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Phanerozoic trends in the global geographic disparity of marine biotas

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Abstract.—Previous analyses of the history of Phanerozoic marine biodiversity suggested that the post-Paleozoic increase observed at the family level and below was caused, in part, by an increase in global provinciality associated with the breakup of Pangea. Efforts to characterize the Phanerozoic history of provinciality, however, have been compromised by interval-to-interval variations in the methods and standards used by researchers to calibrate the number of provinces. With the development of comprehensive, occurrence-based data repositories such as the Paleobiology Database (PaleoDB), it is now possible to analyze directly the degree of global compositional disparity as a function of geographic distance (*geo-disparity*) and changes thereof throughout the history of marine animal life. Here, we present a protocol for assessing the Phanerozoic history of geo-disparity, and we apply it to stratigraphic bins arrayed throughout the Phanerozoic for which data were accessed from the PaleoDB. Our analyses provide no indication of a secular Phanerozoic increase in geo-disparity. Furthermore, fundamental characteristics of geo-disparity may have changed from era to era in concert with changes to marine venues, although these patterns will require further scrutiny in future investigations.

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Introduction

After more than a quarter-century of intensive investigation, the Phanerozoic trajectory of global marine diversity remains as a central theme in macroevolutionary investigations with respect to the relationship among diversity trends at different ecological/geographic scales and the extent of the post-Paleozoic increase exhibited at the family level and below. Depending on one's point of view, depictions of raw diversity trajectories (e.g., Valentine 1969; Sepkoski 1981; Sepkoski 1997) are biologically trustworthy (Sepkoski et al. 1981), or they grossly overestimate (Raup 1972, 1976) or underestimate (Jackson and Johnson 2001) the extent of the Cenozoic increase. Attempts to statistically correct for sampling heterogeneities among Phanerozoic stratigraphic intervals (e.g., Miller and Foote 1996; Alroy et al. 2001) have, themselves, led to concerns about the artifactual effects of secular trends in community-level attributes and even interval durations with respect to the palette of analytical methods used for these purposes (Bush et al. 2004; Stanley 2007), although Alroy et al. (2008) have recently offered a new perspective on this question.

A possible alternative to assessing global diversity trends through aggregate summation at the global level is to evaluate secular transitions at key hierarchical levels, and then to combine the contributions of each of these constituents to develop a global trajectory. Although intended for a somewhat different purpose, Sepkoski's (1988) pioneering assessment of diversity trends at the within-community (alpha) and between-community (beta) levels for the Paleozoic Era was a step in that direction. Sepkoski's analysis, however, was limited primarily to Paleozoic assemblages from the paleocontinent of Laurentia,

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with beta diversity analyzed by combining together in a single onshore-offshore ''gradient'' all of the assemblages contained within a given stratigraphic interval. The possible contribution to global diversity added by geographic differentiation among biotas was discussed by Sepkoski but not analyzed, and he downplayed the likelihood of its importance, at least for the Paleozoic, following on discussions of Paleozoic global provinciality provided by Valentine et al. (1978) and others. In the end, Sepkoski was unable to account for the significant gulf between synoptic, global diversity numbers and the summed contributions provided by his assessments at the alpha and beta levels.

The possible relationship between global biodiversity and Phanerozoic trends in global provinciality was addressed more directly by Valentine and colleagues (e.g., Valentine 1970; Valentine et al. 1978), who argued that the substantial post-Paleozoic rise in diversity at the family level and below, including a possible order-of-magnitude rise at the species level, was paralleled and fueled by an equally profound increase in the number of marine faunal provinces, associated with the breakup of the supercontinent of Pangea. More recently, however, Bambach (1990) and others have noted that Valentine's tabulations of provinciality through time, which were derived from assessments in the literature, were compromised by the use of different standards by workers who focused on different parts of the stratigraphic column.

If we assume, as seems reasonable, that there is a relationship between the degree of global provinciality and the degree of compositional similarity or disparity among biotas arrayed around the world, then we can directly quantify secular changes, if any, in global compositional disparity without attempting to designate provinces. With the development of geographically resolved, occurrence-based fossil data repositories such as the Paleobiology Database (PaleoDB; http://paleodb.org/), it is now possible to numerically assess, for marine biotas, Phanerozoic trends in *geo-disparity*, defined here as *the degree of global compositional disparity among coeval biotas as a function of geographic distance.* The purpose of this paper is to present a methodological framework for an analysis of this kind, and to provide the initial results of a Phanerozoic-scale assessment using data reposited in the PaleoDB for an aggregate set of genera belonging to a major cross-section of taxa from Sepkoski's (1981) three evolutionary faunas. Although these analyses raise several new questions in their own right, they nevertheless suggest that, on a global scale, there has *not* been a secular, global-scale increase in geo-disparity through the Phanerozoic.

Methods

Data.—Genus-level occurrence data from intervals spanning the Phanerozoic were downloaded from the PaleoDB on 17 September 2008; genera with qualified names were excluded (e.g., names preceded by ''aff.,'' ''cf.,'' ''*sensu lato*,'' or a question mark, or contained inside of quotation marks), as were informal names; taxonomic updates available in the PaleoDB were applied to genus identifications, and subgenera were elevated to genus rank.

All genera belonging to the following higher taxa were included in the downloads: Trilobita, Brachiopoda, Bivalvia, and Gastropoda. Collectively, these higher taxa provide a representative cross-section of major elements from each of Sepkoski's evolutionary faunas and are among the higher taxa most consistently cataloged throughout the Phanerozoic in the PaleoDB. Previous studies limited to similar subsets of the marine biota (e.g., Miller and Foote 1996) suggest that aggregate genus-diversity trajectories for these higher taxa capture major attributes of the Phanerozoic trajectory exhibited by the marine biota as a whole. With respect to the Cenozoic in particular, most previous analyses of diversity trajectories have been dominated overwhelmingly by bivalves and gastropods (see Bush and Bambach 2004), so the focus here on the same groups seems especially appropriate (but see later section, ''Remaining Issues and Future Work'').

Stratigraphic Binning of Collections.—In general, depictions of Phanerozoic global diversity trends in the literature are resolved stratigraphically to the level of stage or substage. Although it would obviously be desirable in the present analyses to maintain similar resolution, the coverage of data reposited in the PaleoDB at the time that they were downloaded were rather limited for some stages. As an alternative, therefore, we followed the convention of Alroy et al. (2008) and other recent studies, by using a set of PaleoDB-designated stratigraphic/temporal bins that average about 11 million years in duration (Table 1). The bins used here span the entire Phanerozoic except for the earliest Cambrian (Cambrian 1), which was not included because it does not contain sufficient data. Some of the bins encompass a single stage, but others are broader in extent. As indicated by the wide variation in the number of occurrences of genera and other sampling attributes recognized for each interval, bin-to-bin coverage in the PaleoDB is uneven. Although it is likely that some of this variability, such as the increasingly large samples for Cenozoic bins, directly mirrors the availability of material from the fossil record, other aspects, such as the small number of occurrences for some Carboniferous bins, reflect the need to further enhance the acquisition of data for these intervals. Nevertheless, as we will show below, several stratigraphic bins arrayed throughout the Phanerozoic have adequate coverage for our purposes, and those with more limited coverage do not impart unusual or unique signals with respect to the central questions addressed here.

