

## On the bidirectional relationship between geographic range and taxonomic duration

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**Abstract.**—Geographic range and taxonomic duration are known to be positively correlated in a number of biologic groups; this is usually attributed to the influence of range upon duration rather than the other way about. Here we analyze two distinct components of this correlation within species and genera of marine invertebrates and microfossils by partitioning the total duration into two parts: the time it takes a taxon to attain its maximum geographic range, and the time a taxon persists after attaining its peak range. We find that the longer it takes a taxon to attain its maximum geographic range, the wider is that range. We also find that the broader the maximum range, the greater is the duration after this maximum is attained. These two correlations are equally strong on average. There is thus a reciprocal relationship between duration and geographic range, and there is no compelling evidence that range generally determines duration more or less than duration determines range.

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Accepted: 2 July 2008

### Two Aspects of the Range-Duration Relationship

Since the pioneering work of Simpson (1944), understanding taxonomic differences in the geologic durations of species and genera has been a central problem in paleobiology. The factor that stands out most consistently as a correlate of duration is geographic range: genera and species with broader geographic ranges tend to be longer lived (Jablonski 2005, 2008; Kiessling and Aberhan 2007; Powell 2007). In most paleontological work, the underlying assumption, sometimes tested explicitly (Jablonski 1987) or supported with biological arguments (Powell 2007), is that range determines duration, rather than vice versa (Hansen 1980; Martinell and Hoffman 1983; Jablonski 1986a; Budd and Johnson 2001; Harnik 2007; Liow 2007). This assumption should most obviously hold when we assess ranges over a relatively brief interval of time and compare them with survival versus extinction in some immediately ensuing event (e.g., Foote 2003; Rode and Lieberman 2004; Payne and Finnegan 2007; and summary in Jablonski 2005: Table 1), or when we compare present-day geographic range with an assess-

ment of extinction risk (e.g., McKinney 1997; Purvis et al. 2000).

The causal relationship between range and duration is less obvious when we consider the overall duration of a taxon in relation to the geographic range it attains over its entire lifetime. There are, in principle, at least two components to the relationship: (1) The longer a taxon persists, the more time it has to spread geographically (Willis 1922). Although this idea, based originally on distributions of living taxa, was initially quite controversial (see Willis 1926), it has been supported by a few paleontological studies (Miller 1997; Foote et al. 2007; Liow and Stenseth 2007). In the spirit of Willis (1922) and Miller (1997), we will refer to this as the *age-and-area* effect. (2) The broader the geographic range at some point in time, the greater the future duration, presumably because wider-ranging taxa are not so susceptible to local or regional environmental perturbations or to the demographic effects of population fragmentation and stochastic fluctuations in abundance (Jackson 1974; Stanley 1979: p. 260; Jablonski 2005; Powell 2007). We will refer to this as the *buffering* effect.

When we consider a group of species, what is the relative importance of these two effects,

TABLE 1. Summary of data sets and principal results.

Group	Taxonomic level	N†	Time span
Anthozoa	Genus	247	Ordovician-Permian
Anthozoa	Genus	169	Triassic-Paleogene
Brachiopoda	Genus	880	Ordovician-Permian
Brachiopoda	Genus	135	Triassic-Paleogene
Bivalvia	Genus	159	Ordovician-Permian
Bivalvia	Genus	423	Triassic-Paleogene
Cephalopoda	Genus	175	Ordovician-Permian
Cephalopoda	Genus	357	Triassic-Paleogene
Gastropoda	Genus	215	Ordovician-Permian
Gastropoda	Genus	341	Triassic-Paleogene
Crinoidea	Genus	107	Ordovician-Permian
Bryozoa	Genus	115	Ordovician-Permian
Ostracoda	Genus	137	Ordovician-Permian
Trilobita	Genus	412	Ordovician-Permian
Foraminiferida	Species	100	60 Ma–5 Ma
Radiolaria	Species	127	45 Ma–5 Ma
Nannoplankton	Species	126	60 Ma–5 Ma
Diatoms	Species	82	35 Ma–5 Ma
Bivalvia (New Zealand)	Species	169	Bortonian-Nukumaruan
Gastropoda (New Zealand)	Species	287	Bortonian-Nukumaruan

\*, \*\*, \*\*\*  $p < 0.05$ ,  $p < 0.01$ ,  $p < 0.001$  (one-tailed).

† Number of taxa after culling.

‡ This is equal to  $T_1/T_{tot}$  (see Fig. 1).

in terms of accounting for the variation in range and duration among the species? As stated above, a good deal of paleontological literature would hold that range influences duration far more than duration influences range. To test this idea, we take advantage of recent data compilations that allow us to document temporal changes in geographic range within individual taxa and thereby assess the relative strength of two statistical correlations: (1) that between the time it takes a taxon to reach its maximum geographic range and the magnitude of that maximum; and (2) that between the maximum geographic range and the duration following the attainment of the maximum. Note that the question of the relative strength of these two associations is logically distinct from the question of whether maximal geographic range is achieved early or late in the history of a taxon (Jablonski 1987; Foote 2007b; Foote et al. 2007; Kiessling and Aberhan 2007; Liow and Stenseth 2007).

#### Data and Methods

We have analyzed data on the stratigraphic and geographic occurrences of marine inverte-

brates and microfossils from three sources: (1) Phanerozoic invertebrate genera from the Paleobiology Database (PBDB; www.paleodb.org); (2) Cenozoic molluscan species of New Zealand from the Fossil Record File (FRED; www.fred.org.nz); and (3) Cenozoic species of planktic foraminifera, radiolarians, diatoms, and nannoplankton from the Neptune database, accessed via the PBDB. The PBDB data, downloaded on 5 September 2007, are updated versions of those analyzed by Foote (2007b). Records were restricted to those of the Marine Invertebrate Research Group; subgenera were elevated to genus rank; reidentifications and senior synonyms were used; genus occurrences with specifically indeterminate names were used; and genus names modified with *aff.*, *sensu lato*, or quotation marks were omitted. In an effort to exclude records in which higher taxonomic names were inadvertently entered in the genus field, all records with *indet.* in the species field were excluded. In addition to the genus name and stratigraphic information, class name, paleolatitude, paleolongitude, and collection number were downloaded. The FRED data are the same as those studied recently by Foote et al. (2007), al-

TABLE 1. Extended.

