Geographical range and speciation in fossil and living molluscs

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The notion of a positive relation between geographical range and speciation rate or speciation probability may go back to Darwin, but a negative relation between these parameters is equally plausible. Here, we test these alternatives in fossil and living molluscan taxa. Late Cretaceous gastropod genera exhibit a strong negative relation between the geographical ranges of constituent species and speciation rate per species per million years; this result is robust to sampling biases against small-bodied taxa and is not attributable to phylogenetic effects. They also exhibit weak inverse or non-significant relations between geographical range and (i) the total number of species produced over the 18 million year timeframe, and (ii) the number of species in a single timeplane. Sister-group comparisons using extant molluscan species also show a non-significant relation between median geographical range and species richness of genera. These results support the view that the factors promoting broad geographical ranges also tend to damp speciation rates. They also demonstrate that a strong inverse relation between per-species speciation rate and geographical range need not be reflected in analyses conducted within a single timeplane, underscoring the inadequacy of treating net speciation as a proxy for raw per-taxon rates.

Keywords: speciation; geographical range; sister-group comparisons; species richness; molluscs

1. INTRODUCTION

The relation between geographical range size of species and evolutionary dynamics—speciation rate, extinction rate and species durations—figures in many evolutionary and ecological discussions (for reviews see Jablonski 1995; McKinney 1997; Gaston & Chown 1999; Gaston & Blackburn 2000; Jablonski *et al.* 2003). The inverse relation between geographical range and extinction rate, or the positive relation between geographical range and species duration, has been documented in several fossil molluscan assemblages (see Stanley 1979; Hansen 1982; Jablonski 1987, 1995; McKinney 1997; Gaston & Blackburn 2000; for a possible exception see Stanley (1986)), and is also generally supported by ecological data and theory (Maurer & Nott 1998; Gaston & Blackburn 2000).

The relation between geographical range and speciation rate is more contentious. The notion of a positive relation between geographical range and speciation rate or speciation probability may go back to Darwin (1859, Ch. 2) (Holt 1997; Maurer & Nott 1998; Gaston 1998; Maurer 1999, pp. 186–189), and has had proponents ever since. Many authors have predicted or assumed a positive relation between geographical range and speciation rate from the reasonable argument that, all other factors being equal, broad geographical ranges are more likely to be broken by barriers, or to bud off peripheral isolates, than narrow ranges (Terborgh 1973; Rosenzweig 1975, 1995; Maurer & Nott 1998; Hubbell 2001 adopts a similar view but argues that this model should apply most strongly to vicariant, rather than peripheral-isolate, speciation; and see Roy

(1994) on genus-level patterns). Large ranges should also encompass a greater diversity of selective environments and so might drive greater adaptive divergence among populations (Terborgh 1973; Endler 1977; Holt 1997). This reasoning has been extended beyond speciation rates to the total number of species produced, and to the standing diversity (i.e. species richness) within clades, all of which have been hypothesized to be a positive function of species' geographical ranges (Maurer & Nott 1998).

An equally plausible alternative, however, is that the factors promoting broad geographical ranges, such as relatively high dispersal ability or broad physiological or environmental tolerances, also tend to make those species relatively insensitive to barriers and should thereby damp speciation rates and the accumulation of species numbers (see, for example, Mayr (1963); Jablonski (1986); and other papers cited by Gaston & Chown (1999); see also Maurer & Nott (1998) and Hubbell (2001)). Under this view, species with limited dispersal ability or narrower tolerances tend to have more fragmented populations that will make them more vulnerable to both vicariant and peripheral-isolate speciation despite their more restricted geographical ranges (as also argued by Maurer & Nott (1998)).

Here, we present analyses of Cretaceous and present-day molluscan genera that support this alternative view: speciation rate tends to be inversely related to geographical range, and the total production of species over time or present in a single timeplane is inversely or non-significantly related to geographical range.

2. MATERIAL AND METHODS

(a) Cretaceous

The late Cretaceous (Campanian–Maastrichtian, *ca.* 83–65 million years (Myr) before present) molluscan fauna of the Gulf

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and Atlantic Coastal Plain is one of the richest and most extensively documented fossil faunas in the world. A (discontinuous) outcrop extending over 4000 km from New Jersey to Mexico was affected by sea-level cycles that yielded successive samples of similar depositional environments. Some of these deposits provide exceptionally fine preservation, which combined with a robust and internally consistent species-level taxonomy generated by just a few systematists, have made this region a focus for evolutionary, ecological, biogeographical and taphonomic analyses (e.g. Sohl & Koch 1983; Jablonski 1986, 1987, 1995, 1997; Koch 1996).

