

Genus age, provincial area and the taxonomic structure of marine faunas

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Species are unevenly distributed among genera within clades and regions, with most genera species-poor and few species-rich. At regional scales, this structure to taxonomic diversity is generated via speciation, extinction and geographical range dynamics. Here, we use a global database of extant marine bivalves to characterize the taxonomic structure of climate zones and provinces. Our analyses reveal a general, Zipf–Mandelbrot form to the distribution of species among genera, with faunas from similar climate zones exhibiting similar taxonomic structure. Provinces that contain older taxa and/or encompass larger areas are expected to be more species-rich. Although both median genus age and provincial area correlate with measures of taxonomic structure, these relationships are interdependent, nonlinear and driven primarily by contrasts between tropical and extra-tropical faunas. Provincial area and taxonomic structure are largely decoupled within climate zones. Counter to the expectation that genus age and species richness should positively covary, diverse and highly structured provincial faunas are dominated by young genera. The marked differences between tropical and temperate faunas suggest strong spatial variation in evolutionary rates and invasion frequencies. Such variation contradicts biogeographic models that scale taxonomic diversity to geographical area.

Keywords: taxonomic structure; Zipf–Mandelbrot; bivalves; biogeography

1. INTRODUCTION

Spatial variation in species richness is ubiquitous in modern and ancient systems and tends to be phylogenetically structured. Recent work has mainly focused on the influence of competition on phylogenetic structure at the community scale (Webb *et al.* 2002; Kraft *et al.* 2007; Emerson & Gillespie 2008). However, communities are embedded in regional faunas regulated by longer term ecological and evolutionary factors and their dynamics are not governed solely by interactions between locally co-occurring taxa (Ricklefs 2004, 2008). Understanding how biodiversity is phylogenetically structured over broad spatial scales provides essential context for interpreting finer scale variation and is a necessary precursor for investigating the biotic and abiotic processes that generate large-scale spatial diversity gradients. Yet, remarkably little is known about phylogenetic structure at the regional to global scale (though see Roy *et al.* 1996; Cardillo *et al.* 2008; Krug *et al.* 2008).

Here we investigate the phylogenetic structure of biodiversity globally, within climate zones and within faunal provinces, using a database of extant marine bivalve species. Phylogenetic structure can be measured in a variety of ways (Cooper *et al.* 2008; Emerson &

Gillespie 2008; Cavender-Bares *et al.* 2009). The taxonomic hierarchy is typically used as a proxy in the absence of a formal phylogenetic framework, under the assumption that taxonomic classification accurately reflects phylogenetic relationships. For mammalian and molluscan genera, this assumption has statistical support (Jablonski & Finarelli 2009). We analyse the distribution of species among genera (hereafter referred to as taxonomic structure), and find a general, Zipf–Mandelbrot form to the taxonomic structure of diversity, with provincial faunas from similar climates exhibiting similar taxonomic structure.

It has long been recognized that the shape of the frequency distribution of species among genera is right-skewed, with most genera containing few species (Willis & Yule 1922). This hollow-curve distribution may result in part from the differential evolutionary success of a few clades (Dial & Marzluff (1989) and references therein). However, older genera are expected to contain more species than younger genera, so the hollow curve could simply result from differences in time since origination (Yule 1924; Raup *et al.* 1973; Stanley 1979; Nee 2006). Variation in rates of origination, extinction and range expansion either among clades or over time—for causes ranging from differential survival or recovery from mass extinction to diversity dependence within clades—can reduce or even eliminate the positive relationships expected between genus age and species richness (Ricklefs 2006; Pie & Tschá 2009; Rabosky 2009). We evaluate the contribution of clade age to the taxonomic structure of marine faunas by examining the relationship

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between genus age and species richness at the global scale, and genus age and taxonomic structure at the provincial scale.

The size of a region may also influence the taxonomic structure of its constituent fauna. Larger regions are expected to contain more species (the area–diversity effect), and potentially more congeneric species. Variation in provincial area could generate spatial gradients in taxonomic structure as has been argued for gradients in taxonomic richness (Rosenzweig 1995, 2003). We investigate the contributions of area and climate to provincial taxonomic structure by considering the relationships between provincial taxonomic structure, species richness, area and latitude.

We find marked differences in taxonomic structure in the global ocean, in particular between tropical and extra-tropical faunas. This variation in taxonomic structure is not explained simply by differences in geographical area or by clade age, but instead seems to reflect marked differences in how diversity is generated and accommodated in tropical versus extra-tropical waters.

