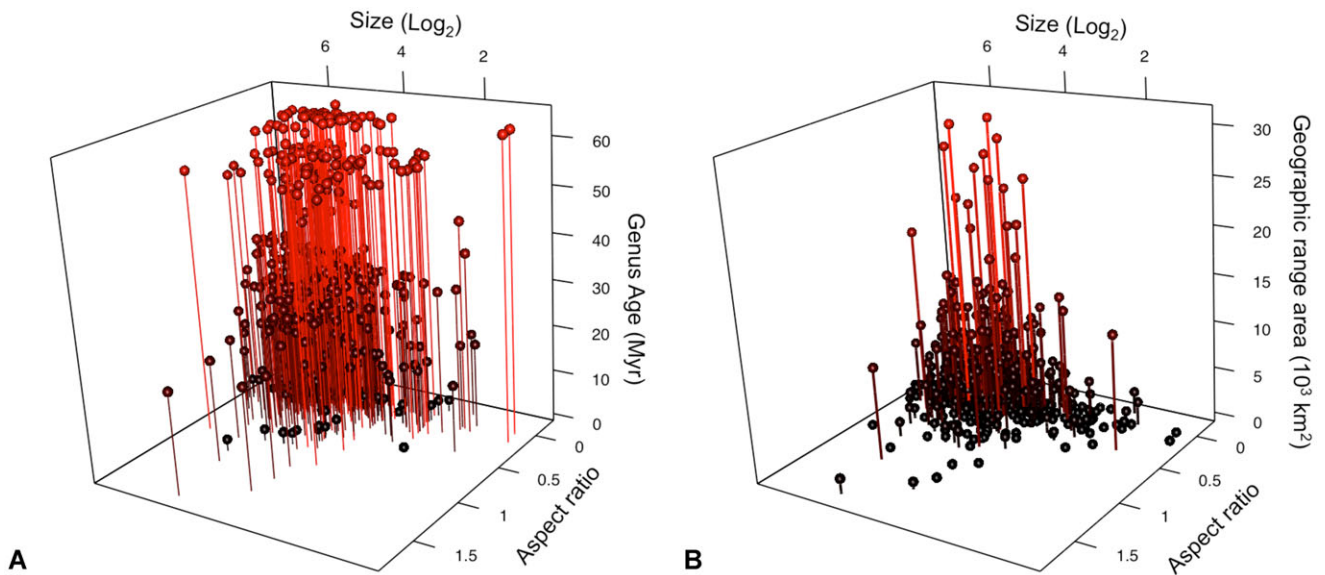
Figure 3. Distribution of species in the morphospace in the most diverse bivalve family, Veneridae, in relation to (A) the age of their genera, and (B) the species' geographic range sizes. Shell size ($\log_2$ transformed) and shape are both in their original scales. The color gradients of the symbols correspond to the values along the vertical axes.
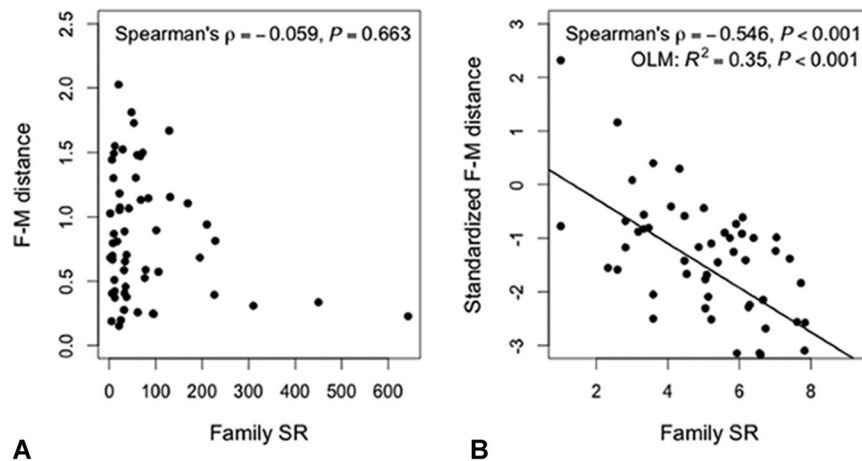
Figure 4. The relation of the number of extant species (SR) to (A) the raw distance and (B) the standardized Euclidean distance between the founder of the family and median (i.e., center of morphospace) of its extant species (F-M distance). Data were $\log_2$-transformed in (B) and the line represents the ordinary linear model fitted to the data.