For gastropod species in the Coastal Plain Cretaceous, we examined the relation between geographical range and

(i) speciation rate;
(ii) the total number of species originating in a genus; and
(iii) standing species richness in a single timeplane.

We calculated speciation rates for each genus on a per-species per Myr basis (= lineage-million years, Lm.y. (Raup 1985)) ($N = 90$ genera and 420 species).

As the stratigraphic ranges of species that originated in the topmost interval (the *bilira* Zone) are truncated by the end-Cretaceous mass extinction event, we omitted species that first appeared in that interval from the speciation-rate analysis; we included them in the total-production and standing-richness analyses. We followed the same protocol for monospecific genera: they were omitted from the speciation-rate analysis, but included in the total-production and standing-richness analyses.

We measured the geographical range of each species as the maximum linear distance (kilometres) along the outcrop belt between geographical range endpoints in any one time interval and calculated a median geographical range for each genus on the basis of all its constituent species. Sampling considerations suggest that palaeobiogeographical analyses are most robust when the kilometre distances along the outcrop are treated as rank-order statistics rather than as absolute distances (Jablonski & Valentine 1990). Many of these genera also occur elsewhere, but the central issue is the relation between the geographical ranges of *species* within a region and the production of species by dividing up—and therefore as a function of—those geographical ranges. The Coastal Plain was a discrete biogeographical unit in the Late Cretaceous (Sohl 1987), with only a few species extending outside it, and so this is a reasonable spatial unit for analysis.

The *bilira* zone, the final interval of the Coastal Plain Cretaceous, has been subjected to detailed re-collecting (see Koch 1996), and so we targeted this interval for our analyses of a single timeplane. Excluding species found only in this interval also makes the speciation analysis conservative for variations in sampling intensity, which can produce artificial pulses of apparent speciation if the differences are extreme (Foote 2000).

This geological record is still far from perfect, of course. A large fraction of the species are known from one or just a few localities, and many have doubtless gone unrecorded. Missing or undersampled species are more likely to be small-bodied (Valentine 1989; Kidwell 2002), and so we repeat the analyses using only the genera where the median body size among species is more than 1 cm. We used the geometric mean of length and diameter, which is a close correlate of shell volume, as a proxy for body size (Stanley 1986; Jablonski 1997). The effects of preservational biases on our results are discussed further below.

(b) *Recent*

We used sister-group comparisons based on published molecular and morphological phylogenies to test whether clades whose species have broad geographical ranges tend to contain more species. We searched the literature for phylogenies of living molluscan groups and selected those that included most or all living species in a particular clade. We excluded the much larger number of cases where species sampling was highly incomplete. Our resulting global dataset contains 13 bivalve and gastropod clades containing 135 species. We estimated the geographical range size for each of these species using published information about their distributions. We measured geographical ranges that ran roughly north–south in degrees latitude but for two-dimensional ranges, as seen in the Indo-West Pacific, we used the geometric mean of latitudinal and longitudinal extent. This metric is, of course, highly correlated with the product of latitudinal and longitudinal extent, which has been used by numerous authors and in turn correlates with several other range metrics (see Quinn *et al.* 1996). For each sister-group comparison, we plotted the difference in species richness between the sister clades against their difference in median geographical range.

3. RESULTS

(a) *Speciation rate*

The Cretaceous gastropod genera show a significant inverse relation between speciation rate and the geographical range of constituent species ($N = 90$ genera, Spearman's rank-order correlation, R, is -0.68, $p < 0.00001$) (figure 1a). This result is unchanged by the exclusion of genera whose median size is less than 1 cm (remaining $N = 62$ genera, Spearman's $R = -0.69$, $p < 0.00001$). Even when we include the species first appearing in the *bilira* zone, the correlation is highly significant ($N = 92$ genera, Spearman's $R = -0.50$; $R = -0.56$ if genera < 1 cm are excluded; $p < 0.000001$ for both tests).

(b) *Total species production*

Even if per-species speciation rates are lower in widespread species, this might be offset by the longer durations of their constituent species. However, Cretaceous genera show a weak inverse relation between geographical ranges of species and the total number of species originating within a genus (Spearman's $R = -0.17$, $p = 0.10$) (figure 1b). The relation is virtually unchanged if we exclude genera whose median size is less than 1 cm (Spearman's $R = -0.20$, $p = 0.12$).

