A macroevolutionary perspective on species range limits

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Understanding the factors that determine the geographic range limits of species is important for many questions in ecology, evolution and conservation biology. These limits arise from complex interactions among ecology and dispersal ability of species and the physical environment, but many of the underlying traits can be conserved among related species and clades. Thus, the range limits of species are likely to be influenced by their macroevolutionary history. Using palaeontological and biogeographic data for marine bivalves, we find that the range limits of genera are significantly related to their constituent species richness, but the effects of age are weak and inconsistent. In addition, we find a significant phylogenetic signal in the range limits at both genus and family levels, although the strength of this effect shows interoceanic variation. This phylogenetic conservatism of range limits gives rise to an evolutionary pattern where wide-ranging lineages have clusters of species within the biogeographic provinces, with a few extending across major boundaries.

Keywords: geographic range limits; macroevolution; biogeography

1. INTRODUCTION

Biologists have long sought to understand the factors that determine the northern and the southern range limits of species because the topic is central to many ecological and biogeographic questions (Gaston 1990, 2003; Holt 2003; Parmesan *et al.* 2005). However, the determinants of range limits of most species remain poorly understood, primarily because such limits arise from complex interactions among a large array of physical, biotic and historical factors (Holt 2003; Parmesan *et al.* 2005; Goldberg & Lande 2007). Empirical analyses of species range limits have mainly focused on the correlations between aspects of the physical environment (e.g. temperature) and species distributions (Gaston 1990, 2003; Holt 2003; Parmesan *et al.* 2005), and such relationships are being quantified for an increasing number of species (Jeschke & Strayer 2008). Theoretical studies of range limits, on the other hand, have explored how biotic parameters such as gene flow, local adaptation, species interactions and dispersal can interact with the physical environment to set species range limits (Caughley *et al.* 1988; Kirkpatrick & Barton 1997; Holt 2003; Case *et al.* 2005; Goldberg & Lande 2007). These models consistently highlight the importance of microevolutionary processes (Holt 2003; Goldberg & Lande 2007), but

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empirical tests of their predictions are still rare (Davis *et al.* 1998; Angert & Schemske 2005; Sanford *et al.* 2006). How macroevolutionary processes set or constrain range limits has received even less attention, as the majority of existing studies, empirical and theoretical, focus on single species or a few closely related species.

The many factors potentially interacting to set species range limits can be divided into three general categories—species niches, dispersal and spatial variations in the environment (Brown & Lomolino 1998; Holt 2003). Both species niches and dispersal ability have been shown to be phylogenetically conserved in some groups (see Chazdon *et al.* 2003 and Wiens & Graham 2005) although this effect is certainly not universal (Knouft *et al.* 2006; Pearman *et al.* 2007) and may be difficult to detect (Gaston & Chown 1999; Losos & Glor 2003). Dispersal is particularly relevant for marine invertebrates where it may play an important role in constraining species' range limits (Gaylord & Gaines 2000; Byers & Pringle 2006; Sanford *et al.* 2006), and the variety of larval and other traits that determine species' dispersal abilities tend to be conserved at the level of higher taxa (Hunt *et al.* 2005; Jablonski *et al.* 2006*b*; Bradbury *et al.* 2008). Local and regional abundances of species, also important determinants of species range limits, can also be influenced by phylogeny (Webb 2000; Webb *et al.* 2002; Kelly *et al.* 2008). Similarly, biogeographers have long recognized that regional species assemblages often consist of groups of closely related species (Pielou 1977, 1978), a pattern that also emerges when regional distributions of species are overlain on molecular phylogenies (e.g. Richman & Price 1992; Hellberg 1998; Meyer 2003; Duda & Kohn 2005;

Latiolais *et al.* 2006; but see Fitzpatrick & Turelli 2006). Furthermore, in some cases, distributions of individual species can be predicted from the ecological characteristics of their sister taxa (Peterson *et al.* 1999). In general, there is a growing recognition that macroevolutionary history can play an important role in determining the spatial distributions of species and structures of communities (McPeek 1996; Webb *et al.* 2002; Chazdon *et al.* 2003; Cavender-Bares *et al.* 2006; Kraft *et al.* 2007). However, large-scale empirical analyses of how evolutionary history affects species range limits are still lacking.

It is important to recognize that focusing on the macroevolutionary scale does not negate the role of ecological and microevolutionary processes long considered to be the key determinants of species range limits. Those processes are indeed likely to be the proximate causes of species range limits, albeit interacting in complex ways whose strengths probably vary among taxa (Jablonski & Hunt 2006). Ultimately, however, the deeper evolutionary history determines how traits that underlie these proximate processes vary among species and thus needs to be taken into account for a better understanding of the causes of species range limits.