2. MATERIAL AND METHODS

Our database contains the occurrences of extant marine bivalves at shelf to intertidal depths (described in Krug *et al.* 2009a; Roy *et al.* 2009b) (electronic supplementary material, figure S1). Marine bivalves are well suited for these analyses as they have been the subject of extensive taxonomic work and have an exceptional fossil record (Kidwell 2005; Valentine *et al.* 2006; Krug *et al.* 2009b), which allows us to incorporate geological data on the ages of first occurrence of most genera. The data analysed here include a sampling of 5178 species distributed among 898 genera and subgenera, spanning all of the major clades of marine bivalves except for the Lucinoidea and Galeommatoida.

Taxonomic structure was analysed at two spatial scales: climate zones and provinces. *Climate zones* included polar and temperate faunas in both the Northern and Southern Hemispheres and a single tropical fauna. *Faunal provinces* were defined using the geographical subdivisions of Valentine (1973), with refinements based on Spalding *et al.* (2007); provinces were defined by these authors on the basis of faunal similarity rather than taxonomic richness. To assess the effects of latitude and of geographical area on taxonomic structure, we estimated the latitudinal mid-point of each province and the length of coastline circumscribing it; this measure of geographical extent underestimates provincial area, but as shelf width is generally trivial relative to shelf length, these data are useful as a measure of relative differences in provincial areas.

Taxon age was taken as the age of first occurrence of each bivalve genus in the fossil record, using an updated compendium of the first and last occurrences of marine bivalve genera over the Phanerozoic (Sepkoski 2002; Jablonski *et al.* 2003; Krug *et al.* 2009a,b). To examine the relationship globally between genus age and species richness, we used linear regression and restricted our dataset to genera with first occurrences in the Cenozoic (less than 65 Ma). The Cretaceous–Paleogene mass extinction (65 Ma) dramatically violates assumptions of time-homogeneous birth and death rates (Krug *et al.* 2009a), and by restricting our analysis to

the Cenozoic, we should be more likely to detect an effect of clade age on species richness if it exists. Cenozoic genera comprise 89 per cent of the total dataset and the results presented below are qualitatively similar when pre-Cenozoic genera are also included. Although some authors have attempted to derive origination and extinction rates directly from data such as ours (e.g. Bokma 2003; Rabosky 2009), uncertainties are often prohibitively large (Rabosky in press), particularly when rates vary among lineages as is known to occur in bivalves (Roy *et al.* 2009a). For interprovincial analyses, we calculated the median age of constituent genera in each province. Note that this age is for the first occurrence of a genus anywhere on the globe, and does not pinpoint the arrival or origin of that genus in a given province; as noted below, the temporal gap between origination and arrival tends to increase with latitude for bivalves. Data on the entry of genera into specific provinces are currently unavailable for much of the globe and so the age of a genus in a given province should be viewed conservatively as an upper bound.

Most previous approaches have quantified taxonomic structure in terms of numbers of species per genus or per family (S/G and S/F ratios) (e.g. Enquist *et al.* 2002; Krug *et al.* 2008). Here we develop an alternative approach, fitting parametric models to the shapes of taxonomic diversity distributions (figure 1a). We use relative abundance models, typically used to describe the distribution of individuals among species (Magurran 2005; McGill *et al.* 2007), to describe the distribution of species among genera (hereafter referred to as relative diversity distribution, or RDD, models). The five models we consider are the broken stick, geometric, lognormal, Zipf and Zipf–Mandelbrot. These models are drawn from the major families of abundance models (Marquet *et al.* 2003; McGill *et al.* 2007), have shapes similar to other models not considered and thus cover the range of possible distributions, and several have already been used to describe the structure of taxonomic diversity (Dial & Marzluff 1989; Burlando 1990, 1993).

RDD models were fit to taxonomic structure data using generalized linear models (GLMs) and the method of maximum likelihood, assuming a Poisson error distribution. The best fit model was selected using Akaike's information criterion (AIC; Akaike 1974; Burnham & Anderson 2002). Akaike weights were calculated to summarize the relative support for each model in the candidate set and for use in model averaging (Burnham & Anderson 2002); averaging parameter estimates across nested models can improve model inference when the support for any single model is equivocal.