The weakness of the correlation may arise from the fact that genera with one or a few species in our study area might represent either of two dynamics: short-lived lineages that became extinct in the Coastal Plain after leaving few or no descendants, or lineages that are highly speciation and extinction resistant. Both kinds of lineage appear to be present in our data, but species in monospecific genera tend to have significantly longer durations than species in polyspecific genera (figure 2). This again suggests that long-lived species have low speciation rates (the monospecific genera would otherwise consist mainly of short-lived species).
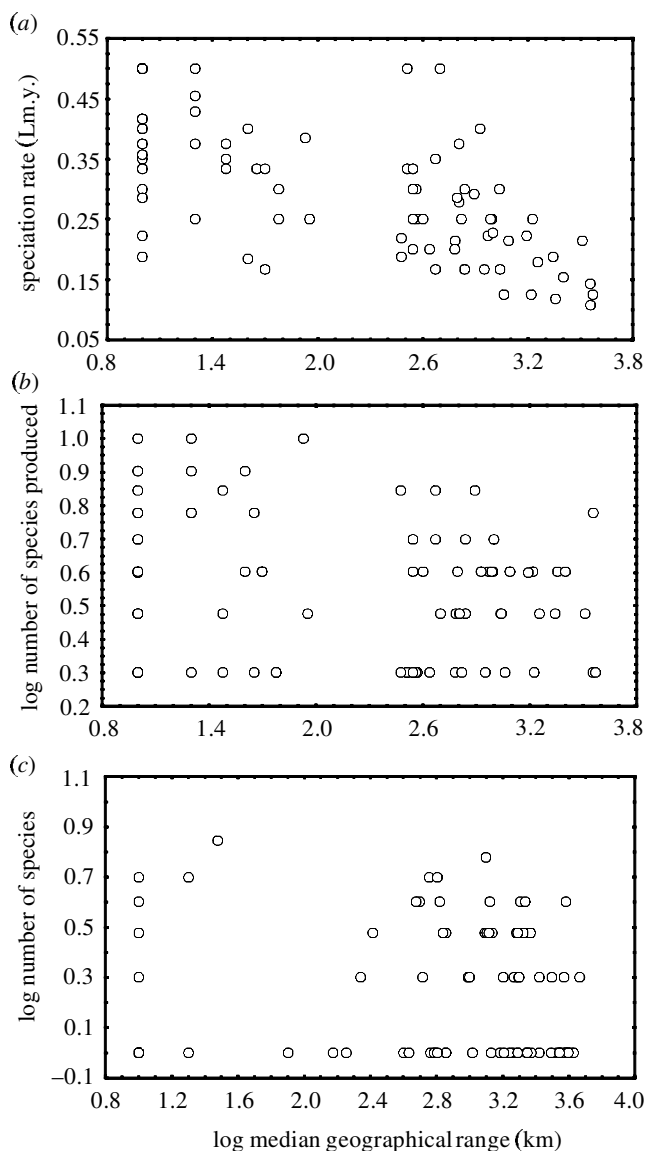
Figure 1. Speciation and geographical range in Late Cretaceous gastropods of the Gulf and Atlantic Coastal Plain. (*a*) Significant inverse relation between speciation rate per species per Myr (Lm.y.) and median geographical range of constituent species. (*b*) Weak inverse relation between the total number of species originating within a genus and the geographical ranges of its species. (*c*) No significant relation between the number of species within a genus in the latest Cretaceous *bilira* Zone and the geographical ranges of its species, although this becomes a significant inverse relation when small-bodied species, most subject to sampling biases, are omitted (see § 3*a* for details).