The range limits of any clade are obviously set by the maximum latitudinal and longitudinal limits achieved by its constituent species, and every clade starts with its range limits defined by that of a single species. As the clade ages, its range limits as well as those of the constituent species change as new species evolve and achieve their geographic distributions, existing species go extinct and the range limits of individual species shift in response to changing environments. The range limits of the living clades and species within them are thus a result of all of these historical processes and ultimately reflect how ecological, physiological and life-history traits interact and evolve to determine these limits. In this paper, we explore how evolutionary history influences the range limits of species and clades by evaluating (i) the relationship between the distributional limits of a clade and its age and species richness and (ii) whether the distributional limits of species are phylogenetically conserved (i.e. whether the range limits of closely related species are more similar compared to those that are more distantly related). These relationships address two issues that have previously been explored in the context of range sizes but not for range limits. Palaeontological data suggest that the geographic distributions of the clades (genera), and hence their distributional limits, increase over time (Miller 1997; Jablonski *et al.* 2006b; Finnegan *et al.* 2008), but whether such changes primarily result from speciation into new regions as the clade diversifies or from the expansion of ranges of existing species remains poorly known. Similarly, there has been considerable discussion about the extent to which the range sizes of species are phylogenetically conserved (Pielou 1977, 1978; Jablonski 1987, 2008; Ricklefs & Latham 1992; Webb & Gaston 2003, 2005; Hunt *et al.* 2005; Jones *et al.* 2005; Fitzpatrick & Turelli 2006; Jablonski & Hunt 2006; Mouillot & Gaston 2007; Waldron 2007), with a substantial phylogenetic signal documented by multiple studies. However, range limits have so far received little attention in this context. Even though these are related questions, it is important to note that a phylogenetic signal in range size does not necessarily imply that range limits are also phylogenetically conserved
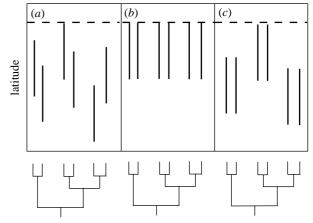

Figure 1. Conceptual models relating range limits of individual species to those of their clades. These hypothetical scenarios show how the northern limits of each species (the top of each line segment) relate to other species in the clade as well as the northern limit of the clade itself (shown by dashed lines). The size of the ranges is kept constant for simplicity and the figure is not meant to make any statement about the southern limits. See text for more details.

(two species can have exactly the same range size but different limits).

In considering the distributions of species within a given clade, we can define three scenarios: (i) the range limits of closely related species diverge from each other during speciation or subsequently (figure 1a), (ii) the range limits of closely related species are similar to each other (figure 1b), and (iii) the range limits of sister species are similar to each other but diverge between different sister species pairs (figure 1c). Scenario (i) leads to poor correspondence between the range limits of clades and their constituent species as would be expected if ecological niches, dispersal abilities, physiological tolerances and other limit-setting properties are not phylogenetically conserved (i.e. species evolve individualistically). Scenarios (ii) and (iii) are based on different levels of phylogenetic conservatism of limit-setting traits, leading to a perfect correspondence between the species and clade range limits in (ii) and a conservatism of range limits at the level of sister species but not a good correspondence between the species and clade range limits in (iii). Of course, real-world patterns are likely to be more complex than these hypothetical scenarios. Nonetheless, they provide a conceptual framework for examining how diversification of species within lineages constrains the distributions of lineages themselves.

We explore these questions using marine bivalves as a focal group and integrating the estimates of stratigraphic ranges of genera from the fossil record with the distributional data for living species on a global scale (5132 species in 854 genera) and, at higher spatial resolution, along the northeastern (NE) Pacific (921 species in 400 genera) and western (W) Atlantic (883 species in 319 genera) coasts. These two coastal databases share 218 genera but only 183 species. We focus on the northern and the southern distributional limits of species simply because the information for those is currently more reliable than those for longitudinal limits. Molecular phylogenetic analyses are starting to provide a more refined picture of the relationships among the deep

nodes of the bivalve tree (Taylor *et al.* 2007; Giribet 2008), but the relationships at or near the tips of the tree (i.e. among species and genera) have been resolved for only a handful of bivalve clades. Consequently, given the spatial scales of our analyses and the number of taxa involved, analyses using a well-resolved phylogeny are not possible at present. Instead, we use the taxonomic hierarchy (following a standardized taxonomic scheme; see below) as an indicator of phylogenetic relationships, and test for phylogenetic effects by comparing the range limits of species within individual genera with those across different genera. For some questions, we also repeat the analyses at the family level. This approach remains the best choice for groups where well-resolved phylogenies are not available (Harvey & Pagel 1991; Ricklefs & Nealen 1998; McGill 2008) and assumes that the relationships between individual taxa are unresolved (i.e. they represent a polytomy), which should make any phylogenetic signal in our data conservative. We use genera (including subgenera, which we elevate to genus rank here; Jablonski *et al.* 2006b) as operational phylogenetic units because they are fairly stable units and morphologically defined molluscan genera map well onto molecular phylogenies in most instances (Jablonski *et al.* 2006a). Finally, some of the analyses presented here take advantage of the excellent fossil record of marine bivalves, which provides direct estimates of the divergence times of genera (Jablonski *et al.* 2003, 2006b).