$r_s(R_{\max}, T_{\text{tot}})$	$r_s(R_{\max}, T_1)$	$r_s(R_{\max}, T_2)$	Median scaled time (0 to 1) preceding maximum range†	Proportion of taxa with maximum range before temporal midpoint	Proportion of original taxa culled because of nonunique maximum range	Proportion of taxa so culled having maximum range of a single cell
0.33 ***	0.35 ***	0.24 ***	0.61	0.39	0.25	0.98
0.41 ***	0.19 **	0.39 ***	0.39	0.61	0.35	1.00
0.45 ***	0.35 ***	0.34 ***	0.50	0.49	0.18	0.99
0.02	-0.12	0.11	0.37	0.61	0.29	1.00
0.54 ***	0.42 ***	0.45 ***	0.54	0.48	0.24	0.98
0.29 ***	0.34 ***	0.07	0.62	0.42	0.20	1.00
0.32 ***	0.12	0.26 ***	0.58	0.46	0.26	0.98
-0.07	0.02	-0.06	0.39	0.56	0.17	1.00
0.42 ***	0.36 ***	0.32 ***	0.53	0.47	0.28	0.99
0.04	0.01	0.06	0.57	0.44	0.37	0.99
0.34 ***	0.19 *	0.17 *	0.39	0.51	0.33	1.00
0.37 ***	0.33 ***	0.29 ***	0.51	0.47	0.24	1.00
0.16 *	0.16 *	0.06	0.39	0.53	0.28	1.00
0.32 ***	0.15 **	0.23 ***	0.58	0.45	0.14	1.00
0.65 ***	0.33 ***	0.69 ***	0.41	0.62	0.33	0.78
0.20 *	-0.03	0.33 ***	0.48	0.51	0.37	0.92
0.39 ***	0.24 **	0.39 ***	0.45	0.55	0.37	0.96
0.34 ***	0.40 ***	0.18	0.37	0.61	0.42	0.92
0.25 ***	0.22 **	0.16 *	0.58	0.45	0.03	1.00
0.20 ***	0.20 ***	0.15 **	0.58	0.44	0.01	1.00

though our culling methods are different herein and we have undertaken additional taxonomic vetting to remove all occurrences with uncertain species identifications. The Neptune data, updated versions of those analyzed by Liow and Stenseth (2007), were downloaded 5 November 2007. Only resolved, valid taxa were used, and the sample number, sample age, latitude, and longitude were recorded.

Data from the PBDB were resolved largely to global stages (Foote 2007b), FRED data were resolved to New Zealand stages (Cooper 2004; Foote et al. 2007), and Neptune data were resolved to million-year time bins. Temporal variation in range cannot be assessed for taxa that are confined to a single time bin. Only taxa with a range of two or more stages (PBDB and FRED) or 2 Myr or more (Neptune) were therefore analyzed. Because of low stratigraphic resolution in the Cambrian, we confined our PBDB analysis to post-Cambrian taxa. We also analyzed Paleozoic and post-Paleozoic data separately. For the FRED and Neptune data, we omitted taxa with first appearances in the earlier intervals of time in which data are sparse (pre-Bortonian for FRED, and prior to between 35 Ma and 60 Ma for Neptune, depending on the taxonomic

group; see Table 1). In order to study the full history of taxa, we included only those taxa with last appearances sufficiently old that we can be reasonably confident they are extinct (through the Paleogene for the PBDB, through the Nukumaruan Stage, i.e., roughly through the Pliocene, for FRED, and through 5 Ma for Neptune). We analyzed higher taxonomic groups, generally phylum- or class-level, separately and (except for diatoms) we included only those groups with 100 or more taxa. All group assignments were based on information in the relevant databases. Unassigned taxa, relevant only to the PBDB, were omitted. The resulting numbers of taxa and spans of time covered are given in Table 1.

Paleolatitude and -longitude for the PBDB data were taken from the PBDB, which uses Christopher R. Scotese's (2008) reconstructions. For the Neptune data, age assignments and present-day latitude and longitude were used to estimate past coordinates. These rotations were kindly carried out by David B. Rowley (personal communication 2007). New Zealand reconstructions are sufficiently uncertain, relative to the comparatively small geographic scale of this region (King 2000), that we would regard the estimation of past

coordinates as spuriously precise. We therefore deem it conservative to use present coordinates for the New Zealand data. One possible bias in using present coordinates is that geographic ranges may be exaggerated more for older than for younger taxa (Foote et al. 2007). The concordance between results based explicitly on geographic range and those based simply on the number of collections suggests that this bias is not dictating the patterns we see in New Zealand molluscs (see below; also Foote et al. 2007).

We measured geographic range as the number of equal-area grid cells,  $N_{ij}$ , occupied by taxon  $i$  in time interval  $j$ . We favor this measure of range because it combines the gross areal extent with the completeness of occupancy within that extent. For the PBDB and the Neptune data, we started with a Lambert cylindrical equal-area projection of the globe with a primary latitude at  $0^\circ$  and then used 100 latitudinal and 100 longitudinal divisions. Each of the resulting 10,000 cells has an area of about 51,000 km<sup>2</sup>, roughly the size of a  $2^\circ \times 2^\circ$  cell at the equator. For the New Zealand data, the cells correspond to standard 1:50,000 topographic map sheets, each of which is about 1200 km<sup>2</sup> in area, with negligible variance among the maps.