Taxonomic structure scales with taxonomic richness and thus the observed relationships should be compared with null models (Simberloff 1970; Gotelli & Colwell 2001; Cardillo *et al.* 2008). However, specification of an appropriate null model is not always straightforward (Kembel & Hubbell 2006; Hardy 2008; Cavender-Bares *et al.* 2009). For each climate zone, we generated a null distribution by randomly sampling species without replacement from the global species pool. This approach allows us to compare regional taxonomic structure with that expected on the basis of species richness alone, while still retaining the global taxonomic structure of marine bivalves. For each random sample, RDD models were fit to the distribution of species among genera and the parameter estimates for the best model recorded. This procedure was repeated 1000

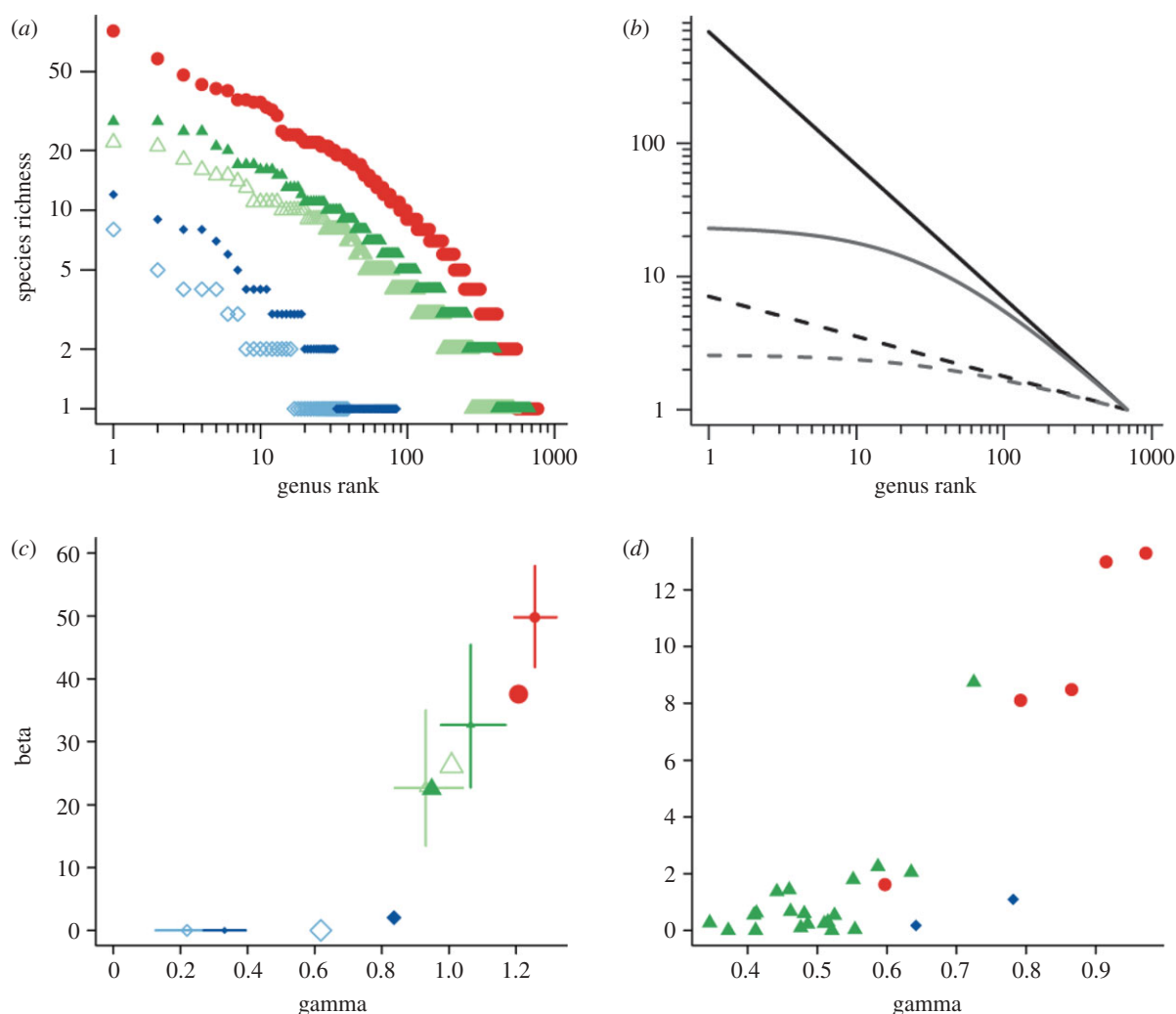


Figure 1. (a) Relative diversity distributions (RDD) of marine bivalves in the tropical, temperate and polar climate zones. (b) Schematic of the Zipf–Mandelbrot (Z–M) distribution; Z–M model parameters describe the evenness of species richness among genera in the overall fauna (gamma) and among the most species-rich lineages (beta). (c) Taxonomic structure of climate zones—as described using the values of the gamma and beta parameters of the Z–M distribution—varies from the tropics to the poles, with both tropical and polar taxonomic structure deviating significantly from that expected on the basis of species richness alone. Observed data are denoted with large symbols and null model distributions with small symbols and 95% bootstrap confidence intervals. (d) Taxonomic structure of provincial faunas. Provincial faunas in the temperate zone exhibit relatively little taxonomic structure and are dominated by monotypic genera. Red circles indicate tropical data, green triangles temperate data and blue diamonds polar data; this scheme is used in all figures. Filled symbols in (a) and (c) are Northern Hemisphere data and open symbols are Southern Hemisphere data. Solid black line, high gamma, beta = 0; solid grey line, high gamma, beta > 0; dashed black line, low gamma, beta = 0; dashed grey line, low gamma, beta > 0.