genera, but tend to have smaller geographic ranges, indicating lower extinction-resistance (see Jablonski 2008; Harnik et al. 2012a). The evidence for a higher proportion of species from younger genera is much weaker, but also suggests a more complex mechanism than simple diffusion. Given that extant shelf-depth bivalves are reasonably well-sampled, and the rich fossil record of the group (Harper 1998; Foote and Sepkoski 1999; Kidwell 2005; Valentine et al. 2006), the patterns documented here are unlikely to be sampling artifacts.

Our results also show that ancestral positions in morphospace tend to be close to the center of present-day morphospace for most species-rich families. This, in combination with the observation that the central part of the morphospace also contains more species-rich genera, suggests that net diversification rates (spanning both background and mass extinctions) are higher there. The fact that in most families (particularly those that are species rich), the ancestral position is within the space occupied by the living descendants further indicates generally stable morphospace occupation over macroevolutionary time. These results are inconsistent with strong or pervasive directional selection on these timescales, or strong driven or active trends in the sense of McShea (1994) and Wagner (1996).

Patterns of bivalve morphospace occupation are similar to those in passerine birds (Ricklefs 2005, 2012), in that the

central zone of morphospace is occupied by a significantly higher proportion of species from species-rich genera than expected by chance. The findings that central species also tend to be significantly more widespread and are more likely to belong to relatively old genera both further suggest that the central zone in the morphospace represents a size/shape combination conducive to species and genus survivorship. This pattern could reflect a direct association between morphology and survivorship, but the median morphology might also be directly or indirectly associated with large geographic range, and thus indirectly linked to high extinction-resistance (Jablonski 1987, 2008; Harnik et al. 2012b). Previous findings from fossil data suggested that high species richness and broad species-level geographic range interact to promote longevity of marine genera (Jablonski 2005), but the mechanism underlying the apparent clustering of such genera in morphospace, giving rise to the family morphological mode, needs further investigation.

Another possibility is that younger lineages have been excluded from the favorable, central morphospace because it is already occupied by older, thriving lineages (discussed in Liow 2007). This incumbency or preemption hypothesis is consistent with the higher proportions of younger genera in the periphery, seemingly suggesting low rates of entry of new genera into that portion of the morphospace. However, this result is sensitive to the placement of the boundary between the morphospace center and periphery (Fig. 2), and our data are better taken to show that young taxa (and geographically restricted species) are rather evenly distributed through the morphospace, and the old taxa (and widespread species) tend to be concentrated in the center. The eight most diverse families all also show complex distribution patterns of species belonging to genera with Cenozoic origins, but no monotonic tendency toward the periphery for species belonging to younger genera (Fig. S2). The fact that young genera contribute to both central and peripheral species assemblage suggests that the central zone of the morphospace is not too full to accommodate the origin and diversification of new taxa, perhaps owing to stochastic extinction of incumbents (e.g., Walker and Valentine 1984; Ricklefs and Jønsson 2014).

The incumbency hypothesis also assumes relatively stable morphospace occupancy, but unlike passerine birds, most bivalve families are old enough to have experienced at least one mass extinction (i.e., the end-Cretaceous event). Because of such catastrophic events (see Foote 2010), the present-day morphological centers need not coincide with, or be close to, the morphology of the earliest member of a clade, and our analyses show that the deviation of a family's modern morphospace center from its founder varies among bivalve families, with the morphospace of 14% of the analyzed families now excluding their starting points (Fig. S1). More detailed analyses of the diversity dynamics in relation to morphological variation through time are needed to investigate the underlying evolutionary mechanisms (Foote 1996, 1997; Hopkins 2013).