Geographic Binning of Collections into Samples.—For all analyses presented here, PaleoDB collections (i.e., faunal lists) in a given stratigraphic interval were combined together into samples by superimposing a 5° latitude by 5° longitude grid on the global paleogeographic distribution of collections, estimated by using Christopher Scotese's *Paleomap* rotations (Scotese personal communication 2001), provided by the PaleoDB when data are downloaded. All collections occurring within a given 5° × 5° cell constituted a sample. Under the protocol used for accessing data from the PaleoDB in the present study, multiple occurrences of species for a given genus in a PaleoDB collection were not recognized, so that all genera in a collection were credited with a single occurrence. In the aggregation of collections into samples, however, genera were credited with multiple occurrences if they occurred in two or more of the collections in a 5° × 5° cell; genera that were particularly common or widespread during a given stratigraphic interval, indeed, had the propensity to occur in multiple PaleoDB collections within a single cell.

Given that the area covered by a 5° × 5° cell varies as a function of latitude, with a systematic decrease toward higher latitudes, it is important to ask whether this geographic-binning protocol might, in itself, compromise the analyses. With this in mind, we analyzed a limited set of stratigraphic intervals dispersed throughout the Phanerozoic both by using an alternative, equal-area binning protocol (i.e., a protocol that holds the area of a bin fixed as a function of latitude), and by varying the areas of individual grid cells as much as fourfold. In all cases, the effects on our analytical results were barely discernable. This may reflect, in part, the relative paucity of data from high latitudes (>60° N or S), where the distortion would be most significant. Furthermore, in cases where substantial data were available from high latitudes (e.g., high southern latitudes for the Ordovician), the data tended to be highly concentrated in a few regions, which in itself would tend to minimize the effects of differences in the scale of geographic-binning because highly concentrated data would likely fall in the same geographic bin regardless of the protocol used.

Quantification of Similarity.—All analyses described below were conducted with computer programs written and executed in *PowerBasic Console Compiler for Windows*, Version 5. At the heart of these analyses was the quantification of similarity between sample pairs as a function of the distances between them; as illustrated later, high similarity is indicative of low disparity, and low similarity is reflective of high disparity. To quantify pairwise faunal similarities among 5° × 5° cells within an interval, two different similarity coefficients were used in the present study:

1. *Assessment with quantified data*. Pairwise comparisons of samples were first conducted using the *Quantified Czekanowski's* coefficient (Sepkoski 1974):

$$C = 2\ \Sigma\ \min(x_{1k}, x_{2k})/(\Sigma\ x_{1k} + \Sigma\ x_{2k}),$$

where x_{1k} is the number of occurrences of the k^{th} genus in one of the cells, x_{2k} is the number of occurrences of the k^{th} genus in the other cell, and min (x_{1k}, x_{2k}) selects the lesser of the two values. Only cells with at least 50 occurrences were included in these analyses. Because the Quantified Czekanowski's coefficient is sensitive to variations in sample size (i.e., the number of occurrences in each cell), and these differences were probably not biologically meaningful in most instances, the number of occurrences for each genus in a given cell were transformed by recasting these values as *proportions* of the aggregate number of occurrences in the cell. The use of the Quantified Czekanowski's coefficient coupled with percent transformation is known widely in the ecological literature as *proportional similarity*.

As an alternative to data transformation, we investigated the use of sampling-standardization to mitigate differences in sample size. It was determined with simulations, however, that sampling standardization is not appropriate in this instance, despite its intuitive appeal. In our simulations, samples initially of different sizes were drawn randomly from the same simulated pool of species in which relative abundances were assigned to species on the basis of a log-normal distribution. When the larger sample was rarefied down to that of the smaller sample, the calculated similarity of the samples tended to *decrease*, rather than increase, relative to similarity values based on simple transformation to proportions. We nevertheless conducted an additional set of analyses on our data in which sampling-standardization *was* used, and found that it made little difference in the end: although sampling standardization tended to reduce calculated similarity values, it did so predictably and uniformly, and had little effect on the geographic and stratigraphic trajectories presented below.

2. *Assessment based on presence/absence*. Although it is often considered desirable to include a quantitative representation of taxonomic dominance in the calculation of similarity between sample pairs, this inevitably places heavy emphasis on the few common taxa that tend to dominate most samples. In the present study, this may be problematical because the Phanerozoic is thought to have been characterized by a secular increase in the number of endemic, possibly rare, taxa that could have been the main sources of increased provinciality posited for the Cenozoic (Valentine 1969; Campbell and Valentine 1977). By de-emphasizing uncommon genera in the calculation of similarity, the Quantified Czekanowski's coefficient might therefore overlook the principal contributors to increased Cenozoic geo-disparity. To assess this possibility, pairwise similarities among samples were also calculated based only on the presence or absence of genera, using the binary version of the Jaccard coefficient, which has been used previously in studies of beta diversity (e.g., Sepkoski 1988):

$$J = m/(m + a + b),$$

where m is the number of genera present in both samples (the number of ''matches''), a is the number of genera uniquely present in one sample, and b is the number of genera uniquely present in the other sample. Because multiple occurrences of genera were ignored in this analysis, the minimum threshold for inclusion of a 5° × 5° cell in this analysis was reduced from 50 occurrences to 20. Importantly, uncommon genera contained within a given cell therefore provided the same contribution to the calculation of Jaccard similarity as common genera, enhancing the opportunity to capture the effects of a secular increase, if any, in the number of uncommon, possibly endemic, genera. Furthermore, as with the Quantified Czekanowski's coefficient, it was determined that sampling standardization was inappropriate.

Graphical Representation of Geo-Disparity.— The central goal of this study was to assess the degree of similarity among the biotas of a given stratigraphic interval with respect to

TABLE 1. PaleoDB-bin protocol used in this study. For each bin, the stratigraphic range and duration are provided, as are several summary attributes of genus-level data extracted from the PaleoDB. Era-level means for numerical attributes are as follows: Duration (Myr): Paleozoic (Pz)—11.7, Mesozoic (Mz)—10.3, Cenozoic (Cz)—10.9; No. occurrences: Pz—4196.7, Mz—3518.8, Cz—12,164.5; No. occurrences/Bin duration: Pz—397.2, Mz—453.3, Cz—1133.2; No. unique genera: Pz—449.7, Mz—341.1, Cz—1321.8; No. unique genera/Bin duration: Pz—42.3, Mz—38.1, Cz—126.4; No. occurrences/No. unique genera: Pz—9.1, Mz—9.3, Cz—8.3. Although means for several of these attributes increase noticeably in the Cenozoic, there is no indication that they affect the analytical results of this investigation. In fact, analytical results presented for Cenozoic 4, 5, and 6 are remarkably similar to one another, despite dramatic differences among these bins in the number of aggregate occurrences and the number of unique genera.