2. MATERIAL AND METHODS

(a) *Databases*
Our global, NE Pacific and W Atlantic databases for living bivalves, along with the database on first occurrences of genera in the fossil record, are described in the electronic supplementary material.

(b) *Statistical analyses*
We explored the relationship between the range limits (in degrees latitude) of a genus and its age and species richness using multiple regressions (the data for age and species richness were natural-log transformed). For the analyses of species range limits within and among genera, we focused on two of the best sampled coasts in the world—the NE Pacific and the W Atlantic (Roy *et al.* 2000, 1998). In each case, we computed the differences between the species range limits (in absolute degrees of latitude, separately for the northern and the southern limits) within individual genera as well as between the species in different genera, and used the difference in the medians of these two distributions (between-genus differences minus within-genus differences) as a test statistic. If range endpoints are not conserved within the genera, the within- and between-genus distributions should be similar, and the test statistic should be close to zero. Conversely, if endpoints are conserved, we expect large positive values of the test statistic, reflecting systematic differences between the genera. We assessed the significance of this statistic by comparing it to a null expectation generated by randomly assigning species to the genera. Randomizing taxonomic affinities preserved the observed distributions of range sizes as well as range limits, so that the difference between the observed and expected values of the test statistic reflects the phylogenetic component. Because the genera of marine bivalves represent relatively small clades (median

species : genus ratio in our global data is 3), we repeated the same analyses at the family level to explore the effects of the taxonomic scale. We also used a nested analysis of variance (Harvey & Pagel 1991; Ricklefs & Nealen 1998; McGill 2008) to explore how the variance in species range limits is partitioned among the taxonomic levels. Species were nested within the genera within families and each level was treated as a random effect. In addition, for the northern range limits along the NE Pacific and the W Atlantic, we also computed two commonly used metrics for phylogenetic signal: λ (Freckleton *et al.* 2002) and K (Blomberg *et al.* 2003), using taxonomy to provide a crude proxy for phylogeny. Together, these tests can differentiate between figure 1a and the other two scenarios. To differentiate between the scenarios in figure 1b,c, we calculated the differences between the northern and southern range limits of each species and the corresponding limits for the genus they belong to, and compared the median of these differences to the null distribution derived by the randomizing algorithm described above. All analyses were carried out in R STATISTICAL ENVIRONMENT (R Development Core Team 2006), and further details are provided in the electronic supplementary material.

3. RESULTS
For the global data, age and species richness of a genus are both significantly and positively related to its northern range limit (table 1; multiple $R^2 = 0.18$, $n = 711$). Age, however, has a very small effect compared with species richness as revealed by the changes in Akaike weights as each variable is removed from the full model (table 2). By contrast, only species richness is significantly correlated with the southern range limits of genera for the global dataset (table 1; multiple $R^2 = 0.25$, $n = 711$). For the NE Pacific, the results for the northern and the southern range limits are qualitatively similar to the global results (tables 1 and 2). However, the total variance explained by richness and age is much smaller along this coast than in the global data (for the northern limits, multiple $R^2 = 0.05$, and for the southern limits, multiple $R^2 = 0.06$; $n = 366$). Finally, for the W Atlantic, the age of a genus is not significantly related to either its northern or southern limits but the species richness of a genus is positively related to both (tables 1 and 2). In contrast to the NE Pacific, the W Atlantic variance explained by multiple regression is comparable to the global data (for the northern limits, multiple $R^2 = 0.12$, and for the southern limits, multiple $R^2 = 0.20$; $n = 319$). In all cases, the variance inflation factor is less than 2, indicating that the collinearity between age and richness is unlikely to be a problem in these analyses (Bowerman & O'Connell 1990).

For the NE Pacific, the northern range limits of species within a genus are significantly closer to one another than expected if species were distributed randomly within the genera (observed test statistic is 8.5°, $p < 0.001$). Similar clustering is also evident for the southern range limits (observed test statistic is 7°, $p < 0.001$). The results are not affected if monotypic genera are excluded from the analyses ($p < 0.001$ in both the cases). The same results also hold for the analyses at the family level ($p < 0.001$ for both the northern and the southern limits). Estimates of the variance components show that most of the variation in range

Table 1. Summary of the multiple regression coefficients. (Note that the range limits in the Southern Hemisphere are coded as negative numbers in our data, which lead to the negative slopes for the analyses of the southern range endpoints. Significant relationships are shown in italic.)