The proximity of the present-day morphospace center to the starting point of most diverse families is qualitatively similar to the expectation from simple (unbounded) diffusion and so should not be overinterpreted, as it may not require any special adaptive explanation. Evaluating whether the extant species are more tightly clumped around the starting point than expected by a diffusion model requires a well-resolved phylogeny of living and fossil species that is currently not available. Information about fossil species would be particularly valuable in that context because it would otherwise be difficult to determine (1) whether present-day disparity represents the maximum for each clade, and (2) whether the expectation from random diffusion scales to the number of extant species or the total number of speciation events in the clade's history. Other results, however, cannot be attributed to stochastic processes, most strikingly the concentration of widespread species near the family near the center of the morphospace (see Figs. 2, 3).

Here, we have emphasized results for the most diverse families. The fossil record also shows that low-diversity families have had a variety of histories and so their present-day morphospace patterns should be interpreted cautiously. If a group has suffered at least one major extinction event, the link between ancestral and descendant morphologies can be disrupted (which would of course undermine ancestral state reconstruction from modern data). This is well illustrated by preliminary data from the Cretaceous (Maastrichtian) fossil record for six bivalve families known to have been more diverse in the Mesozoic than in the present day. In each if these families, the founders' position fell within the Maastrichtian morphospace of the clade, but not in the space occupied by the extant species (Fig. 5; data available upon request). Clades that are diverse today either suffered qualitatively different losses from the clades bottlenecked at the end of the Cretaceous, or more readily reoccupied their founders' morphospace during successful recoveries from the extinction. These alternatives need to be evaluated in the future.