To account for temporal variation in the spatial coverage of data, we scaled ranges relative to the maximum possible for time interval  $j$ , given the total number of grid cells ( $N_{totj}$ ) occupied by at least one collection in the corresponding data set. We are interested in the realized coverage of a taxon relative to its potential, and we are comparing taxa that lived at different times, represented by data that vary in quantity and spatial extent. This scaling is therefore appropriate whether the temporal variation in amount and extent of data reflects primarily what is preserved and sampled, or primarily the actual habitable space available to species at times in the past. We nonetheless find compatible results with unscaled data (Appendix). Because the total number of cells occupied varies among time intervals, the minimum possible scaled range (i.e., that corresponding to a single cell) varies considerably. We therefore subtracted the minimum possible range to achieve a new scaled range with a minimum at zero. Thus,

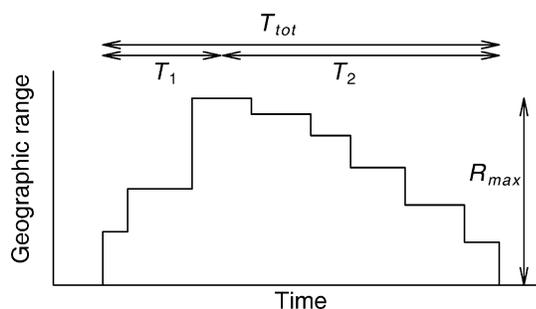


FIGURE 1. Protocol for partitioning duration of taxon ( $T_{tot}$ ) into components preceding ( $T_1$ ) and following ( $T_2$ ) the time of attainment of maximal geographic range ( $R_{max}$ ).

$R_{ij} = (N_{ij} - 1) / N_{totj}$ , where  $R_{ij}$  is the range of taxon  $i$  in time interval  $j$ . For each taxon we then determined its maximum scaled geographic range,  $R_{max}$ , and we omitted taxa in which the maximum range is repeated in more than one time interval. The proportion of taxa removed because of this last protocol varies from group to group, but in the great majority of cases these taxa with multiple maxima are sparsely distributed and do not vary in geographic range, being known from at most a single grid cell in any given time interval (see the last two columns of Table 1).

We tabulated the total stratigraphic range of each taxon ( $T_{tot}$ ), from the base of the interval of first appearance to the top of the interval of last appearance, as well as the time preceding the maximum ( $T_1$ ), from the base of the interval of first appearance to the midpoint of the interval of peak range, and the time following the maximum ( $T_2$ ), from the midpoint of the interval of peak range to the top of the interval of last appearance (Fig. 1). These protocols assume that originations and extinctions are concentrated at the beginnings and ends of stages, an assumption that appears to be consistent with both the PBDB and New Zealand data (Foote 2005; Crampton et al. 2006). Numeric ages for stage boundaries are based on Gradstein et al. (2004; see Foote 2007b) for global stages and on Cooper (2004) for New Zealand stages.

For each group, we calculated the Spearman rank-order correlation  $r_s$  between  $R_{max}$  on the one hand and  $T_{tot}$ ,  $T_1$ , and  $T_2$ , on the other hand. All calculations were carried out in the R programming environment (R Development Core Team 2007). Although the magnitude of

these correlations could in principle be inflated because the taxa are phylogenetically related and therefore not statistically independent (Felsenstein 1985), we are mainly interested in comparing pairs of correlation coefficients within a given group, and we would expect these correlations to be similarly influenced by phylogenetic effects. We will return to this problem below for one group in which we can take phylogenetic information into account explicitly.

*Testing for Sampling Artifact.*—It is possible in principle for a positive association between range and duration to be an artifact if better-sampled taxa have spuriously wider ranges and spuriously longer durations merely because they are more completely sampled (Jablonski 1988; Russell and Lindberg 1988). To assess this possibility, we estimated the per-time-interval sampling probability for each taxon, using a modification of the standard gap statistic (Paul 1982; Foote and Raup 1996) proposed by John Alroy (in press). To mitigate the effects of gaps created by spuriously long ranges that result from misidentification and other taxonomic errors, we follow Alroy in determining, for each species in each time interval, whether it is sampled in the intervals *immediately* before and *immediately* after. The total sum of such instances ( $S_{\text{potential}}$ ) represents the net number of opportunities for sampling. We then tabulated the number of such instances in which the taxon is also sampled in the intervening time interval ( $S_{\text{actual}}$ ). For each taxon, the estimated sampling probability ( $P$ ) is then simply  $S_{\text{actual}}/S_{\text{potential}}$ . For example, suppose a species ranges from time intervals 1 through 5, and is sampled in intervals 1, 3, 4, and 5. Then there are two intervals (2 and 4) for which it is sampled immediately before and after, and it is actually sampled in one of these two intervals (number 4). Its estimated sampling probability would therefore be 0.5. Like the conventional gap statistic, this statistic by its very nature can be calculated only for taxa with durations of three or more time intervals.

If three variables are interrelated, the nature of the relationship can be misunderstood if only two of the variables are analyzed. Under the artifact hypothesis,  $P$  directly affects both  $R_{\text{max}}$  and  $T_{\text{tot}}$  but  $R_{\text{max}}$  and  $T_{\text{tot}}$  are not directly associated.

If this hypothesis were true we would expect to find a substantial correlation between  $R_{\text{max}}$  and  $T_{\text{tot}}$  but a diminished partial correlation between these two variables, with the effects of sampling ( $P$ ) held fixed. We therefore compared raw and partial correlations to determine whether they are consistent with the expectations of the artifact hypothesis.

## Results

*Total Geologic Duration.*—Nearly all groups (19 of 20) show a positive correlation between  $R_{\text{max}}$  and  $T_{\text{tot}}$  and this relationship is statistically significant at  $p < 0.05$  (one-tailed) in most cases (17 of 19) (Table 1). These results are thus in accord with the previously documented correlation between range and duration in many groups that have been studied. The one negative correlation, for post-Paleozoic cephalopods, is statistically indistinguishable from zero.