times and the mean model parameters and 95% confidence intervals compared with the observed data.

At finer provincial scales, in which larval dispersal is more likely to homogenize biotas, the appropriate species pool to be used in generating a null distribution is unclear. Given that our results at the scale of climate zones (presented below) agree with other finer scale analyses of taxonomic structure (Roy *et al.* 1996; Krug *et al.* 2008), we interpret our provincial-scale results at face value while emphasizing the need for future development of appropriate null models in regional marine faunas.

3. RESULTS

The structure of taxonomic diversity in marine faunas globally conforms to a consistent family of distributions. The Zipf and Zipf–Mandelbrot distributions were selected as the best RDD models for four of the five

climate zones (electronic supplementary material, table S1) and 26 of the 27 provinces (electronic supplementary material, table S2). The similarity in the form of RDDs across the major biogeographic subdivisions of the global ocean is not owing simply to compositional similarity between faunas. For example, the Surian and Nova Scotian provinces have similar parameter values (electronic supplementary material, table S2) but share only 37 genera (=21% of the generic diversity of the Surian province). The tropical climate zone and the tropical Western Pacific province were general exceptions, both best fit with a lognormal distribution. In these two related instances (i.e. the Western Pacific contains 72% of tropical genera), the Zipf–Mandelbrot RDD was ranked second, and for the Western Pacific, the difference in support between these two models was equivocal ($AIC_{\text{lognormal}} = 1572$; $AIC_{\text{Zipf-Mandelbrot}} = 1575$). In order to compare the taxonomic structure of climate zones