Collectively, our results seem to suggest that morphospace centers represent morphologies that are at least conducive to species and/or genus persistence. However, the genus-level dynamics in the taxonomically most diverse family (Veneridae) present a more complex picture (Fig. 6). When evaluated in the two-dimensional morphospace, 65% of the genera ($N = 51$) have moved closer to the family center, but the change in distance to the family center is only weakly associated with the species diversity in the genus ($\rho = 0.23$, $P = 0.099$; data available upon request). In fact, the venerid genera show no clear displacement from their respective founders toward the family morphospace center (Fig. 6). Of the 15 genera that moved in the general direction of the family center (see Fig. S3 for analysis),
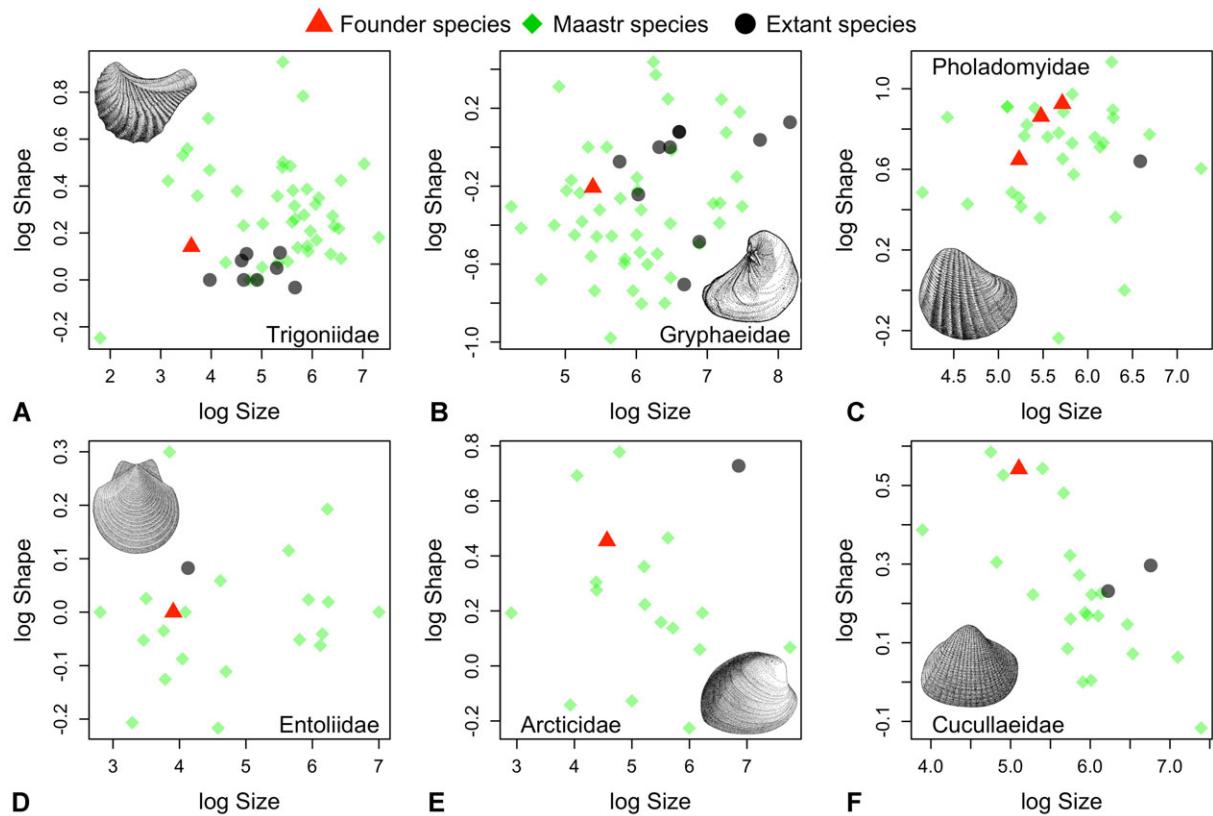
Figure 5. Shell size and shape distributions of the founder species (triangle), Maastrichtian species, that is, just before the end-Cretaceous extinction (diamonds), and modern species (dots) in six bivalve families that have low diversity today. All size and shape data are log$_2$ transformed (so that each unit represents a doubling in size). Line drawings of Cretaceous fossils from Natural History Museum (2013b).
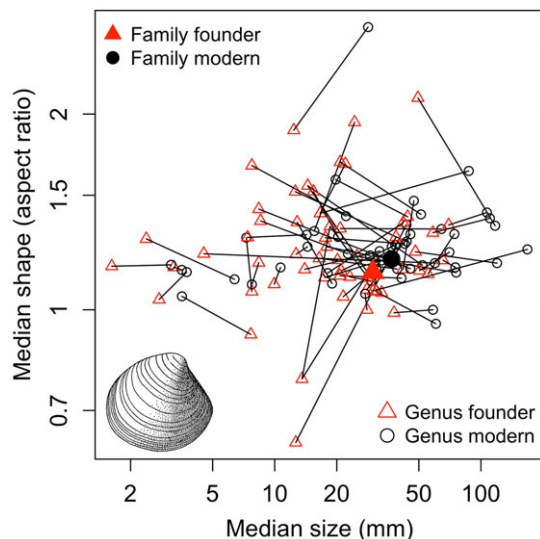
Figure 6. Sizes and shapes of founders (triangles) and the median sizes and shapes of present-day extant species (circles) in 51 genera in the most diverse bivalve family, Veneridae. The family founder and median of all extant venerid species combined are shown in the solid symbols. Line drawing from Natural History Museum (2013a).

seven of them "overshot," that is, the distance between genus founder and median value for the genus today is greater than the distance between genus founder and median for the family. Further, we found no correlation between the age of a genus and the distance between its founder and the present-day center for the family ($P = 0.348$), suggesting little priority effect close to the center of family morphospace. Many factors can cause shifts in morphospace occupancy (e.g., reviewed in Foote 1997; Roy and Foote 1997; McShea 2000; Wagner 2010), including directional selection shifting the center and extremes (often termed an active or driven trend; e.g., see McShea 1994; Wagner 1996; Alroy 1998, 2000); selective barriers producing expansions in range without the loss of initial phenotypes (often termed a passive trend; Stanley 1973; McShea 1994, 2000); soft boundaries that damp but do not fully disallow evolution in particular directions (e.g., Gherardi et al. 2013); local attractors within the morphospace; or biotic or physical environmental factors that might promote differential diversification among clades (e.g., Poulin 1995a,b; Gardezi and Silva 1999; Alroy 2008).