Interval name	Included stages/epochs	Duration (Myr)	No. occurrences	No. occurrences/ bin duration	No. unique genera	No. unique genera/bin duration	No. occurrences/ no. unique genera
Cambrian 2	Tommotian–Toyonian	19.0	1002	52.7	298	15.7	3.4
Cambrian 3	Middle Cambrian	12.0	2899	241.6	371	30.9	7.8
Cambrian 4	Late Cambrian	12.7	2632	207.2	453	35.7	5.8
Ordovician 1	Tremadocian	9.7	2060	212.4	384	39.6	5.4
Ordovician 2	''Arenigian''	12.6	2912	231.1	514	40.8	5.7
Ordovician 3	Llanvirnian–Llandeilian	5.5	2298	417.8	421	76.5	5.5
Ordovician 4	Caradocian	11.0	12830	1166.4	699	63.5	18.4
Ordovician 5	Ashgillian	5.8	5773	995.3	540	93.1	10.7
Silurian 1	Llandoverian	15.5	5954	384.1	496	32.0	12.0
Silurian 2	Wenlockian–Pridolian	9.5	10285	1082.6	756	79.6	13.6
Devonian 1	Lochkovian–Pragian	11.7	5642	482.2	684	58.5	8.2
Devonian 2	Emsian	9.5	3327	350.2	666	70.1	5.0
Devonian 3	Eifelian–Givetian	12.2	8477	694.8	702	57.5	12.1
Devonian 4	Frasnian	10.8	2355	218.1	295	27.3	8.0
Devonian 5	Famennian	13.8	2570	186.2	289	20.9	8.9
Carboniferous 1	Tournaisian	15.4	2889	187.6	376	24.4	7.7
Carboniferous 2	Chadian–Asbian	13.3	2244	168.7	296	22.3	7.6
Carboniferous 3	Brigantian–Serpukhovian	13.9	2456	176.7	288	20.7	8.5
Carboniferous 4	Bashkirian–Moscovian	11.6	3438	296.4	312	26.9	11.0
Carboniferous 5	Kasimovian–Gzhelian	7.5	3661	488.1	181	24.1	20.2
Permian 1	Asselian–Sakmarian	14.6	2268	155.3	326	22.3	7.0
Permian 2	Artinskian–Kungurian	13.8	5198	376.7	510	37.0	10.2
Permian 3	Guadalupian	10.2	5222	512.0	551	54.0	9.5
Permian 4	Lopingian	9.4	2329	247.8	385	41.0	6.0
Triassic 1	Induan–Olenekian	6.0	982	163.7	135	22.5	7.3
Triassic 2	Anisian–Ladinian	17.0	2449	144.1	269	15.8	9.1
Triassic 3	Carnian	11.5	1852	161.0	329	28.6	5.6
Triassic 4	Norian–Rhaetian	16.9	2656	157.2	370	21.9	7.2
Jurassic 1	Hettangian–Sinemurian	10.0	2808	280.8	253	25.3	11.1
Jurassic 2	Pliensbachian	6.6	3067	464.7	205	31.1	15.0
Jurassic 3	Toarcian–Aalenian	11.4	3079	270.1	247	21.7	12.5
Jurassic 4	Bajocian–Bathonian	6.9	2275	329.7	348	50.4	6.5
Jurassic 5	Callovian–Kimmeridgian	13.9	8379	602.8	519	37.3	16.1
Jurassic 6	Tithonian	5.3	2510	473.6	258	48.7	9.7
Cretaceous 1	Berriasian–Valanginian	9.1	1904	209.2	279	30.7	6.8
Cretaceous 2	Hauterivian–Barremian	11.4	896	78.6	231	20.3	3.9
Cretaceous 3	Aptian	13.0	1658	127.5	391	30.1	4.2
Cretaceous 4	Albian	12.4	1901	153.3	394	31.8	4.8
Cretaceous 5	Cenomanian	6.1	2833	464.4	334	54.8	8.5
Cretaceous 6	Turonian–Santonian	10.0	2242	224.2	376	37.6	6.0

TABLE 1. Continued.

Interval name	Included stages/epochs	Duration (Myr)	No. occurrences	No. occurrences/ bin duration	No. unique genera	No. unique genera/bin duration	No. occurrences/ no. unique genera
Cretaceous 7	Campanian	12.9	3622	280.8	486	37.7	7.5
Cretaceous 8	Maastrichtian	5.1	18225	3573.5	716	140.4	25.5
Cenozoic 1	Paleocene	9.7	5212	537.3	890	91.8	5.9
Cenozoic 2	Ypresian–Lutetian	15.4	5668	368.1	860	55.8	6.6
Cenozoic 3	Bartonian–Priabonian	6.5	6873	1057.4	1029	158.3	6.7
Cenozoic 4	Oligocene	10.9	8539	783.4	997	91.5	8.6
Cenozoic 5	Early–Middle Miocene	11.4	16731	1467.6	1819	159.6	9.2
Cenozoic 6	Late Miocene–Pleistocene	11.6	29964	2585.3	2336	201.6	12.8

their distances from one another. For this purpose, in all cases where a similarity value was determined for a 5° × 5° cell pair, the great-circle distance between the cells was also determined. Then, for each stratigraphic interval, similarity values were grouped into 2000-km distance bins, and mean similarities of each group were illustrated graphically for sequential distance bins. Results for different stratigraphic intervals were superimposed, facilitating direct comparisons among them. As an alternative means of assessing secular trends in similarity, time-series depictions of similarity were also produced for several distance bins.

Finally, to better understand the nature of geo-disparity on a global scale, we constructed paleogeographic maps for each stratigraphic interval to illustrate secular changes in the fundamental nature of paleobiogeographic distributions. On each of these maps, a line was drawn between the centroids of any 5° × 5° cell pair for which a similarity value had been calculated; the line was color-coded to reflect the similarity value. As will be demonstrated below, these maps were valuable for diagnosing the effects of the secular Phanerozoic decline in the importance of epicontinental seas and the concomitant increase in the data derived from open-ocean facing settings.

Results and Discussion

Geo-disparity versus Distance.—Mean pairwise similarities between 5° × 5° cells in relation to the distances between them are illustrated in Figure 1 for the Ordovician 4 stratigraphic bin (Caradocian), based on the Quantified Czekanowski's coefficient. This interval was chosen as an initial exemplar not only because it is well sampled, but also because it captures the culmination of the Ordovician Radiation and establishment of the Paleozoic Evolutionary Fauna, which dominated seafloors for the remainder of the Paleozoic Era (Sepkoski 1981). Not surprisingly, there is a strong inverse relationship between similarity and distance, although this levels off at distances of about 8000 km. The small increase observed in the 14,000–16,000 km distance bin relates to slightly elevated similarities between a few locales in South China and cells in Avalonia and Baltoscandia.