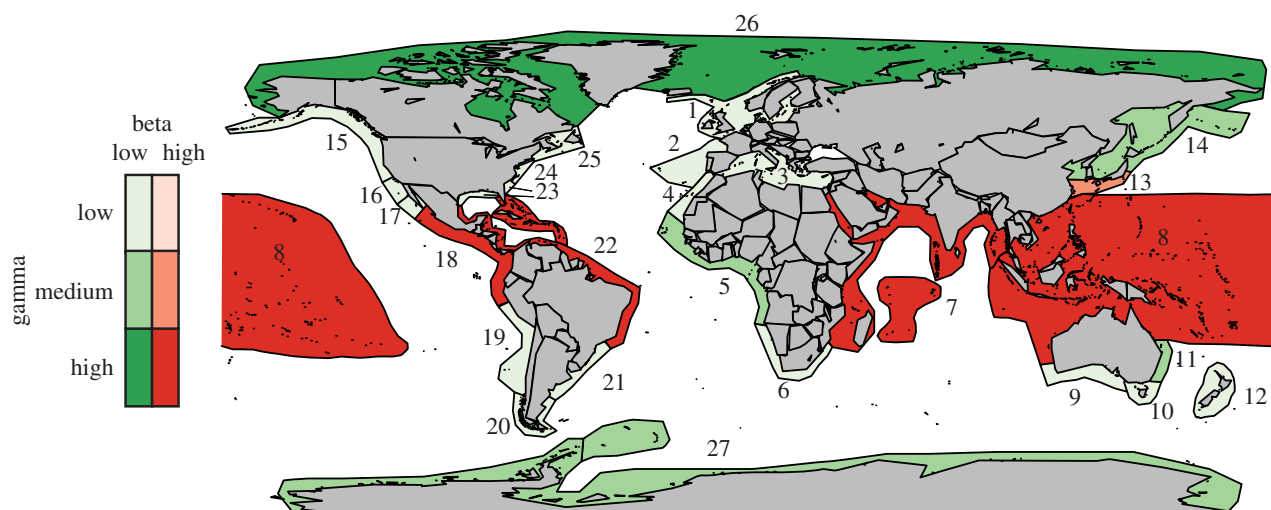


Figure 2. Geographical distribution of taxonomic structure in marine provinces. Colour and shading summarize two measures of diversity structure, beta and gamma; scale generated by dividing the range of beta values in half and gamma values in thirds. The combination of low beta and high gamma is mathematically and biologically unlikely; low gamma indicates little difference in species richness among genera, a situation in which parsimony would favour a single-parameter (gamma) model over a two-parameter (gamma and beta) model. Provinces are: (1) North European; (2) Lusitanian; (3) Mediterranean; (4) Mauritanian; (5) Guinean; (6) South African; (7) Indian Ocean; (8) Western Pacific; (9) South Australian; (10) Maugean; (11) Peronian; (12) Zealandian; (13) Warm Japonic; (14) Cool Japonic; (15) Oregonian; (16) Californian; (17) Surian; (18) Panamanian; (19) Peruvian; (20) Magellanic; (21) Patagonian; (22) Caribbean; (23) Carolinian; (24) Virginian; (25) Nova Scotian; (26) Arctic; (27) Antarctic.

and provinces globally, we use the model-averaged parameter estimates for the Zipf and Zipf–Mandelbrot distributions in all subsequent analyses.

The consistency in the parametric form of RDDs at the scale of climate zones and provinces allows geographical variation in taxonomic structure to be investigated using two parameters of the Zipf–Mandelbrot model: gamma and beta (figure 1*b*); a pure Zipf distribution uses only the parameter gamma and is thus equivalent to a Zipf–Mandelbrot distribution in which beta equals zero. These two parameters describe the evenness of species richness among genera in the fauna overall (gamma) and among the most diverse genera (beta). Greater values of gamma indicate increasingly uneven RDDs in which genera vary in a more step-wise manner in their species richness, whereas greater values of beta indicate increasingly even distributions of species among the most diverse genera (figure 1*b* and electronic supplementary material, figure S2).

This model-fitting approach to quantifying taxonomic structure reveals features of diversity overlooked using existing methods. When examined separately, both gamma and beta significantly covary with provincial S/G ratios (Spearman rank-order correlation ρ -values of 0.97 and 0.68, respectively, $p < 0.001$ for both). However, when the unique contributions of gamma and beta to S/G ratio values are assessed using a multivariate GLM, gamma is the only significant predictor of S/G ($p < 0.001$). Beta is uncorrelated with S/G ($p > 0.05$) and describes a novel feature of taxonomic structure: the equitability of diversity among the most species-rich genera.

The taxonomic structure of climate zones shifts from the tropics to the poles (figure 1*c*). The tropical fauna exhibits greater values of gamma owing to the marked disparity in species richness among genera in the overall fauna, and greater values of beta owing to the pronounced

equitability of richness among species-rich genera (figure 1*a,c*). Our null model results indicate that the observed structure of diversity cannot be explained solely by variation in species richness: tropical and polar faunas deviate significantly from the null expectation, whereas the structure of temperate faunas approximates that expected from a random sampling of the global species pool (figure 1*c*). These results are consistent with other studies that have found that S/G ratios in tropical and polar faunas but not temperate faunas differ significantly from that expected on the basis of species richness alone (Roy *et al.* 1996; Krug *et al.* 2008).

Analyses at the provincial scale reveal a more complex biogeographic pattern (figures 1*d* and 2). Temperate provinces deviate from the latitudinal trend observed at the zonal scale by exhibiting very even RDDs overall (gamma values closer to zero), with faunas dominated by monotypic genera. The intermediate taxonomic structure of faunas in the Northern and Southern Hemisphere temperate zones (figure 1*c*) thus results from the amalgamation of many weakly structured temperate provincial faunas (figure 1*d*). Polar provinces are more taxonomically uneven overall when compared with temperate provinces (i.e. have higher gamma values), but differ from tropical faunas in their lack of species-rich clades of comparable diversity (i.e. have lower beta values).