analysis	coefficient	estimate	s.e.	*p*-value
global north limits (*n*=711)	*intercept*	*17.69*	*2.3*	*0.000*
	ln(genus age)	*1.69*	*0.76*	*0.026*
	ln(species richness)	*9.80*	*0.95*	*0.000*
global south limits (*n*=711)	*intercept*	*−5.45*	*2.22*	*0.0142*
	ln(genus age)	0.03	0.73	0.9648
	ln(species richness)	*−13.04*	*0.92*	*0.000*
NE Pacific north limits (*n*=366)	*intercept*	*31.78*	*2.59*	*0.000*
	ln(genus age)	*1.50*	*0.72*	*0.0379*
	ln(species richness)	*5.36*	*1.34*	*0.000*
NE Pacific south limits (*n*=366)	*intercept*	*6.14*	*2.70*	*0.02*
	ln(genus age)	1.20	0.75	0.11
	ln(species richness)	*−6.89*	*1.40*	*0.000*
W Atlantic north limits (*n*=319)	*intercept*	*17.04*	*5.13*	*0.001*
	ln(genus age)	2.37	1.47	0.109
	ln(species richness)	*11.87*	*2.14*	*0.000*
W Atlantic south limits (*n*=319)	intercept	−1.80	5.42	0.739
	ln(genus age)	−0.15	1.55	0.922
	ln(species richness)	*−18.33*	*2.26*	*0.000*

Table 2. The effects of genus age and species richness on Akaike weights in the multiple regressions. (The full models included both genus age and species richness. Note that the Akaike weights are comparable only within datasets. In every case, removing the genus age has a much smaller effect than removing the species richness (see text for details).)

comparison	model	Akaike weights
global north limits (*n*=711)	full	0.818
	ln(genus age)	0.182
	ln(species richness)	0.000
global south limits (*n*=711)	full	0.269
	ln(genus age)	0.731
	ln(species richness)	0.000
NE Pacific north limits (*n*=366)	full	0.817
	ln(genus age)	0.182
	ln(species richness)	0.001
NE Pacific south limits (*n*=366)	full	0.622
	ln(genus age)	0.378
	ln(species richness)	0.000
W Atlantic north limits (*n*=319)	full	0.622
	ln(genus age)	0.378
	ln(species richness)	0.000
W Atlantic south limits (*n*=319)	full	0.269
	ln(genus age)	0.731
	ln(species richness)	0.000

endpoints is accounted for by phylogenetic (taxonomic) grouping. For the northern range limits, 60 per cent of the variance is associated with genus membership and 24 per cent with family membership. Similarly, for the southern limits, 54 per cent of the variance is associated with the genus level and 15 per cent with the family level.

The results for the W Atlantic are qualitatively similar to those for the NE Pacific, with both the northern and the southern range limits of species within genera and within families being significantly closer to each other than would be expected in the absence of phylogenetic effects ($p < 0.001$, in all cases). However, the variance

components are partitioned differently for this coast, with much less of the variation accounted for by taxonomy. For the northern limits, 22.7 per cent of the variance is associated with the genus level and 13.8 per cent with the family level. For the southern limits, 21.3 per cent of the variance is associated with the genus level and only 5.7 per cent with the family level.

For the northern range endpoints, metrics of the phylogenetic signal (Freckleton *et al.* 2002; Blomberg *et al.* 2003) are moderate to high in the NE Pacific ($\lambda = 0.32$, $K = 0.78$) and somewhat lower in the W Atlantic ($\lambda = 0.11$, $K = 0.53$). Non-parametric tests for the phylogenetic signal (Blomberg *et al.* 2003) are significant ($p < 0.001$) for both the coastlines.

The median difference between the range limits of species and the genus they belong to is significantly smaller than expected in the absence of phylogenetic effects for both the northern (observed test statistic $= 6°$, $p < 0.0001$) and the southern limits (observed test statistic $= 4°$, $p < 0.0001$) for the NE Pacific taxa. For the W Atlantic, the test statistic is highly significant for the northern range limits (observed $= 11°$, $p < 0.0001$) but marginally so (observed $= 28°$, $p = 0.05$) for the southern limits.

4. DISCUSSION

Previous analyses have shown that the genera of marine bivalves tend to originate preferentially in the tropics and over time extend their range limits polewards with the older taxa reaching further towards the poles (Goldberg *et al.* 2005; Jablonski *et al.* 2006*b*; Roy & Goldberg 2007). The analyses presented here are consistent with this 'out of the tropics' dynamic (see below) but they also find an interesting asymmetry in the behaviour of the northern versus the southern range limits of genera. Older genera have more poleward northern limits on a global scale, as well as along individual coasts, but age is not a significant correlate of the southern range limits. The reason for this asymmetry is unclear but could result from different processes being responsible for setting the northern versus the southern ranges of taxa (MacArthur 1972;
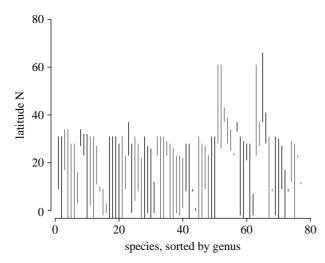
Figure 2. A plot showing the distribution of the northern range limits of the species of the family Veneridae along the NE Pacific. The top of each line represents the northern limit of that species. Clusters of species with the same line type represent individual genera and only non-monotypic genera are shown. The lines that intersect the *x*-axis represent the species whose southern limits are south of the equator. In this case, the test for phylogenetic conservatism is marginally significant ($p = 0.07$), although the power of the test is low because of small sample size.