An initial comparison of similarity versus distance in Paleozoic versus Cenozoic stratigraphic bins is also presented in Figure 1, where similarity values for the youngest Phanerozoic bin, Cenozoic 6 (late Miocene–Pleistocene), are compared directly with values for Ordovician 4. As with the Ordovician, there is a drop-off with distance in the Cenozoic example that levels off at about 8000 km. Over the range of distances analyzed, Ordovician 4 similarities were significantly greater than those for Cenozoic 6 for distances of 6000 km and less, but there was little variation at greater distances, except for a small difference in the aforementioned 14,000–16,000 km interval. As we will illustrate later, the greater mean similarities among Ordovician-4 biotas at distances less than 4000 km, and especially less than 2000 km, may reflect an ''epicontinental-sea

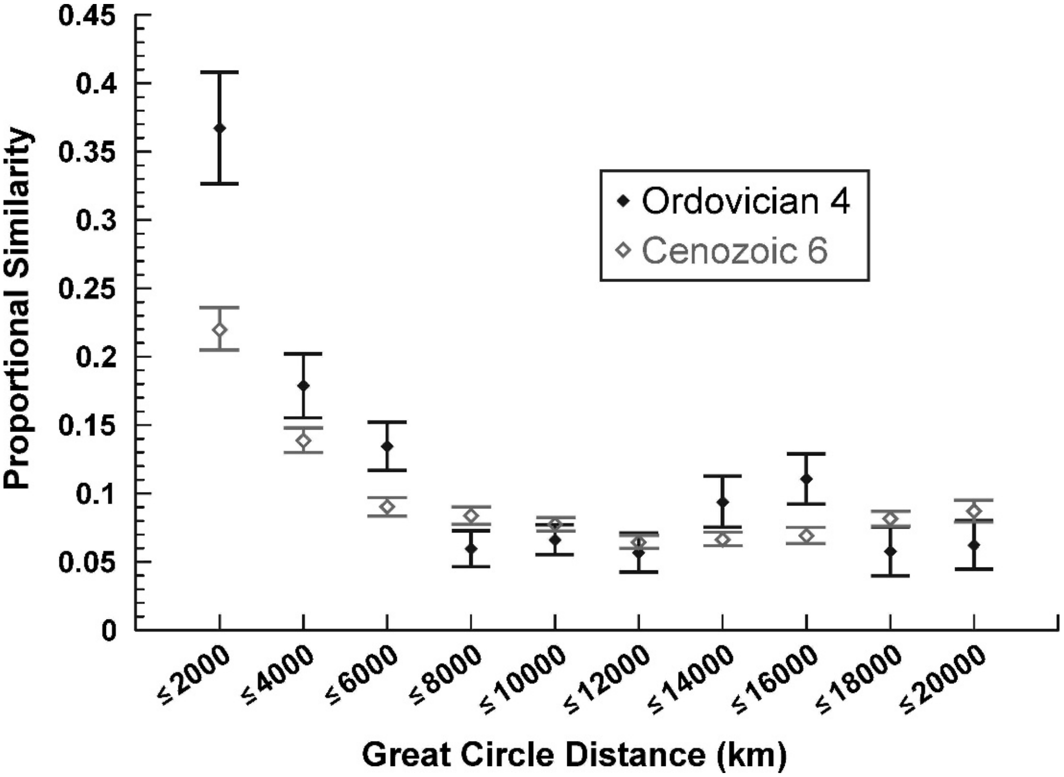

FIGURE 1. Graph depicting mean similarities among 5° × 5° cells versus great-circle distance for Ordovician 4 (Caradoc; solid lines and solid diamonds) and Cenozoic 6 (late Miocene–Pleistocene; dotted lines and open circles), based on proportional similarity. Error bars are 95% confidence intervals about the mean. Note that the Ordovician and Cenozoic intervals both exhibit a decrease in similarity with distance, but mean similarities for the three smallest distance bins are significantly greater for Ordovician 4 than for Cenozoic 6. Mean similarity at greater distances, however, are highly comparable for both intervals, except for distances in the 14,000–16,000 km range.

effect.'' At the same time, Cenozoic 6 biotas are generally *not* more disparate compositionally than their Ordovician 4 counterparts at greater, transoceanic-scale distances.

A broader comparison of the Paleozoic with the Cenozoic is presented in Figure 2A, for stratigraphic intervals in each era that contained at least 8000 occurrences (Table 1). Perhaps most striking is the tendency for Silurian 2 to exhibit markedly greater similarity at most distances than all of the other Paleozoic and Cenozoic intervals included in the illustration. Importantly, the Silurian has long been thought to be a time of heightened cosmopolitanism for trilobite and brachiopod faunas, brought about by the closing of the Iapetus Ocean and the Late Ordovician mass extinction (Sheehan 1975, 2008; Adrain and Westrop 2000; Adrain et al. 2000), and this appears to be well reflected in the heightened similarities among Silurian biotas observed here.

A comparison of the same stratigraphic intervals based on analyses of presence-absence data using the Jaccard coefficient is presented in Figure 2B. Because they accentuate the importance of rare taxa, it is not surprising that, overall, Jaccard presence-absence values are substantially lower than the corresponding Quantified Czekanowski's values. Nevertheless, both sets of curves exhibit the same pattern of declining similarity with increasing distance between cells; both analyses point to Silurian 2 as an interval of unusually high similarity; and, except for Silurian 2, there is little indication that Cenozoic intervals exhibit consistently lower or higher similarities than their Paleozoic counterparts, particularly at distances greater than 6000 km when one might expect to see increased effects of provinciality manifested in lower similarities for Cenozoic intervals. Furthermore, the similarities of the trajecto-