To address the potential factors underlying geographical variation in provincial taxonomic structure, we first assess the relationships between latitude, area and species richness. A latitudinal diversity gradient in species richness is observed among provincial faunas ($\rho = -0.48$, $p < 0.05$), but only a weak relationship exists between species richness and provincial area ($\rho = 0.28$; $p = 0.15$ across all provinces; $\rho = 0.19$ and $p = 0.33$ when the large West Pacific province is omitted) (figure 3); this result is contrary to findings for terrestrial systems (e.g. Rosenzweig 1995; Ricklefs *et al.* 2007) but consistent

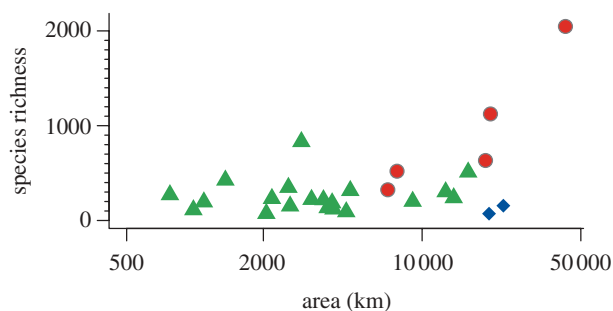


Figure 3. Relationship between species richness and the geographical area encompassed by shallow marine provinces. Provincial area and species richness are decoupled. Symbols as in figure 1.

with other analyses in the marine realm (e.g. Roy *et al.* 1998). Within climate zones, we find a positive area–diversity relationship among tropical provincial faunas ($\rho = 1$, $p < 0.05$), but not among temperate provincial faunas ($\rho = 0.15$, $p = 0.53$). Indeed, in the temperate zone, provincial area can increase by roughly an order of magnitude with no effect on species richness.

With respect to taxonomic structure, gamma increases significantly with provincial area ($\rho = 0.65$, $p < 0.001$), meaning larger provinces contain faunas with more uneven overall RDDs (electronic supplementary material, figure S3a). However, this relationship largely results from the large areas of tropical and polar provinces. The temperate provinces alone exhibit a substantially weaker correlation that is no longer significant ($\rho = 0.30$, $p = 0.19$). A model-selection approach yielded similar results, with a single linear regression describing the effect of area on gamma across temperate and tropical provinces preferred (AIC = 31.04) over a more complex model in which the effects of area on gamma varied between climate zones (AIC = 45.12). There is no relationship between beta and area (electronic supplementary material, figure S3b), regardless of whether the analysis is conducted across all provinces ($\rho = 0.29$, $p = 0.14$) or is constrained to only temperate provinces ($\rho = -0.02$, $p = 0.91$). Polar provinces cannot be analysed separately as there are only two of them.

At the global scale, genus age positively covaries with species richness ($p < 0.05$) but explains little of the variation ($r^2 = 0.09$). At the provincial scale, taxonomic structure covaries with the median age of constituent genera (gamma versus median genus age: $\rho = -0.62$, $p < 0.001$; beta versus median genus age: $\rho = -0.59$, $p < 0.01$; electronic supplementary material, figure S4). However, contrary to expectation, provinces that are more taxonomically structured tend to be dominated by younger rather than older faunas. The relationships between age and taxonomic structure remain when analyses are restricted to temperate provinces, though the relationship between beta and genus age weakens (gamma versus median genus age: $\rho = -0.69$, $p < 0.001$; beta versus median genus age: $\rho = -0.47$, $p < 0.05$). A multivariate GLM of the effects of absolute latitude and median age on gamma and beta, respectively, indicate that both predictors are important contributors to provincial taxonomic structure: median age is a significant predictor of both gamma ($p < 0.01$) and beta ($p < 0.05$), whereas latitude is a significant predictor only of beta ($p < 0.05$).

Many of the factors that potentially contribute to geographical variation in taxonomic structure covary (e.g. latitude and provincial area). However, the multivariate relationships between these factors are frequently nonlinear and can be non-monotonic (electronic supplementary material, figure S5), which precludes the application of standard statistical approaches for partitioning the variance among multiple factors.