Jablonski & Valentine 1990). We also cannot rule out the possibility that the asymmetry reflects poorer sampling of the southern oceans (see Clarke *et al.* 2007). However, for the majority of taxa used here the southern range limits are in the comparatively well-sampled Northern Hemisphere and so some of this asymmetry is likely to be real. More importantly, our results show that the correlation between the age and distributional limit, when it exists, is largely due to increased species richness in older clades rather than being a direct effect of age. In fact, for the global data, species richness emerges as a much stronger correlate of distributional limits of the genera than does age (see also Krug *et al.* 2008).

The range limits of marine bivalve species show significant phylogenetic conservatism at both the genus and family levels (figure 2; also figure 3 in the electronic supplementary material). Our estimates of *K* are similar to those previously documented for morphological, life-history and physiological traits (Blomberg *et al.* 2003). Estimates of λ for our data are lower but still comparable with those for ecological characters (Freckleton *et al.* 2002). While these estimates should be interpreted with caution given the crude and largely unresolved phylogeny used here, they do suggest that the phylogenetic signal in range limits may be substantial in marine bivalves. The strength of the effect and how variation in range limits is partitioned among taxonomic levels also clearly differs between the NE Pacific and the W Atlantic coasts. Overall, the nested ANOVA as well as the estimates of λ and *K* suggest a stronger phylogenetic signal in the NE Pacific than in the W Atlantic. These differences presumably reflect interoceanic differences in compositions of species assemblages as well as the past and present differences in environmental conditions. Furthermore, the range limits of species and the genus they belong to are significantly closer to each other than would be expected by chance,

but again the interoceanic differences are present with the concordance much higher in the NE Pacific than in the W Atlantic.

Marine biogeographers have long known that species range limits tend to cluster in certain areas, marking the boundaries between the biotic provinces and subprovinces (Valentine 1966; Roy *et al.* 1998; Briggs 1999; Spalding *et al.* 2007; Reaka *et al.* 2008). Many of these boundaries coincide with the convergences between major water masses or other changes in coastal oceanography (Valentine 1966; Spalding *et al.* 2007), and both the theoretical models (Gaylord & Gaines 2000; Byers & Pringle 2006) and empirical studies (Doyle 1985; Gilman 2006) suggest that such barriers to dispersal may be important determinants of the range limits of some marine species. Our results indicate that the responses of species to such barriers are, in part, determined by their phylogenetic affinities; if barriers affected all species equally then the analyses above would not have found conservatism of range limits at the level of genera and families. Thus, for marine bivalves, traits that determine the dispersal abilities of species are likely to be conserved at the level of genera and to a lesser extent the families. The specific traits involved remain poorly known, but for broadcast spawning species they should include those that enhance the transport and survival of larvae in the plankton as well as attributes that lead to post-settlement growth and survival (Morgan 2001; Sanford *et al.* 2006). Rafting of adults may also be significant in some clades, particularly at smaller body sizes, another trait that has a strong phylogenetic component (e.g. Smith *et al.* 2004). Physiological tolerances have also been shown to be important determinants of the range limits of some marine species (Tomanek & Somero 1999; Stillman & Somero 2000). In some groups of intertidal gastropods and crabs, closely related species have been shown to have similar physiological tolerances (Tomanek & Somero 1999; Stillman & Somero 2000) but such information is still scarce for most species. There is, however, a growing interest in measuring the physiological traits across large spatial scales with the aim of integrating ecological physiology with macroecology. Such macrophysiological studies (*sensu* Chown *et al.* 2004) are being undertaken for both marine and terrestrial organisms (Chown & Gaston 1999; Chown *et al.* 2004; Compton *et al.* 2007; Osovitz & Hofmann 2007; Deutsch *et al.* 2008; Tewksbury *et al.* 2008) and these data, analysed in a phylogenetic context, should be useful for exploring the interactions between the evolutionary history, physiology and range limits.

The finding that the range limits of living bivalve species show a phylogenetic signal strongest at the genus level but detectable even at the family level, supplements and illuminates previous findings on the historical under-pinnings of the present-day bivalve biogeography. The Cenozoic Era witnessed a general cooling trend during which tropical climates retreated equatorward, interrupted by local climatic optima as during the Eocene and the mid-Miocene and by warm interglacial episodes during the Pleistocene (Zachos *et al.* 2001). The fossil record indicates that during the last 11 Myr most bivalve genera originated in the tropics, and their persistence there helps to explain the formation and maintenance of the latitudinal diversity gradient (Jablonski *et al.* 2006*b*). Over time, the range limits of many of these genera extended poleward even as high latitudes cooled. In fact,