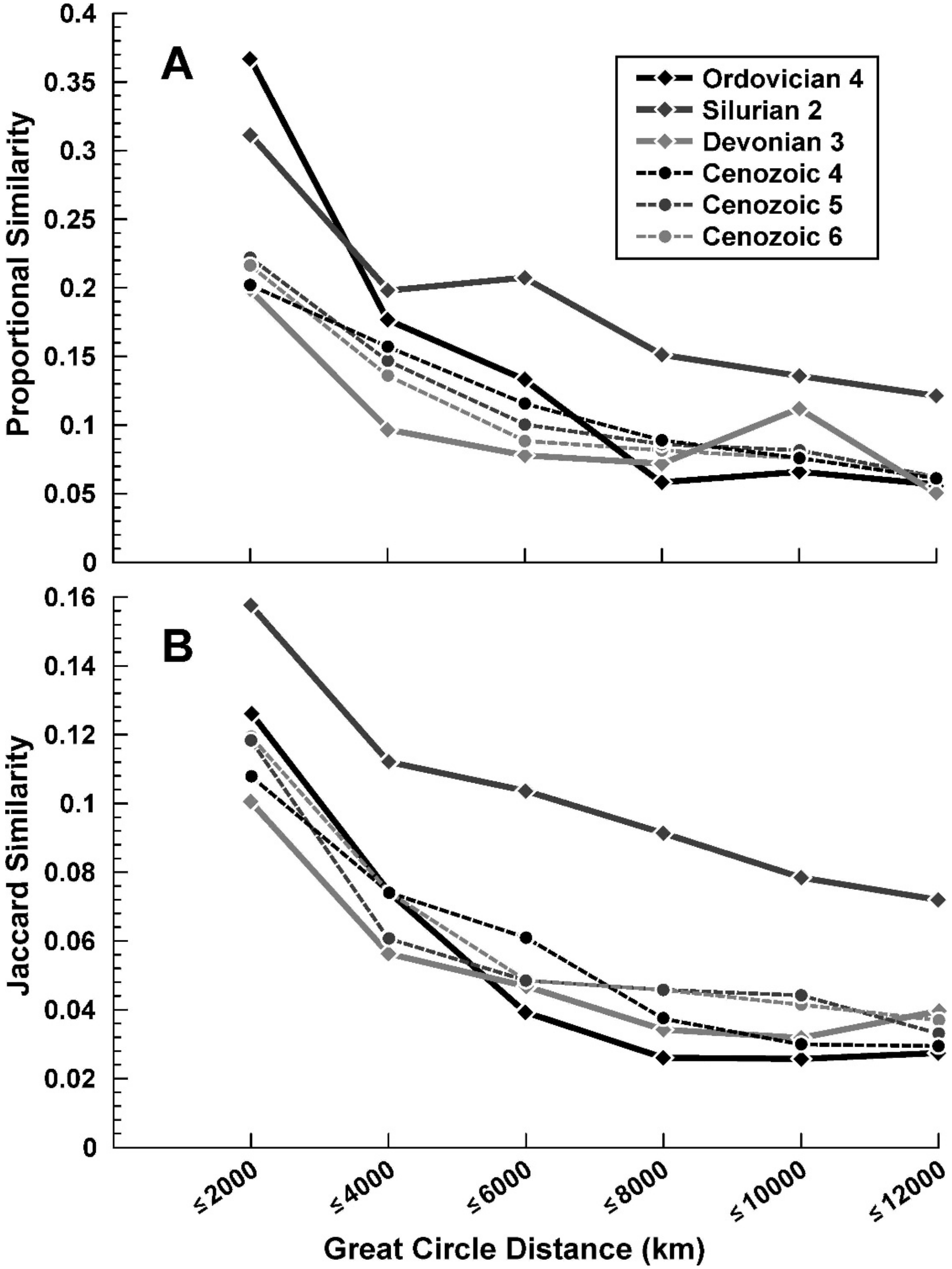

FIGURE 2. Graphs depicting mean similarities among 5° × 5° cells versus great-circle distance for representative Paleozoic and Cenozoic stratigraphic intervals. Here and in Figure 3, distances are truncated at 12,000 km because the majority of change occurs at distances less than that, and, for some stratigraphic bins, the number of inter-cell comparisons becomes fairly limited at greater distances. A, Based on proportional similarity. B, Based on Jaccard presence-absence similarity. For visual clarity, error bars are not included. Note the tendency in both cases for Silurian 2 (Wenlock-Pridoli) to exhibit markedly greater similarities than all other intervals at most distances.

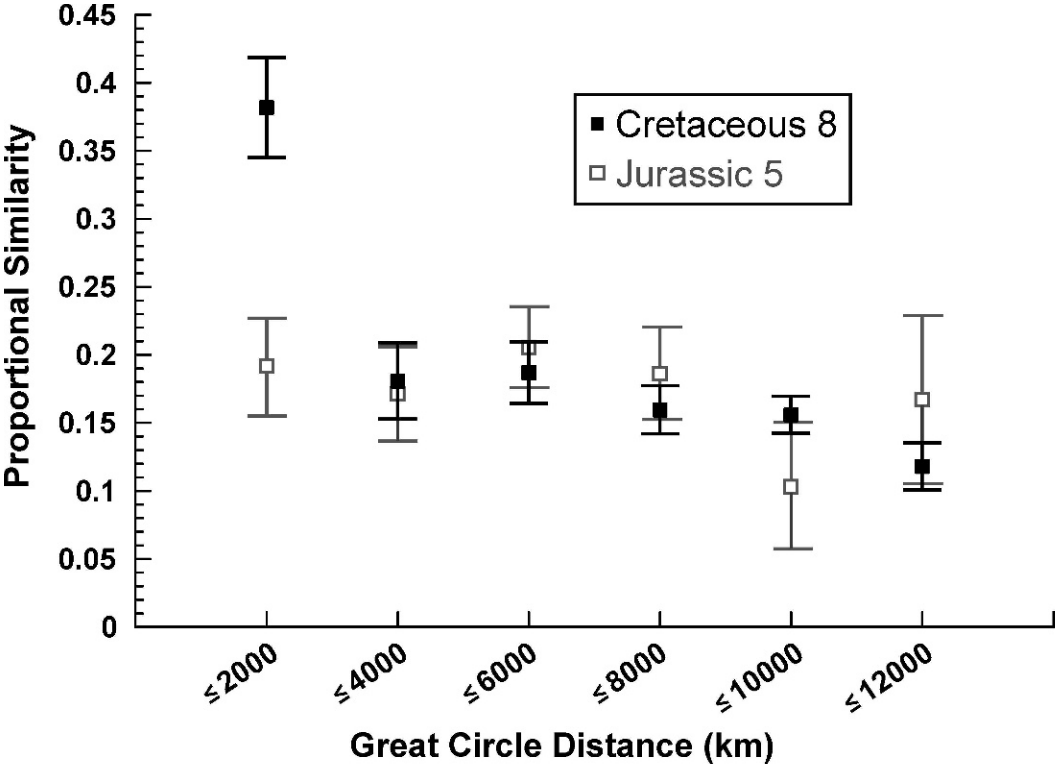

FIGURE 3. Graph depicting mean similarities among 5° × 5° cells versus great-circle distance for Cretaceous 8 (Maastrichtian) and Jurassic 5 (Callovian–Kimmeridgian). As in Figure 2, the graph is truncated at 12,000 km. Note the comparative flatness of both trajectories relative to those depicted for the Paleozoic and Cenozoic, suggesting a less definitive relationship between similarity and distance. These trajectories are emblematic of most other Mesozoic stratigraphic bins.

ries for Cenozoic 4, 5, 6 are particularly striking, given the dramatic differences in overall sampling among these three bins (Table 1). This attests to a strong signal in the data that appears impervious to these sample-size differences.

In contrast to the similarity-versus-distance curves for Paleozoic and Cenozoic intervals, those for the Mesozoic do not all exhibit trends of decreasing similarity with increasing distance. The curve for Cretaceous 8 (Maastrichtian), for example (Fig. 3), shows a decline from the 0–2000 km distance bin to the 2000–4000 km bin, but then flattens out thereafter. Jurassic 5 (Callovian–Kimmeridgian), exhibits a nearly flat trajectory (Fig. 3), and other Mesozoic stratigraphic intervals, not illustrated here, exhibit highly irregular trajectories, compared with Paleozoic and Cenozoic stratigraphic intervals.

Geo-Disparity and Paleogeography.—It remains to be determined whether the Mesozoic patterns reflect peculiarities in the database that will be overcome with continuing updates or, instead, suggest something unique about the global paleogeographic distribution of Mesozoic biodiversity (see the later section, ''Remaining Issues and Future Work''). A direct assessment of similarity with respect to paleogeography suggests, however, that each of the three Phanerozoic eras may carry its own unique signature (Figs. 4–6), related to the positions of paleocontinents and the relative contributions of epicontinental-sea biotas. In the case of Ordovician 4, for example, the greatest similarities among 5° × 5° cell pairs are limited primarily to individual paleocontinents (Fig. 4A), most apparent in the case of a group of cells associated with Laurentia, and traversing the Iapetus Ocean, which was closing at that time. Other, more limited pods of high similarity include small portions of South China, Avalonia to Baltoscandia, and the Mediterranean Province.