Overall, the failure of the genera to shift preferentially toward the morphospace center of their family or the founder of the family argues against the diversity maximum as an adaptive peak

or evolutionary attractor at the species level (see also Roy et al. 2000), and is further evidence that the frequency distribution of phenotypes in a morphospace does not necessarily map onto an adaptive landscape (as also noted by McGhee 2006, p. 70). The apparent preference for the central morphology (morphospace close to the center and founder for Veneridae) does not appear to be the outcome of the dynamics (or trajectory) of morphospace occupancy within individual genera, but seems to be a product of differential survivorship among genera (e.g., clade-level effects of geographic range or species richness).

Evaluating the different scenarios of temporal morphospace occupancy dynamics would require additional morphological data for the clade over its evolutionary history. Both median size (Blomberg's $K = 0.78$, $P = 0.002$) and median shape (Blomberg's $K = 0.86$, $P = 0.001$) of bivalve families show significant phylogenetic structure among families, but the deviations of extant morphospace centers from founders' positions do not (Blomberg's $K = 0.64$, $P = 0.39$). These findings suggest that extinction is either nonselective at the family level, or showed selectivity that is independent of phylogeny, pushing survivors relatively far from the founder positions in some families irrespective of evolutionary relationships. Extinction *intensity* can be phylogenetically conserved (Purvis 2008; Roy et al. 2009), but at our current level of phylogenetic resolution in bivalves, we have no evidence that its effect in morphospace is patterned phylogenetically (but see fossil evidence for selective extinction with respect to body size in Smith and Roy 2006). We acknowledge that our results of a simple two-dimensional morphospace might not represent those for other traits, especially ones that are not strongly correlated with shell size and shape. Clearly, analyses using additional traits are needed to establish the generality of these results. Also, although previous analyses of morphospace occupation have tended to focus on patterns of morphological variance (see Roy and Foote 1997; Huang et al. 2012; Ricklefs 2012), the analyses here compared positions of species relative to the centers of individual family morphospaces. Simple analyses relating clade age to present-day diversity and disparity will not be very informative because diversification within bivalve families (most likely, any other long-lived clade) has clearly not been time-homogeneous (e.g., Krug and Jablonski 2012; see also Pie and Weitz 2005). As more information about morphological traits of extinct relatives of living bivalves becomes available, analyses of temporal trends in morphological variances for this group should become increasingly feasible.

In summary, we used marine bivalves as a model system to examine patterns of morphospace occupation in relation to lineage diversity and persistence. Several lines of evidence indicate that the central zone of a family's morphospace reflects a region of long-term diversity accumulation, rather than a simple adaptive peak generated by evolutionary trends among species,

with species-poor taxa (genera in our case) more evenly spread throughout a family's morphospace, and thus overrepresented near the periphery. Clades that maintain position in morphospace over time appear most likely to accumulate high standing diversity, but the causal mechanism is uncertain, and may not support simple optimality arguments. Most extant bivalve families have experienced catastrophic disturbances in their evolutionary history, and the fossil record of these bottlenecks and their aftermath provides an excellent opportunity for further investigation of the mechanisms underlying the apparent link between morphospace occupation and diversity accumulation.

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Associate Editor: P. D. Polly
Handling Editor: J. Conner

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1. Frequency distribution of the percentage of extant species whose positions in their family morphospace are closer to the family center than the oldest fossil species of the family (founder).

Figure S2. For the eight most diverse bivalve families, the distance of species to the family morphospace center is not related to the age of their genera.

Figure S3. Frequency distribution of the direction of genus movement in morphospace in relation to the family morphospace center, that is, median for both size and shape (angle α, in inset diagram), showing a wide variety of trajectories.

Table S1. The size and shape of extant (medians) and founder species in 57 bivalve families.

ERRATUM

This article corrects:

Origins, bottlenecks, and present-day diversity: Patterns of morphospace occupation in marine bivalves

Vol 69, Issue 3, 735–746, Article first published online: 25 FEB 2015

An incorrect version of Figure 2 was included in the final draft of our manuscript "Origins, bottlenecks, and present-day diversity: Patterns of morphospace occupation in marine bivalves" (Huang et al.), which was published in the March 2015 issue of Evolution Vol 69, No. 3, pp. 735–746.