75 per cent of today's polar bivalve genera also occur in the tropics, and many of these are likely to have originated in tropical waters (Goldberg *et al.* 2005). These poleward extensions of the genus range limits probably occurred mainly through speciation since less than 1 per cent of bivalve species extend from the tropics to the poles, and the more widely distributed genera tend to have more species in each climate zone (and in each province), including the tropics, than the genera that are more restricted geographically (Krug *et al.* 2008). These patterns are consistent with the results shown here, with distributional limits of the genera correlating more strongly with species richness than with genus age. The phylogenetic conservatism of range limits leads to wide-ranging lineages having clusters of species within the biogeographic provinces, with a few extending across these major boundaries. This pattern suggests a diversity-dependent dynamic, with the chance of breaking the phylogenetic conservatism (presumably through larger than the usual divergences of the underlying traits during speciation) increasing with the number of speciation events. This probabilistic model is further supported by the fact that the difference between range limits of species and the limits of their genus tends to be positively correlated with the species richness of the genus but not with the age of the genus. For example, for the NE Pacific species in the Northern Hemisphere, the median difference in the northern limits is significantly correlated with species richness ($p < 0.0001$) but not with age ($p = 0.68$). A positive relationship between the richness of a genus and the median difference in range limits is expected from sampling, but taxonomic clustering of range limits should make the slope shallower than expected from sampling alone. We estimated the slope expected in absence of taxonomic clustering by randomizing the taxonomic affinities of individual species and repeating the regression 1000 times. The observed slope (0.74) is indeed significantly shallower than that expected from sampling alone (95% confidence interval of the expected slope is 0.77–1.2). Thus, the general phylogenetic conservatism of range limits holds irrespective of the species richness of the genus (table 3), but as more species are added to a genus, there is evidently more opportunity for niche and dispersal-related traits of the species to diverge and the pattern becomes closer to figure 1*c* than to figure 1*b*.

Macroevolutionary history clearly plays a role in determining the range limits of marine bivalve species, but the spatial scale and/or the phylogenetic level at which such factors are most important remains poorly explored. Here, we focused on large spatial scales involving large numbers of species from most of the major bivalve lineages, with the distributional data for individual species resolved at a moderately coarse resolution. We suspect that the phylogenetic conservatism of range limits is likely to be most evident at these macroecological scales with population-level mechanisms becoming more important for setting distributional limits at local scales (e.g. Gross & Price 2000). Similarly, given that speciation and extinction rates differ substantially among taxa, the degree to which range limits are phylogenetically conserved is also likely to vary among the living genera and families and may even be absent in some. Both simulation studies and empirical analyses have already demonstrated such scale

Table 3. Randomization tests for phylogenetic conservatism of range limits (see text for details) in the NE Pacific bivalve genera with different levels of species richness. (Separate tests were performed for each range of species richness. The results are qualitatively the same for the W. Atlantic genera.)

species richness	total number of genera	total number of species	*p*-value (north, south)
2–4	147	380	$<0.001, <0.001$
5–7	36	207	$<0.001, <0.001$
8+	8	89	$<0.001,\ \ 0.001$

dependence (both spatial and taxonomic) of phylogenetic conservatism for community structure (Cavender-Bares *et al.* 2006; Kraft *et al.* 2007). Furthermore, detection of phylogenetic conservatism becomes more difficult for clades and/or assemblages with smaller numbers of species since the power of the statistical tests declines with sample size (Kraft *et al.* 2007). So, for marine bivalves, tests of phylogenetic conservatism of range limits at finer spatial and taxonomic scales than attempted here will require better phylogenetic resolution at the level of individual genera and better spatial sampling, especially in the tropics and the southern oceans.

For the vast majority of marine and terrestrial species, the processes determining distributional limits remain unknown. Given the complex interactions between the organismic traits and the biotic and abiotic environments involved in setting range limits, this situation is unlikely to change in the near future. On the other hand, such knowledge is essential for addressing a number of real-world problems, from the responses of species to climate change to the success and spread of introduced species. The assumption that the traits involved in setting range limits are phylogenetically conserved is common in predictions of how the distributional limits of species will change in response to future climate change (Peterson *et al.* 1999; Wiens & Graham 2005; Jeschke & Strayer 2008), but without explicit tests it is impossible to know how well the assumption holds for various groups. Finally, we note that it remains an open question whether macroevolutionary history plays a similar role to that seen here in setting the range limits of terrestrial animals, where long-distance larval dispersal and recruitment dynamics, key components of marine population biology, have virtually no analogues (Paine 2005). Comparative analyses using better-resolved phylogenies and across different groups of marine and terrestrial organisms are needed to understand how evolutionary history constrains the distributional limits of species and lineages.