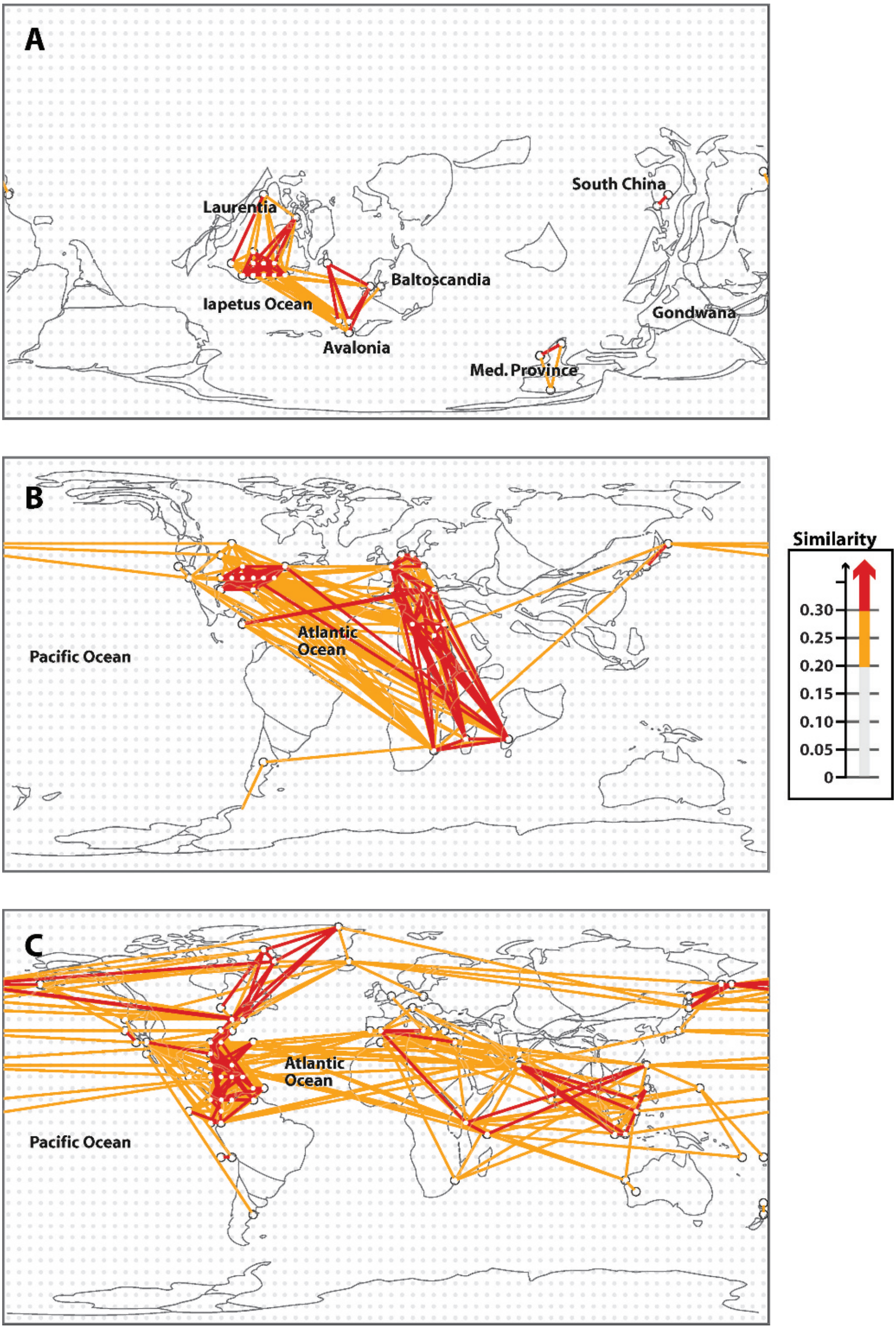

FIGURE 4. Proportional similarities plotted on paleogeographic maps for Ordovician 4 (A), Cretaceous 8 (B), and Cenozoic 6 (C) with color-coded lines connecting centroids of 5° × 5° cells when both cells exceed the 50-occurrences threshold required for calculation of similarity between the cell pair. Only similarities ≥0.30 (red) and ≥0.20 to <0.30 (orange) are depicted. For Ordovician 4, the majority of these linkages are observed for cells in close proximity to one another (e.g., among nearby cells on Laurentia or across the closing Iapetus Ocean). By contrast, most such linkages for Cenozoic 6 are transoceanic (note the linkages between eastern and western North American and eastern Asia). Cretaceous 8 includes some linkages that are in close proximity and others that are transoceanic.