The correlation between  $R_{\text{max}}$  and  $T_{\text{tot}}$  is not substantially weaker when sampling ( $P$ ) is explicitly taken into account (Fig. 2); if anything, the partial correlations are slightly higher than the raw correlations because of slight negative correlations between  $P$  and  $T_{\text{tot}}$ , the nature of which is not entirely clear (for a similar negative correlation, see Powell 2007: p. 535). (Note that fewer of the correlations between  $R_{\text{max}}$  and  $T_{\text{tot}}$  are significant here than in Table 1. This largely reflects the fact that the analyses in Figure 2 necessarily exclude taxa with durations of two time intervals, and therefore have smaller sample sizes and reduced statistical power. The average correlations are about the same, however, with 11 of 20 values greater in Figure 2 than in Table 1 and the two means equal to 0.31 and 0.30.) From this analysis we conclude that sampling is not a major determinant of the relationship between geographic range and total duration.

*Time Preceding Maximum Range versus Time Following Maximum Range.*—In most groups, there is a positive correlation between  $R_{\text{max}}$  and both  $T_1$  and  $T_2$  (18 of 20 for  $T_1$  and 19 of 20 for  $T_2$ ), and this association is statistically significant at  $p < 0.05$  (one-tailed) in 15 of 18 cases for  $T_1$  and in 14 of 19 cases for  $T_2$  (Table 1, Fig. 3). Some associations are negative, but none of these are statistically distinguishable

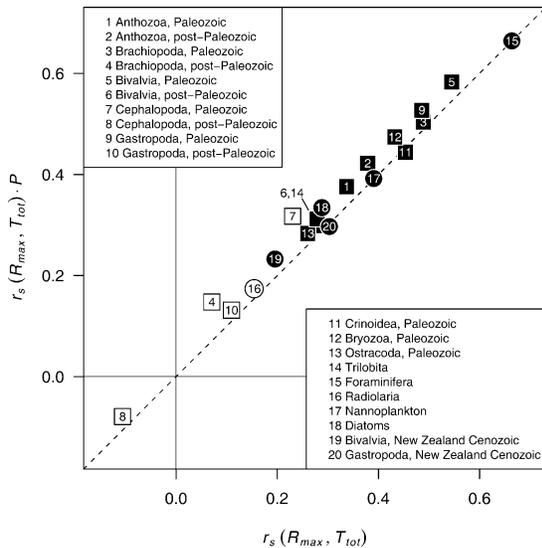


FIGURE 2. Comparison of correlation between maximum geographic range and total duration when sampling is ignored versus included as a factor. Square symbols: genera. Round symbols: species. Black symbols denote effects that are statistically significant at  $p < 0.05$  (one-tailed), based on Spearman rank-order correlation between  $R_{\max}$  and  $T_{\text{tot}}$ . Abscissa, correlation between  $R_{\max}$  and  $T_{\text{tot}}$ . Ordinate, partial correlation between  $R_{\max}$  and  $T_{\text{tot}}$  with sampling ( $P$ ) held fixed. Correlation is not diminished when sampling is partialled out, implying that the association between  $R_{\max}$  and  $T_{\text{tot}}$  does not result simply from each of these factors being driven independently by sampling.

from zero. The relative strength of the two associations, which we take as proxies for the age-and-area effect and the buffering effect, is assessed by comparing the correlations between  $R_{\max}$  and  $T_1$  and between  $R_{\max}$  and  $T_2$ . The line of isometry in Figure 3 denotes equal strength of the two correlations; points below and above the line indicate greater strength of the age-and-area and buffering effects, respectively. Large points in Figure 3 indicate cases in which the two correlations differ significantly at  $p < 0.05$  (two-tailed), using the normal approximation to the rank-order correlation with an estimated standard error of  $(N - 1)^{-0.5}$  (Siegel and Castellan 1988: p. 243). (We obtain similar results if we estimate the standard error via bootstrap resampling [Efron and Tibshirani 1993].) Of the four cases in which at least one correlation is significant and the difference between them is also significant, three differences are positive (post-Paleozoic Anthozoa, Foraminiferida, and Ra-

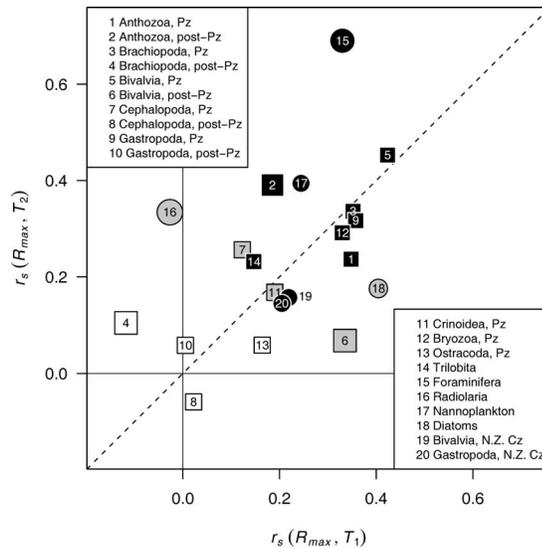


FIGURE 3. Correlations between maximal geographic range ( $R_{\max}$ ) and the time taken to attain this range ( $T_1$ , abscissa) and between maximal geographic range ( $R_{\max}$ ) and the duration after the attainment of this range ( $T_2$ , ordinate). The dashed diagonal line is the line of isometry. Points above and below this line indicate greater strength of the buffering and age-and-area effects, respectively. Square symbols, genera. Round symbols, species. Black symbols, both associations significant at  $p < 0.05$  (one-tailed). Gray symbols, one association significant. White symbols, neither association significant. Large symbols indicate cases in which the two correlations are significantly different from each other. Neither association is generally stronger, implying that the age-and-area effect and the buffering effect are of equal importance on average.

diolaria) and one is negative (post-Paleozoic Bivalvia). On the whole, there is no clear tendency for one effect to be stronger or weaker than the other.