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Materials and Methods – Supplement

Biogeographic databases:

(i) *Global* - We significantly expanded and revised a previously constructed spatially explicit database (Flessa & Jablonski 1996) of global occurrences of shallow water (<200 m) living marine bivalves (Jablonski et al. 2006b), which now includes 854 genera and subgenera, 5132 species, and 28,264 occurrences from 322 localities spanning the world oceans. Supplementary Table 1 provides a list of the bivalve families included in this database. Many parts of the world oceans still remain very poorly sampled (Bouchet 1997) and the spatial resolution of the global dataset was chosen to maximize spatial coverage while simultaneously limiting the biasing effects of variable sampling and taxonomic treatment. We only included data from well studied regions where large portions of the fauna are unlikely to be absent or misidentified. Spatial resolution of individual localities varies, ranging from single islands to regions along continental shelves, but the latitudinal extent of a locality rarely exceeds 5° of latitude, with most representing 3° or less. Though higher resolution is obviously desirable, this subdivision of the world makes it is unlikely that additional sampling will result in large shifts in the distributions of taxa represented in the database. Occurrences are defined here as the presence of a species at a locality, and are compiled from literature sources and museum collections. Genus and higher-level taxonomic assignments are standardized using the recent taxonomic literature and consultation with specialists (see below). Of the 854 genera, 83% are known from the fossil record, a value similar to previously reported percentages (Flessa & Jablonski 1996; Krug et al. 2007; Valentine 1989) despite substantial expansion of the database and extensive taxonomic revisions.

(ii) *NE Pacific* – The northern and southern range limits of 921 species (from 400 genera) were determined for bivalves from the northeast Pacific ocean (from the southern edge of the Panamic Province at 5°S to Point Barrow, Alaska, in the Arctic Ocean at 71°N). Unlike the global database, these data are not binned by locality, but rather focus on determining the latitudinal extremes for each species (and hence for each genus). The extratropical portion of this database differs only in minor details, primarily updates and a few taxonomic modifications, from Coan et al. (2000); the tropical portion has been heavily updated from Keen (1971) based on more recent publications, major museum collections, and consultation with taxonomic experts (see below). Of the 400 genera recorded from this coast, only those 366 with reliable age estimates from the fossil record are used here.

(iii) *W Atlantic* – Data for Western Atlantic analyses come from the W Atlantic localities within the global dataset, from north Greenland (80°N) to Tierra del Fuego, Chile (55°S) and include 883 species, 319 genera (90% of which have been identified as fossils), and 5284 occurrences from 89 localities. Most range limits correspond closely to those in the online database Malacolog (Rosenberg 2005), but some differ because of taxonomic revisions to standardize the data to our global scheme.

Paleontological database:

The geologic ages of genera were taken from an extensively revised and updated version of Sepkoski's 2002 compendium (Jablonski et al. 2003, 2006). To date, we have made 1334 changes in Sepkoski 2002 (who listed 2872 genera), from minor adjustments of range endpoints through significant stratigraphic range extensions and contractions to the addition of newly described (or newly recognized, via our own work or that of others)

genera and the deletion of genera now synonymized with other genera in the database. Of these changes, 620 are Cenozoic, 517 are Mesozoic, and 197 are Paleozoic – roughly proportional to the number of genera recorded from each Era, although the Cenozoic frequency falls well short. The absolute ages of genera were assigned using the midpoint of the geological interval according to the timescale of Gradstein et al (2004).

Statistical analyses:

We explored the relationship between range limits (in degrees latitude) of a genus and its age and species richness using stepwise multiple regressions. Because the raw data for age and species richness are highly skewed, they were natural log-transformed for all the analyses but range limits were not. This transformation substantially reduces the skew in the regression residuals but does not completely remove it. So we also explored other methods for transformation, namely square-root and Box-Cox transformations. In all of these cases some skew in the regression residuals remain, because of the nature of the species richness data. However, given that the qualitative results are the same under all types of transformation it is highly unlikely that our regression results are artifactual. Another concern here is the potential for collinearity between age and species richness. To assess whether our regression results are affected by collinearity, we calculated variance inflation factors (VIF) for all analyses. Collinearity is normally considered to be an issue if VIF is greater than 10 (Bowerman and O'Connell, 1990). We computed the relationships for northern and southern range limits separately for the global dataset, the NE Pacific and the W Atlantic coasts. While these are not independent analyses in the sense that the data for individual coasts are a subset of the global data, they are useful for exploring how the relationship between range limits, age, and richness varies with spatial

scale and among different regions. Because coasts differ in terms of geological, environmental, and biotic histories (e.g. O'Dea et al. 2007; Renema et al. 2008; Todd et al. 2002), comparisons of results from two different coasts can be viewed as comparisons of the results of two natural experiments.

(ii) We compared the distribution of species range limits within and among genera using multiple approaches. Because shelf regions of the world ocean are sampled to differing degrees (Bouchet 1997), range limits of individual species are often poorly constrained. In order to avoid problems due to this sampling bias, for the analyses of species range limits we focused on two of the best-sampled coasts in the world - the NE Pacific and the W Atlantic (Roy et al. 2000; Roy et al. 1998). In each case, we first computed the differences between species range limits (in absolute degrees of latitude) within individual genera as well as between species in different genera. Differences were calculated separately for northern and southern limits. We then used the difference in the medians of these two distributions (between genus differences minus within genus differences) as a test statistic and compared its value to that of the null expectation generated by randomly assigning species to genera 1000 times. By randomizing taxonomic affinities, we preserved the observed distributions of range sizes as well as range limits and so the difference between the observed and expected values of the test-statistic is simply a function of changing taxonomic affinities of species. Because genera of marine bivalves represent relatively small clades (the mean species: genus ratio in our global data is 6 and the median is 3) we repeated the same analyses at the family level to explore the effects of taxonomic scale. These randomizations are appropriate for testing the significance of the relationships but provide little insight about effect size, so we used