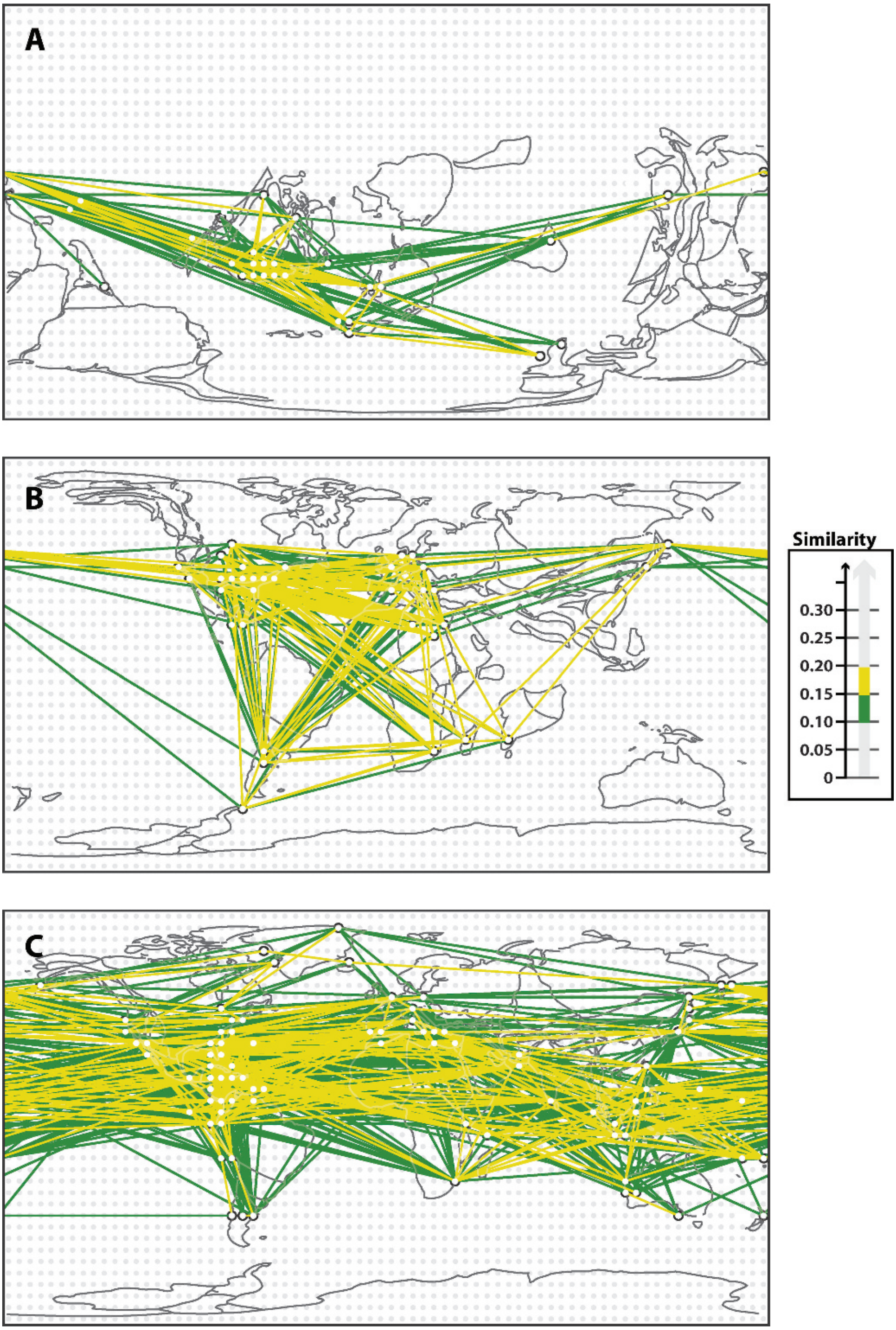

FIGURE 5. Paleogeographic maps for Ordovician 4 (A), Cretaceous 8 (B), and Cenozoic 6 (C) with color-coded lines as in Figure 4, but with linkages depicted for similarities ≥ 0.15 to <0.20 (yellow) and for those ≥ 0.10 and <0.15 (green). An increased number of transoceanic linkages at this level is observed even for Ordovician 4. In addition a number of linkages are observed in Cenozoic 6 between the Northern and Southern Hemispheres that were not as pervasive at higher similarity, suggesting significant compositional differences between the two hemispheres.

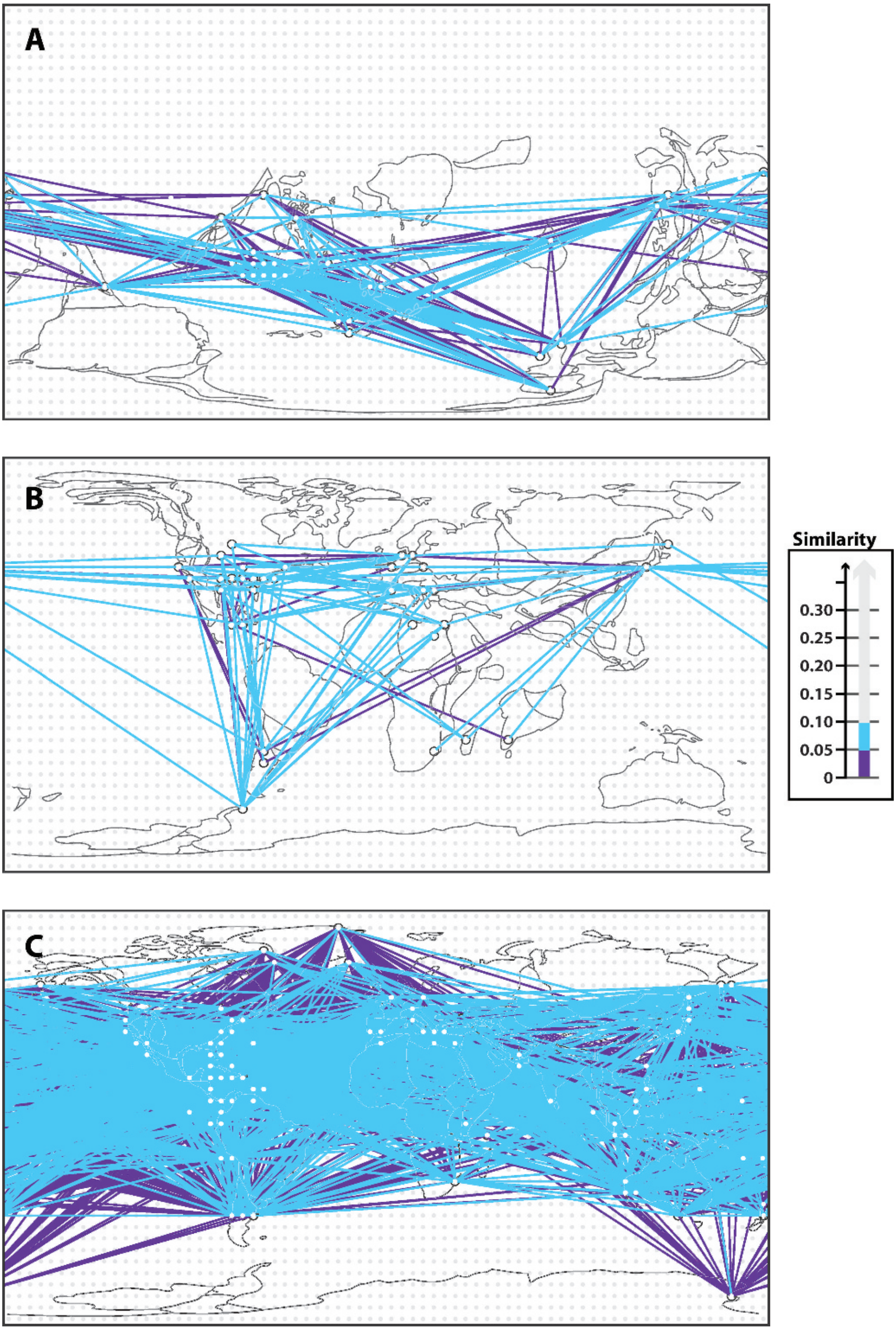

FIGURE 6. Paleogeographic maps for Ordovician 4 (A), Cretaceous 8 (B), and Cenozoic 6 (C) with color-coded lines as in Figures 4 and 5, but with linkages depicted for similarities ≥0.05 to <0.10 (blue) and for those >0.0 and <0.05 (violet).

By contrast, for Cenozoic 6 (Fig. 4C), a greater proportion of the high-similarity linkages between cells are transoceanic, although a set of strong links can also be observed at smaller distances, in the Caribbean Sea and elsewhere. In particular, high similarities are observed across the Pacific and Atlantic Oceans between biotas of western and eastern North America and eastern Asia. The pattern for Cretaceous 8 (Fig. 4B) resembles a kind of ''hybrid'' of the Ordovician and Cenozoic examples: a preponderance of high similarity among cells of the North American coastal plain and Europe–North Africa, coupled with linkages across the expanding Atlantic Ocean.

At lower levels of similarity (Figs. 5, 6), an increasing number of transoceanic links are observed among biotas in all intervals. Interestingly, links for Cenozoic 6 between several localities in the Northern and Southern Hemispheres that are not observed at higher similarities can be observed at these lower levels, suggesting compositional disparity between the hemispheres. This almost certainly reflects the confinement of major oceanic circulation cells to the Northern and Southern Hemispheres, which would tend to inhibit biotic dispersal between the two hemispheres.