(c) *Standing richness*

Standing-species richness represents the net outcome of speciation and extinction, and need not be related to speciation alone. Late Cretaceous data again show a weak and non-significant relation between geographical ranges within the *bilira* zone and the number of species present in that time interval ($N = 91$ genera, Spearman's $R = -0.14$, $p = 0.18$) (figure 1*c*). If we omit genera having a single species in this interval (which of course may be polyspecific in the broader study interval) then the inverse relation between geographical range and species richness becomes statistically significant (Spearman's $R = -0.33$,
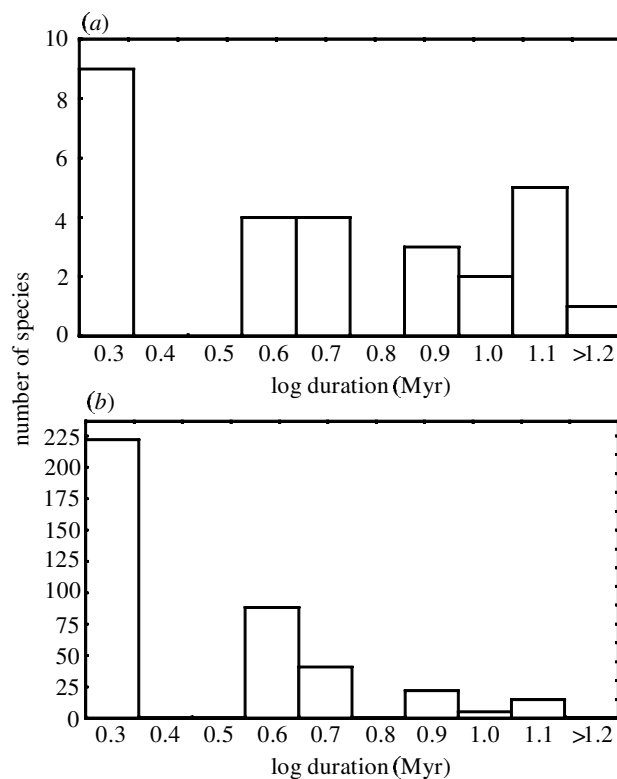
Figure 2. Species in genera that are (*a*) monospecific in the Coastal Plain Cretaceous tend to have significantly greater durations than species in (*b*) polyspecific taxa (Mann–Whitney *U*-test, $p = 0.001$). (*a*) $N = 28$, median = 0.78; (*b*) $N = 392$, median = 0.30.

$p = 0.02$). A similar outcome occurs if we retain the single species genera but omit the small-bodied species most subject to undersampling (Spearman's $R = -0.31$, $p = 0.01$).

Sister-group comparisons of extant clades corroborate the palaeontological results. We find no evidence for a positive relation between species richness and geographical range in these data, where, by definition, the comparison involves groups that have been diversifying for the same period of time. If anything, these data indicate a negative, although non-significant, trend (figure 3) (Spearman's $R = -0.46$, $p = 0.17$; if the outlier in the upper left corner of the plot is excluded, Spearman's $R = -0.26$, $p = 0.46$).

4. DISCUSSION

Contrary to some predictions and model assumptions, we find a significant *inverse* relation between speciation rate and species' geographical ranges in Cretaceous gastropods. We also find non-significant or inverse correlations between total number of species produced and geographical range in the Cretaceous, and between standing species richness and range in both Cretaceous and Recent molluscs. The palaeontological results are unlikely to be the result of sampling or preservation. One of the major determinants of molluscan preservation is shell mineralogy (Harper 1998), but the Cretaceous gastropods studied here, with only one or two exceptions, all consist of the same form of calcium carbonate (aragonite).
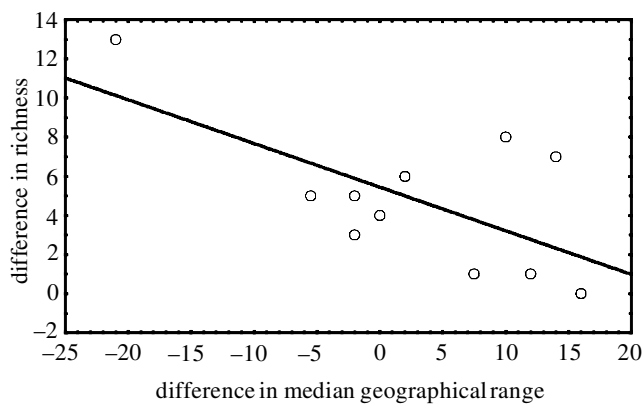
Figure 3. Geographical range and present-day species richness in marine molluscan clades, plotted as the difference in species richness versus the difference in the median geographical ranges (in degrees latitude) of their constituent species for each pair of sister groups. The inverse relation (Pearson's $r = -0.68$, $p = 0.02$) remains but becomes non-significant in a rank-order analysis (Spearman's $R = -0.45$, $p = 0.17$), or when the outlier in the upper left corner is omitted (Pearson's $r = -0.31$, $p = 0.38$). Taxa and sources: *Adelphitectonica* versus *Architectonica* s.s., Bieler (1993); *Littorina* s.s. versus *Neritrema*, Reid *et al.* (1996); *Tegula*, Hellberg (1998); (*Lirastrombina* + *Spiralta*) versus (*Strombina* + *Recurvina* + *Costangula*), Fortunato (1998); *Helcion* versus *Cymbula*, Koufopanou *et al.* (1999); *Acanthinucella* versus *Nucella*, Marko & Vermeij (1999); *Littoraria* (*Littorinopsis*) versus *L.* (*Palustorina*) versus 'clade 6', Reid (1999); *Chionopsis* s.s. versus *Puberella*, Roopnarine (2001).