4. DISCUSSION

At least 75 per cent of the bivalve genera that originated over the past 11 Myr are recorded first in the tropics (Jablonski *et al.* 2006; Krug *et al.* 2009b), and median genus age increases progressively with latitude, suggesting similar dynamics throughout the Cenozoic. Taken together, these data indicate that most bivalve lineages now found in extra-tropical provinces have expanded poleward from tropical origins, even in the face of high-latitude cooling (Jablonski *et al.* 2006). Each temperate province that directly flanks a tropical province, represents a separate example of a fauna of bivalve lineages whose chief phylogenetic source is a tropical neighbour, though certainly both temperate originations and recruitment among temperate provinces have occurred (e.g. Vermeij 1991; Beu *et al.* 1997; Beu 2004; Vermeij 2005). High-latitude faunas that are separated from the tropics by an intervening temperate province are inferred to have received most of their lineages from the tropics but via the intervening province. The regional values of both gamma and beta, should be closely linked to both the frequency of range expansion across provincial boundaries and the nature of the expansion process, either through species range-expansion or speciation events across climatic barriers (Krug *et al.* 2008). These processes should result in spatial autocorrelation in taxonomic structure, owing to the sharing of species and genera between adjacent provinces; accounting for such autocorrelation will be an interesting component of future research.

The shape of regional RDDs must also be owing in part to the environmental variability of the different climate zones, which is highest in temperate zones today and was also high during Pleistocene climate swings (Jansson 2003). This variation has potentially imposed higher local and global extinction rates on temperate bivalves than seen in tropical and polar settings (Valentine *et al.* 2008), and probably creates additional environmental filters for the lineages expanding out of the tropics. Higher extinction rates and/or reduced immigration rates in temperate provinces may have generated the low gamma and beta values we observe here, as well as the breakdown of such canonical biogeographic relationships as the scaling of taxonomic richness and structure to geographical area (see for example, the substantial Pliocene extinctions suffered by large temperate provinces such as the Mediterranean and North European; Raffi *et al.* 1985; Monegatti & Raffi 2001). Regional age–diversity relationships will also be disrupted by these processes: tropical provinces will contain many genera whose species have invaded and diversified in higher latitudes, whereas temperate and polar provinces will contain species derived from lineages that originated, and in most instances persist, at lower latitudes.

Proximity to the tropics partially counterbalances these environmental impacts on taxonomic structure. For example, temperate provinces flanking the diverse tropical Western Pacific province exhibit elevated beta and gamma values when compared with other temperate provinces (figure 2 and electronic supplementary material, table S3). These temperate provinces are either receiving multiple invasions of species from the richer tropical genera, or some invading genera are speciating in these temperate zones at near-tropical rates; our data currently lack the resolution to distinguish between these possibilities.

This spillover or proximity effect on the taxonomic structure of the handful of tropical-like temperate provinces may reflect their oceanographic setting, as they are fed in part by currents flowing from the tropics; the Japonic provinces are chiefly washed by the Kuroshio Current and its offshoot the Tsushima Current (Longhurst (1998) and references therein), the Peronian by the East Australian Current and the South Australian by the Leeuwin Current (Church & Craig (1998) and references therein). These inflows of tropical waters evidently create spreading routes and support the maintenance of lineages spreading from tropical sources, resulting not only in relatively high taxonomic diversity in these provinces, but taxonomic structures of near-tropical aspect. This effect is strongest in the Warm Japonic, but attenuated in its northern neighbour, the Cool Japonic (figure 2). These tropical-flanking temperate faunas would be valuable targets for detailed analysis to evaluate potential factors behind their intermediate structures, which presumably include unusually high Late Cenozoic diversification or invasion rates owing to warmer regional histories for their respective latitudes. More detailed extinction and origination histories are needed at the provincial scale to decipher these historical effects.

The Arctic provides an opportunity to separate taxonomic structure from richness, and we hypothesize an atypical diversity dynamic for the region. The fossil record allows only a Pliocene–Pleistocene window onto Late Cenozoic bivalve history in the Arctic, but faunal composition at the generic level appears to have been quite stable over that interval, with few originations, invasions or extinctions (Valentine *et al.* 2008). The Arctic's high gamma value and relatively high beta value (compared with other mid- to high-latitude faunas) can be interpreted as a result of the presence in the Arctic of a high percentage of older lineages, which we infer have persisted in high latitudes for a long time and have taken advantage of opportunities to diversify that have been opened either via extinctions or by ameliorating episodes. As Arctic diversity accommodation is low, even those richer genera tend to have low species diversities and thus the fauna exhibits only a slightly elevated beta value. Other scenarios are possible, however, and more data are required to test these ideas.