a nested analysis of variance (Harvey & Pagel 1991; Ricklefs & Nealen 1998) to explore how the variance in species range limits is partitioned among taxonomic levels. Species were nested within genera within families and each level was treated as a random effect. Variance components were calculated by first estimating the model using a restricted maximum likelihood algorithm implemented in R (R Development Core Team 2005) and then calculating the variances using the *varcomp* function in the ape package (McGill 2008; Paradis et al. 2004). In addition, for the northern range limits along the E. Pacific and W. Atlantic we computed two commonly used metrics for phylogenetic signal: λ (Freckleton et al. 2002) and *K* (Blomberg et al. 2003). Because there is no comprehensive phylogeny available for bivalves, we used taxonomic structure as a surrogate, creating a tree with nodes for families, and genera within families (Kelly & Woodward 1996). While this is certainly a crude phylogenetic approximation, it does allow comparison of the effect size for phylogeny to other published compilations (Freckelton et al. 2002; Blomberg et al. 2003), bearing in mind that the metrics of phylogenetic structure are likely underestimates because of the coarse and unresolved phylogeny (Freckleton et al. 2002, p. 724). The statistic λ was estimated using the function *fitContinuous* in the R package geiger (Harmon et al. 2007) and *K* was computed using the function *phylosignal* in the R package picante (Kembel et al. 2008). We also report the results of the nonparametric test for phylogenetic signal recommended by Blomberg et al. (2003) and computed by *phylosignal*.

The analyses above are designed to test whether closely related species have range limits closer to one another than those of more distantly related species, but they do not address whether species range limits are a good predictor of genus range limits. In

other words, they can differentiate between the scenario in Fig 1a versus Fig. 1b or Fig. 1c but they are not sufficient to differentiate between the scenarios in Fig 1b and Fig 1c. For the latter, we calculated the differences between the northern and southern range limits of each species and the corresponding limits for the genus they belong to. We then used the median of these differences as a test statistic and compared that to the null distribution derived by the randomizing algorithm described above. Because species and genus range limits are the same for monotypic genera, we excluded them from these analyses. Finally, we used linear regression to explore the relationships between the median difference between species limits and genus limits for each genus relative to its age and species richness. All analyses were done in the R statistical environment (R Development Core Team 2005).

Supplementary Table 1. List of orders and families currently contained in the global database of living bivalves analyzed here. Taxonomic nomenclature follows Bieler and Mikkelsen (2006); Giribet (2008; see also Taylor et al. 2008) combines Arcoida, Mytiloida, Pterioida, Limoida, and Pectinoida into Pteriormorphia; terms the families listed here under Carditoida as Archiheterodonta, and groups the Anomalodestmata and Veneroida (plus Myoidea, not yet incorporated into our database) into Euheterodonta.

Order	Family
Nuculoida	Nuculidae
Solemyoida	Nucinellidae, Solemyidae
Nuculanoida	Malletiidae, Neilonellidae, Nuculanidae, Phaseolidae, Siliculidae, Tindariidae, Yoldiidae
Arcoida	Arcidae, Cucullaeidae, Glycymerididae, Limopsidae, Noetiidae, Philobryidae
Mytiloida	Mytilidae
Pterioida	Gryphaeidae, Isognomonidae, Malleidae, Ostreidae, Pinnidae, Pteriidae, Pulvinitidae
Limoida	Limidae
Pectinoida	Entoliidae, Pectinidae, Propeamussiidae, Spondylidae
Trigonoida	Trigoniidae
Carditoida	Astartidae, Carditidae, Condylocardiidae, Crassatellidae
Anomalodesmata	Clavagellidae, Cleidothaeridae, Cuspidariidae, Laternulidae, Lyonsiidae, Myochamidae, Pandoridae, Parilimyidae, Penicillidae, Periplomatidae, Pholadomyidae, Poromyidae, Thraciidae, Spheniopsidae, Verticordiidae (including Euciroidae and Lyonsiellidae of previous authors)
Veneroida	Anatellidae, Cardiidae (including Tridacnidae of previous authors), Cardilidae, Donacidae, Glauconomidae, Hemidonacidae, Kelliellidae, Mactridae, Mesodesmatidae, Pharidae, Psammobiidae, Semelidae, Solecurtidae, Solenidae, Tellinidae, Trapezidae, Veneridae (including Cooperellidae, Petricolidae, and Turtoniidae of previous authors)

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Figure 4. Northern range limits of NE Pacific marine bivalve species separated by families. Each color represents a family. Because of the large number of families, the same eight colors had to be repeated. Where species ranges (individual lines) intersect the x-axis, the southern limit is south of the equator. These data indicate significant phylogenetic conservatism of northern limits at the family level (see text for details)