To test the robustness of these results, we tabulated two additional measures: (1) occupancy, i.e., the proportion of collections (PBDB and FRED) or samples (Neptune) in a given time interval in which a given taxon is found, scaled exactly as the number of grid cells so that the minimum possible occupancy is zero; (2) convex-hull area (for the PBDB and Neptune data sets) and maximum great-circle distance between occurrences (for the New Zealand data). Convex-hull areas were estimated by first projecting the data onto a cylindrical Lambert equal-area projection, and then constructing the convex hull around the projected points in the plane. We used the great-circle distance for the New Zealand data because it

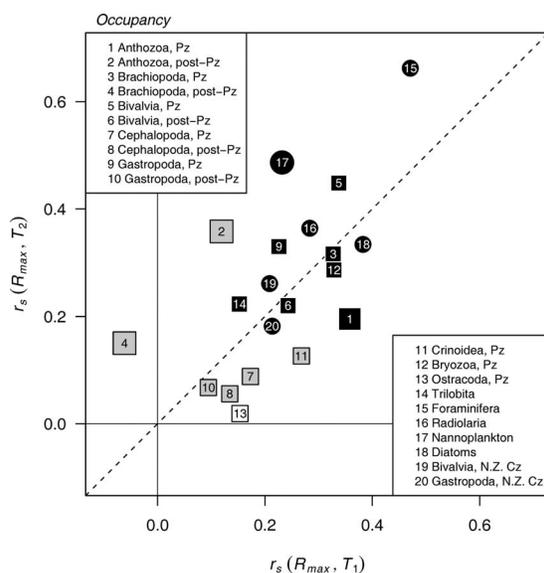


FIGURE 4. Correlations between  $R_{\max}$  and  $T_1$  and between  $R_{\max}$  and  $T_2$ , using occupancy to measure geographic range. See Figure 3 for explanation of symbols.

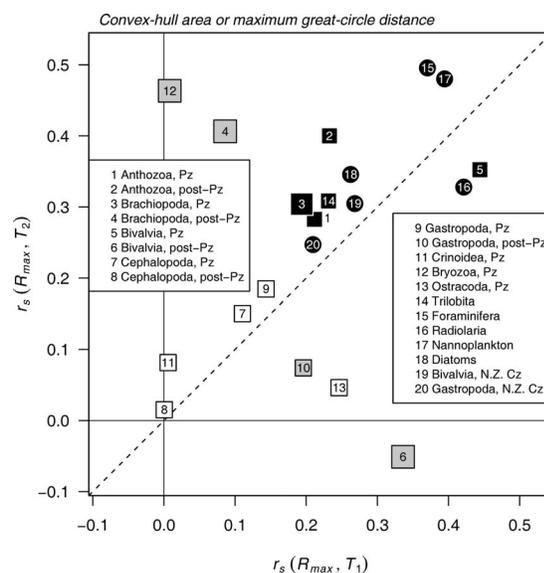


FIGURE 5. Correlations between  $R_{\max}$  and  $T_1$  and between  $R_{\max}$  and  $T_2$ , using maximum great-circle distance (New Zealand molluscs) or convex-hull area (other data sets) to measure geographic range. See Figure 3 for explanation of symbols.

is reasonable given the roughly linear distribution of outcrop, and because it allowed the inclusion of more taxa (only two occurrences are required to measure a distance, whereas three are required to measure an area). Each measure was scaled to the maximum possible for the given time interval, based on the total spatial extent of collections in that interval. The results of these additional analyses, summarized in Figures 4 and 5, are compatible with those in which the number of grid cells is used to assess geographic range. There is a greater tendency for the correlation between  $R_{\max}$  and  $T_2$  to exceed that between  $R_{\max}$  and  $T_1$  when range is measured by area or distance (Fig. 5), but we hesitate to assign much biological significance to this tendency since it is not matched by other measures of range, nor is it evident in the unscaled data (Appendix).

How should mass extinctions affect these results? Because taxa may be truncated at broad geographic range by mass extinction events (Jablonski 1986b; Foote 2007b; Payne and Finnegan 2007), it is possible that the general magnitude of the buffering effect is underestimated by the inclusion of mass extinctions in the analysis. At the same time, if taxa become extinct while they are increasing in geographic range, the age-and-area effect may

be diminished. To explore these possibilities, we conducted a separate analysis in which we excluded all taxa that last appear in the “Big Five” mass extinction events (end-Ordovician, Frasnian/Famennian, end-Permian, end-Triassic, and end-Cretaceous). Because the FRED and Neptune data used here are Cenozoic only, this analysis was restricted to the PBDB genera. The results (Fig. 6) are similar to those of the main analysis, although there is a slight tendency for the relative strength of the age-and-area effect to be enhanced when we ignore the genera that disappear in the major mass extinctions.

## Discussion

In the majority of groups studied here, the time a taxon has in which to spread is a significant predictor of the maximum geographic range it ultimately attains, and this range is in turn a significant predictor of how much longer it endures. Perhaps these results are not surprising, but they are noteworthy because most paleontological literature on geographic range and duration has tacitly or explicitly posited a particular direction of causality, i.e., range giving rise to duration (Hansen 1980;

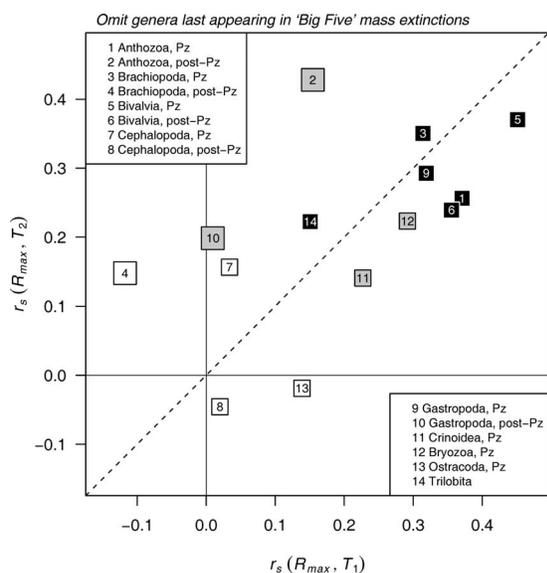


FIGURE 6. Correlations between  $R_{\max}$  and  $T_1$  and between  $R_{\max}$  and  $T_2$ , omitting genera that disappear in the major mass extinctions. See Figure 3 for explanation of symbols. A priori, mass extinctions might be expected to distort evidence for both the age-and-area and the buffering effects. The equal importance of these effects is evident in the data irrespective of whether we include genera that last appear in the major mass extinctions.