A biological explanation for beta—the equitability of species richness among diverse genera—is challenging. Interprovincial comparisons could help identify the factors that structure beta, yet most of the analyses presented here only rule out factors hypothesized to be important. First, the very high beta within tropical provinces (the poorly sampled Guinean province of tropical West Africa being the lowest) suggests a possible effect

of heterogeneous tropical reef habitats. However, the Panamanian province, which lacks reef structures comparable to those in the Pacific or Caribbean, has a beta that is higher than the Caribbean. Second, beta is highest among the largest provinces, but this is because tropical provinces tend to be large; beta does not vary significantly with area among the 20 temperate provinces. Third, beta varies with the median age of genera when all provinces are included, but this relationship weakens when analyses are restricted to temperate provinces. One relationship that seems to hold is that beta is higher in low-latitude provinces in which taxonomic structure is generated overwhelmingly via high speciation and low extinction (Jablonski *et al.* 2006). Yet, beta cannot be explained simply by the logistic diversification of taxa of comparable age, as the ages of species-rich lineages in these provinces vary by an order of magnitude (electronic supplementary material, figure S6).

These comparisons suggest that beta is high in tropical provinces because the dynamics of origination, range expansion and extinction of genera and of species are different there than at higher latitudes. Perhaps tropical environments support greater ecological differentiation, and it is through the combination of multiple independent RDDs—each characterizing the taxonomic structure of a narrower ecological zone—that beta is generated. Another related possibility is that diversity-dependent factors (Valentine 1972; Valentine *et al.* 2008) limit tropical species richnesses (see also Phillimore & Price 2008, 2009; Ricklefs 2008, 2009; Reznick & Ricklefs 2009). Presumably, most genera have adaptive zones or niches of their own, however overlapping, that result in a slowing of diversification rates within each genus with increased packing of conspecifics: genera farther from their limiting richnesses attain higher speciation rates than those nearer their limits, and thus tend to catch up with the diversities of the richest lineages. In such a model, the final responsibility for relative diversity distributions rests with the interplay between the structure of the environment—the potential niches available in a particular setting—and the evolutionary potential of lineages.

Modelling the contributions of extinction, speciation and dispersal to regional-scale taxonomic structure may be particularly fruitful for dissecting the mechanisms underlying these spatial diversity patterns. Such a modelling effort is particularly tantalizing, given the discordance between the RDD expected under a simple birth–death model, wherein rates of extinction and speciation are time- and clade-homogeneous, and the RDDs we observe empirically in the global ocean. The expectation under simple birth–death is for taxonomic structure in any given time step to follow a geometric distribution (Nee *et al.* 1994). However, the best fit of the Zipf–Mandelbrot to the provincial- and zonal-scale data, and specifically the support for beta values greater than zero, implies that additional processes operate to reduce the richness of older species-rich clades, thereby evening out their relative diversity. Candidate processes include diversity-dependent dynamics (e.g. Rabosky 2009) and rates of higher-level branching (e.g. Patzkowsky 1995), both of which should be considered alongside rates of immigration and emigration in future efforts to model regional taxonomic structure.

5. CONCLUSIONS

The taxonomic structure of marine bivalve faunas can be described using a related set of parametric distributions (Zipf and Zipf–Mandelbrot). This general form allows us to investigate geographical variation in taxonomic structure at two different spatial scales, climate zones and provinces, and also quantify two neglected aspects of the taxonomic structure of these biotas: the equitability of species richnesses in each fauna overall (γ) and among their most diverse lineages (β). Tropical provinces, and temperate provinces washed by currents arising in the tropics, differ markedly in structure from temperate provinces washed by cooler currents. We hypothesize that this difference is owing to the relative stability of diversity-dependent factors in tropical latitudes, resulting in high speciation rates and species accommodation levels, in contrast to the instability of such factors at both ecological and evolutionary scales in cool-temperate latitudes, which have lower rates of speciation and immigration as well as higher extinction rates. Polar provinces have exceptionally low species accommodation levels but different climate histories, and differ by almost an order of magnitude in β values; their faunal histories are still too poorly known to support robust hypotheses concerning their taxonomic structures.

The size of a province seems to have little relationship to its taxonomic structure. While it is true that most of the larger provinces are tropical, the polar provinces are also quite large, and size, richness and taxonomic structure are not significantly correlated among temperate provinces. These data suggest that tropical provinces owe their diversity structure to being tropical rather than simply to being large, and thus implicate diversity-dependent factors that are related to latitude as modified by regional conditions. Our results also suggest that relatively young, diversifying clades have had a disproportionate effect on the taxonomic structure of modern marine faunas globally. We hypothesize that the geographical variation in taxonomic structure in the global ocean results from differential origination and extinction rates among clades and regions as constrained by spatial variation in the diversity accommodation space of provinces and climate zones.

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