Shell size is another factor known to influence preservation and sampling, but exclusion of Cretaceous gastropod genera where the median size of species is less than 1 cm only strengthens the relations reported here. These results are also unlikely to be artefacts of spatially restricted sampling, because we obtained similar results in both the palaeontological analyses (which are biogeographically localized, albeit on scales of thousands of kilometres), and in the sister-group comparisons (which are effectively global). *Accumulation* of species within a province may be a different process from the global increase in species numbers via speciation into distant provinces, but our results are consistent in both province-based and global analyses.

Although only the extant species could be analysed in an explicit phylogenetic framework, the results from the larger palaeontological dataset are unlikely to be phylogenetic effects. The genera in each quadrant of figure 1*a* are drawn from a wide range of distantly related families, so that the pattern is unlikely to be driven by the intrinsic characteristics of individual clades. For example, the upper quartile of the geographical-range distribution in figure 1*a* is occupied by species belonging to 26 families, and the lower quartile by species belonging to 24 families, most of which also occur in the upper quartile.

Our results, therefore, corroborate the idea that factors imparting broad geographical ranges also tend to damp speciation rates. Those factors are probably an amalgam of dispersal abilities, environmental tolerances and biotic interactions. Positive linkages among broad geographical range, larval dispersal ability inferred from early ontogen-

etic stages, and low speciation rates have been documented in several biogeographical and palaeontological analyses of marine gastropods (Scheltema 1977, 1989; Hansen 1982; Jablonski 1986, 1995, and references therein; Gili & Martinell 1994). Although exceptions exist, the positive relations among dispersal, gene flow and geographical range are generally well supported for marine and terrestrial taxa (Pechenik 1999; Bohonak 1999; Kittiwattanawong 1999), and there is increasing evidence from marine taxa that species with limited dispersal capabilities tend to show more spatial structuring in phylogeographical data compared with those with planktonic larvae (Hellberg *et al.* 2001; Collin 2001).

The relations among geographical range, dispersal, speciation and species richness may be different in terrestrial systems, given their many contrasts with marine systems (see, for example, Jablonski *et al.* 2003). However, Cowling & Holmes (1992) and Oakwood *et al.* (1993) discuss botanical results consistent with those presented here, although the mechanisms remain unclear and other authors argue that greater dispersal enhances taxon richness in plants (see Chown 1997).

The relatively weak relation between geographical range and total number of species produced over time, or species richness at any one time, is not surprising. Restricted species tend to have shorter durations, so that many die young and leave few descendants, but some will be in lineages that persist via rapid turnover and high speciation rates (Gould & Eldredge 1977). This can be seen in figure 2, and helps to explain the scatter at the left side of figure 1*b,c*. One sampling effect that we cannot remove analytically is the under-representation of the rarest and most spatially restricted species in the palaeontological data (Raup 1979; Jablonski 1995). If these most-restricted species are even more ephemeral than the shortest-ranging species captured by palaeontological sampling, as seems probable, then their extinction probability may exceed their speciation probability. Adding them to figure 1*a* would thus probably produce a downturn of the relation between speciation rate and geographical range at the lowest ranges, resulting in a peaked function such as that suggested by Gaston & Chown (1999). It will be difficult, however, to test this suggestion empirically by probing beyond the palaeontological 'veil line'.

5. CONCLUSIONS

All other factors being equal, speciation rate might be a positive function of geographical range. However, all factors are not equal, and our results from both living and fossil molluscs suggest that for these groups at least, the factors that impart broad geographical ranges also tend to damp speciation rates. A positive relation between origination and extinction rates has often been observed in palaeontological data (Stanley 1979, 1990; Van Valen 1985; Gilinsky 1994; Sepkoski 1998; Kammer *et al.* 1998), and may be a general rule. Obviously, exceptions where extinction exceeds origination will not persist, and exceptions where origination significantly outstrips extinction must yield diversification. Testing whether the relations documented here are maintained during major diversification episodes would bring a much-needed spatial dimension to such macroevolutionary analyses.

We also find that neither the total number of species produced through time, nor the number of species within a single time interval, is a positive function of the geographical ranges of species in a clade. The weak or non-significant correlations seen in the Cretaceous dataset, despite the highly significant results regarding speciation rate, show how poorly analyses based solely on species richness may capture one of the critical parameters in clade dynamics, i.e. the per-taxon speciation rate. Integration of palaeontological and neontological analyses is thus an essential approach to addressing many macro-evolutionary and macroecological questions.

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