Martinell and Hoffman 1983; Jablonski 1986a; Budd and Johnson 2001; Liow 2007). We do not cast doubt on this direction of causality—in fact we confirm it—but we also show that it is only half the story. When we consider the whole story, we find that the two aspects of the relationship are about equally important on average. Of course, it is possible in principle that range and duration are not directly related causally but instead are independently governed by some third factor that we have not considered. Although we have ruled out the possibility that the quality of sampling could be the third factor, other possibilities should also be entertained (Harnik 2007).

Rapid range shifts of living species (Gaston 2003) have been used to support the idea that geographic range determines duration rather than vice versa (Powell 2007). Although we accept this logic, we cannot overlook the fact that range expansion and contraction in the fossil record are drawn out over millions of years. We have previously suggested that the apparent discrepancy can be resolved if species rapidly occupy the geographic and eco-

logical space available to them, but that what is available is governed by slowly varying geological processes (Foote et al. 2007; see also Powell 2007: p. 543).

Given our previous results showing approximate symmetry of average geographic-range histories (Foote 2007b; Foote et al. 2007), one might have supposed that the age-and-area and buffering effects must necessarily be equally strong, but they need not be. The salient issue here is the relative variation in  $T_1$  and  $T_2$  and how it correlates with variation in  $R_{\max}$ . Irrespective of the *average* values, we would like to know whether *individual* taxa that have lower or higher than average values of  $T_1$  or  $T_2$  have corresponding deviations in  $R_{\max}$ , and whether the paired deviations between  $T_1$  and  $R_{\max}$  are similar to those between  $T_2$  and  $R_{\max}$ . That these paired deviations need not be similar, even if average histories are symmetric, can be seen with a hypothetical case of four species having durations of 3, 4, 5, and 6 time intervals and the following range histories, respectively: (1) 0.033, 0.067, 0.10; (2) 0.067, 0.133, 0.20, 0.1; (3) 0.1, 0.2, 0.3, 0.2, 0.1; (4) 0.133, 0.267, 0.4, 0.3, 0.2, 0.1. Of the individual species, the first two are top-heavy, the next is symmetric, and the last is bottom-heavy. In this example, there is no variation in  $T_1$ ;  $R_{\max}$  varies by a factor of four; and  $T_2$  is linearly proportional to  $R_{\max}$ . Thus there is no correlation between  $T_1$  and  $R_{\max}$ , and there is a perfect correlation between  $R_{\max}$  and  $T_2$ . If, however, each species' duration is scaled to unit length and the average range history is calculated (in the manner of our previous analyses [Foote 2007b; Foote et al. 2007]), this history is nearly symmetric.

Symmetry and the relative strength of the two effects are not only logically distinct; our results show that they are largely distinct empirically as well. The rank-order correlation between the difference  $[r_s(R_{\max}, T_2) - r_s(R_{\max}, T_1)]$  and the median scaled time of maximum range ( $T_1/T_{\text{tot}}$ ) is negative. This correlation suggests that a tendency to reach maximum range early might be a fair proxy for the relative strength of the buffering effect. However, the correlation is not statistically significant ( $r_s = -0.24$ , one-tailed  $p = 0.16$ ). Moreover, Table 1 shows that, of eleven groups

with a stronger age-and-area effect, four consist of taxa that tend to reach maximum range *before* their temporal midpoint, and that, of nine groups with a stronger buffering effect, five consist of taxa that tend to reach a maximum *after* their temporal midpoint.

Earlier we raised the question of whether the correlation between range and duration could be exaggerated by non-independence of observations, reflecting phylogenetic relatedness. As a preliminary exploration of this problem, we have analyzed geographic range for 52 postulated sister-species pairs of New Zealand gastropods, based on ongoing systematic work by one of the authors (AGB; see Beu et al. 1990). These sister-species pairs are tentative and likely to be revised in the future, but the salient point is that the postulated relationships are based on morphology rather than geographic range. We calculated the correlations among  $R_{\max}$ ,  $T_{\text{tot}}$ ,  $T_1$ , and  $T_2$  for the subset of species that constitute our sister-species pairs, and we then calculated the correlations among the phylogenetic contrasts in these variables, i.e., the difference between each pair of sister species (Felsenstein 1985). The correlations are all positive, albeit not significant in every case. Moreover, correcting for phylogenetic relatedness substantially increases the correlation in two of three cases (for species treated as independent:  $r_s(R_{\max}, T_{\text{tot}}) = 0.16$ ,  $p = 0.067$ ;  $r_s(R_{\max}, T_1) = 0.12$ ,  $p = 0.15$ ;  $r_s(R_{\max}, T_2) = 0.26$ ,  $p = 0.0082$ ; for phylogenetic contrasts:  $r_s(R_{\max}, T_{\text{tot}}) = 0.34$ ,  $p = 0.0071$ ;  $r_s(R_{\max}, T_1) = 0.22$ ,  $p = 0.055$ ;  $r_s(R_{\max}, T_2) = 0.25$ ,  $p = 0.040$ ; all tests one-sided). From this we conclude that, at least for the one group where we have the means to conduct the test, the correlation between range and duration is not likely to be an artifact of the phylogenetic relatedness, and resulting lack of statistical independence, among species. It is worth noting in passing that the lower correlations in the “uncorrected” data compared with the phylogenetically “corrected” data are consistent with simulation results reported by Rohlf (2006). Similarly, in studying survivorship of Plio-Pleistocene pectinid bivalves from California, Roy and Smith (2006) detected no extinction selectivity with respect to body size when they combined all species into a single

analysis, but they found preferential survival of larger-bodied species when they analyzed their data genus by genus.