Panel B in the correct Figure 2 now shows the patterns correctly described in the *Results* section, specifically, that significant differences occur only at 40% and 50% for YG species (with no difference from randomly simulated data, as indicated by the lack of asterisk) and that when more extreme cutoffs are used to separate central and peripheral assemblages, the proportions of YG species in the two assemblages become similar, indicating little tendency for genus origination on the periphery. The authors apologize for the error and any misunderstanding this may have caused. We thank T. Betzner for bringing it to our attention.
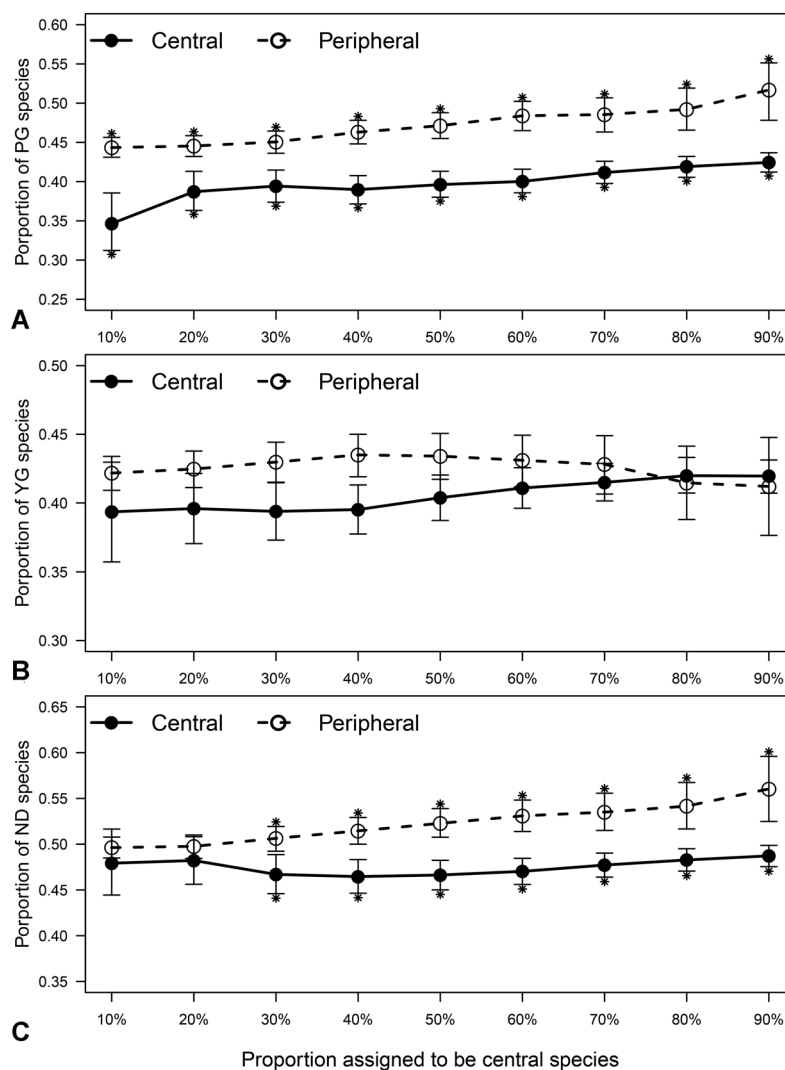
Figure 2. Proportions of central and peripheral species (A) from species-poor genera (PG species), (B) from young genera (YG species), and (C) with narrow distribution (ND species). PG species, YG species, and ND species were defined based on the 50 percentiles of all species of the same family. To test for sensitivity to the cutoffs, central versus peripheral species were iteratively defined using the 10–90 percentiles of all species' distances to their families' morphospace center (medians in size and shape). The error bars represent the 5 and 95 percentiles generated from bootstrapped data. Asterisk (*) indicates the observed proportion is higher or lower than 95% of the random simulations (i.e., $P < 0.05$). We only included the 49 families that each contain at least 10 species and three genera (a total of 5061 species) to ensure statistically meaningful variations in D_{morpho} and other variables within a family.