This study has been exploratory in nature, motivated largely by recent work on systematic variation in geographic range within the history of species and genera (Jernvall and Fortelius 2004; Foote 2007b; Foote et al. 2007; Kiessling and Aberhan 2007; Liow and Stenseth 2007) that has led us to question the common working assumption that geographic range determines taxonomic duration rather than vice versa. Knowing now that the causal relationship between range and duration is reciprocal in many cases, we consider some implications of these results and point to some observations that deserve further attention.

It is important first to emphasize that our results, and others demonstrating systematic variation in geographic range within the history of species (Foote et al. 2007; Liow and Stenseth 2007), do not contradict previous demonstrations of the heritability of geographic range (e.g., Jablonski 1987; Hunt et al. 2005; Jablonski and Hunt 2006; see Jablonski 2008), which were tied in part to arguments that geographic range is attained early in a species’ history (Jablonski 1987). It is certainly possible in principle for geographic range to vary greatly through the lifetime of a species and for closely related species nonetheless to have similar characteristic ranges.

Methodologically, an important implication of our results is that it is not generally appropriate to treat geographic range as an independent variable and taxonomic duration as a dependent variable in macroecological and macroevolutionary studies—the clear exception being the effect of geographic range within a relatively short time interval on the chances of extinction through a comparatively discrete event (e.g., Jablonski 1986b, 2005). The feedback between these two variables implies that simple linear models may fall short. Our approach of breaking the duration into two components represents just one possible way to handle the problem, and it is admittedly oversimplified. We have divided each taxon’s history into a waxing and waning phase, but there is the potential for feedback between range and duration at every increment of time

within each phase, so that both age-and-area and buffering are likely to be at work throughout the lifetime of each taxon.

If, as we suppose, this feedback is ongoing throughout a taxon's life span, we would suggest that the reciprocal nature of range and duration has the potential to amplify small, perhaps stochastic, differences among taxa. Up to a point, enduring longer leads to a wider range, which in turn contributes further to enhanced duration. This is very much like the situation with species richness in homogeneous branching models (Raup 1985; Foote 2007b: Appendix). Clades that live longer tend to accumulate more species, which in turn makes them more resistant to extinction. But nothing lasts forever, and small decreases in species richness and range can also be amplified as taxa drift to extinction.

Our discussion of age-and-area and buffering effects may sound incompatible with the possibility that individual taxa follow random walks in geographic range (with absorbing boundary at zero), but these effects, as well as symmetric average histories, are exactly what one would expect with a random walk, provided that only extinct taxa are considered (Foote 2007b). Under this model, the longer a taxon persists, the greater a geographic range it will attain on average, and the greater the peak range, the longer it will take to drift to zero. In other words, the random walk model does not mean that there is no causal relationship between range and duration; quite the contrary, this causal relationship emerges naturally from it. So, the random walk model predicts equally strong age-and-area and buffering effects, and this is exactly what we see. This agreement, however, does not necessarily mean that individual taxa are in reality following such a model, because other processes can also give rise to similar large-scale patterns. We are currently testing alternatives and hope to report on the results in a future contribution.

One last result worth mentioning is that, within four of five higher taxa in which Paleozoic and post-Paleozoic genera were analyzed separately, the strength of the relationship between geographic range and duration (whole or part) is greater in the Paleozoic than the

post-Paleozoic. In these four groups, this difference is robust and not sensitive to the measure of geographic range (Table 1; also, compare points 3 versus 4, 5 versus 6, 7 versus 8, and 9 versus 10 in Figs. 2–5). With three measures of geographic range and three correlations (between maximum range on the one hand and the total duration, time preceding the maximum, and time following the maximum on the other hand), there are nine measures of range-duration correlation for each higher taxon, although these measures are not independent of each other. The great majority of measures indicate a stronger association in the Paleozoic: eight of nine for Brachiopoda; nine of nine for Bivalvia; eight of nine for Cephalopoda; and eight of nine for Gastropoda. Foote (2007b: Fig. 7) previously found that occupancy, based on the number of collections in which a genus is found, varied less within the durations of post-Paleozoic genera, and speculated on why this might be. We can offer no compelling explanation for the new results, which add to the growing body of cases in which paleoecological and evolutionary dynamics appear to be distinct in the Paleozoic and the Meso-Cenozoic (Bambach 1977: pp. 159–160; Sepkoski 1981, 1984; Foote 2000, 2007a,b; Miller and Foote 2003; Wagner et al. 2006; Peters 2007).

### Summary

1. Geographic range of species and genera within nearly all groups of marine invertebrates and microfossils studied is significantly and positively correlated with taxonomic duration.
2. Explicit consideration of the completeness of sampling of each taxon shows that the relationship between range and duration is unlikely to be an artifact of sampling.
3. Most groups show what is reasonably interpreted as an age-and-area effect: the longer it takes a taxon to achieve its maximum geographic range, the broader is that range.
4. Most groups also show what is reasonably interpreted as a buffering effect: the broader the maximum range, the longer a taxon persists after that range is attained.
5. In general, these two effects are about equally strong. This implies that duration

influences geographic range as much as geographic range influences duration.

6. For unknown reasons, the correlations between range and duration tend to be stronger in the Paleozoic than the post-Paleozoic.

### Acknowledgments

We acknowledge the use of information contained in the New Zealand Fossil Record File. C. M. Jones and I. Matcham assisted with data preparation. We are grateful for discussions with P. G. Harnik, D. Jablonski, A. I. Miller, S. E. Peters, and M. Webster. P. G. Harnik, A. I. Miller, J. L. Payne, and M. G. Powell provided helpful reviews of the manuscript. This work was supported by the Marsden Fund (contract GNS0404) and the National Science Foundation (grant EAR0105609). M.F. is grateful for the use of facilities at GNS Science, where this work was partially carried out. This is Paleobiology Database publication number 82.

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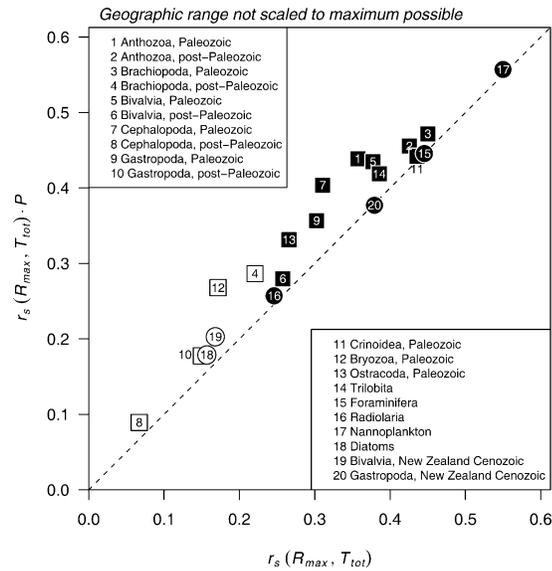
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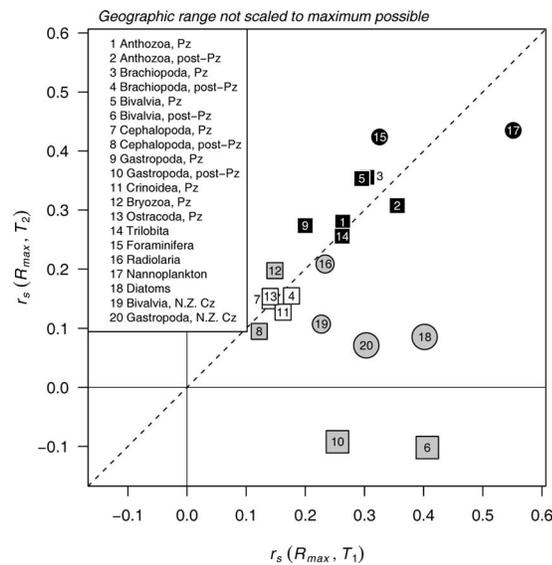
Appendix

Analysis of Unscaled Geographic Ranges

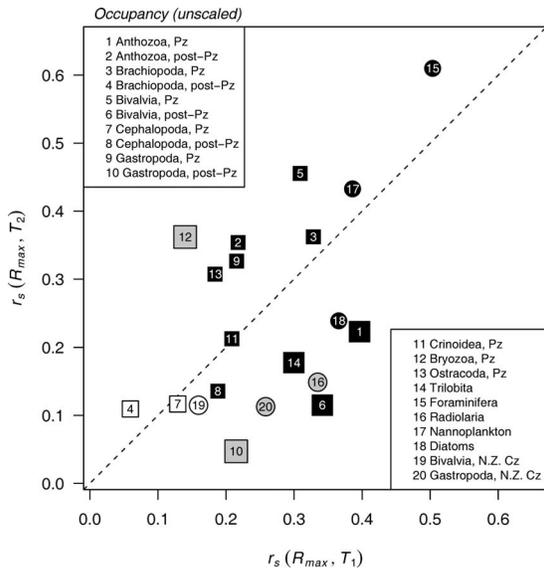
Here we present results without scaling geographic ranges to the maximum range possible in each time interval (Appendix Figs. 1–4). The results are compatible with the analysis of scaled data (Figs. 2–5).



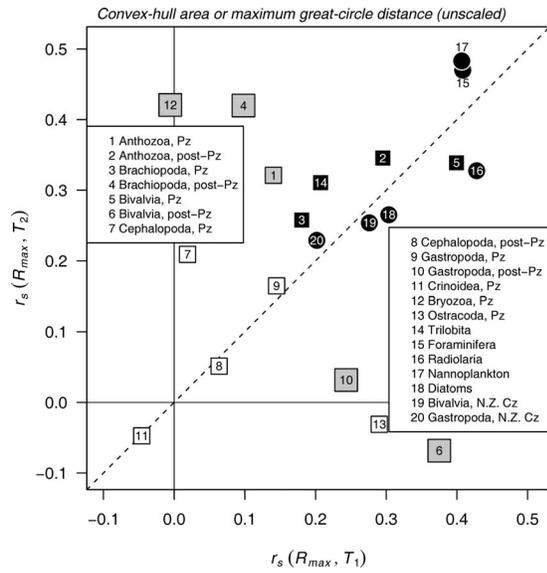
APPENDIX FIGURE 1. Correlations between maximum geographic range and total duration when ranges are not scaled to the maximum possible in each time interval. Compare with Figure 2.



APPENDIX FIGURE 2. Correlations between  $R_{max}$  and  $T_1$  and between  $R_{max}$  and  $T_2$ , when ranges are not scaled to the maximum possible in each time interval. Compare with Figure 3.



APPENDIX FIGURE 3. Correlations between  $R_{\max}$  and  $T_1$  and between  $R_{\max}$  and  $T_2$ , using occupancy to measure geographic range and not scaling ranges to maximum possible in each time interval. Compare with Figure 4.



APPENDIX FIGURE 4. Correlations between  $R_{\max}$  and  $T_1$  and between  $R_{\max}$  and  $T_2$ , using maximum great-circle distance (New Zealand molluscs) or convex-hull area (other data sets) to measure geographic range and not scaling ranges to maximum possible in each time interval. Compare with Figure 5.