An ''epicontinental-sea effect'' illustrated for Laurentia in particular in Ordovician 4 (Fig. 4A) may explain the tendency of most Paleozoic intervals to exhibit greater similarities than their Cenozoic counterparts at smaller distances (Fig. 2). At the same time, the lack of high-similarity links at greater distances among Paleozoic 5° × 5° cell pairs may reflect a relative scarcity of data in the PaleoDB for Paleozoic shallow ocean-facing settings, given the likelihood that much of the area covered by these settings for the Paleozoic was subsequently subducted. Collectively, these patterns serve as reminders of a pair of secular trends in the sedimentary record: a growth in the contribution of strata from shallow, ocean-facing settings and a decline in strata representative of epicontinental seas. Whereas the latter apparently relates to an actual loss of epicontinental seas through the Phanerozoic, the former is in part a preservational artifact, and should probably be incorporated more routinely into future analyses of Phanerozoic biodiversity (Allison and Wells 2006; Peters 2007).

Secular Trends in Geo-Disparity.—Phanerozoic trends in geo-disparity are illustrated in Figures 7 (Quantified Czekanowski's coefficient) and 8 (Jaccard coefficient) for three of the distance bins included in Figures 1–3: 0–2000 km, 2000–4000 km, and 8000–10,000 km. These three intervals were chosen to provide a sense of how the trajectory varies, if at all, in relation to the distance between 5° × 5° cells. Values for some stratigraphic bins are not provided because the available data at the distances in question are insufficient to quantify geo-disparity (for a given distance bin, at least two pairwise comparisons between 5° × 5° cells were required). In addition, similarity values in these figures decrease upward to reflect *increasing* geo-disparity.

With respect to transitions between adjacent stratigraphic bins, the trajectories should be viewed as preliminary because these fine-scale variations may relate to bin-to-bin transitions in data quality and coverage that will be investigated in our future analyses; for some potentially critical transitions (e.g., Triassic 1, immediately following the end-Permian mass extinction), the data remain insufficient to quantify geo-disparity. At broader scales, however, the pattern is likely to be meaningful even now because many of the stratigraphic bins throughout the Phanerozoic, including those highlighted earlier, contain large numbers of occurrences arrayed among 5° × 5° cells at a range of distances from one another. Overall, neither the analysis based on the Quantified Czekanowski's coefficient nor that based on the Jaccard coefficient exhibits a substantial Phanerozoic increase in geo-disparity. There is some hint of an increase about midway through the Cenozoic (in particular for the 8000–10,000 km distance bin) but, in itself, this would be insufficient to drive a major Phanerozoic increase in global diversity. Furthermore, similarity values for the Cenozoic are well in line with those for several

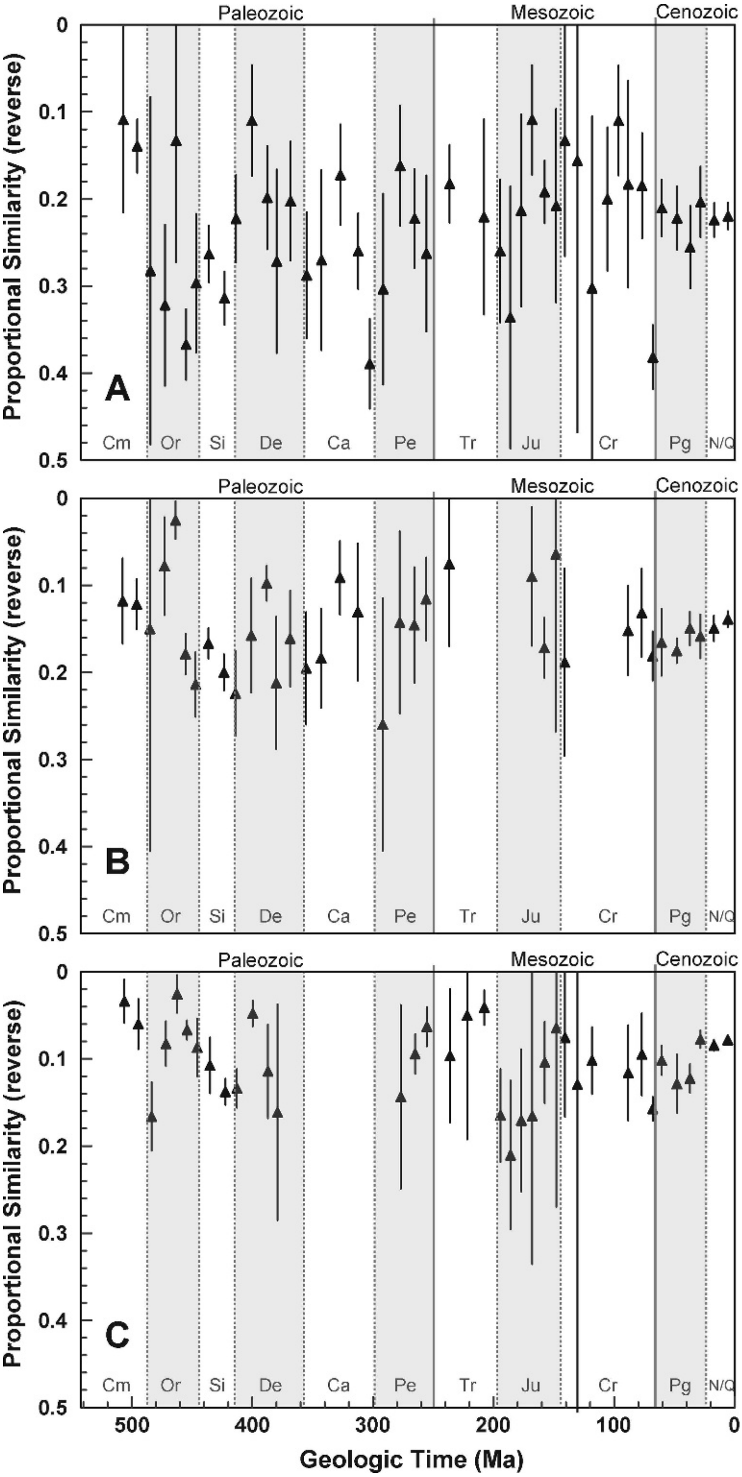

FIGURE 7. Time-series depictions, based on proportional similarity, of mean geo-disparity through the Phanerozoic among 5° × 5° cells for three of the distance bins included in Figures 1–3: 0–2000 km (A), 2000–4000 km (B), and 8000–10,000 km (C). These distances were chosen to illustrate similarities among samples that are relatively closely spaced (A and B), such as cells confined to the same epicontinental sea or continental coastline, as well as others approaching transoceanic distances (C). At greater distances, the paucity of data available for inter-cell comparisons in several stratigraphic bins makes it difficult to construct a meaningful time series. Values are illustrated only in cases where two or more comparisons between cells were available for a given stratigraphic bin. Note that similarity values *decrease* upward in these figures, reflecting an upward increase in geo-disparity.

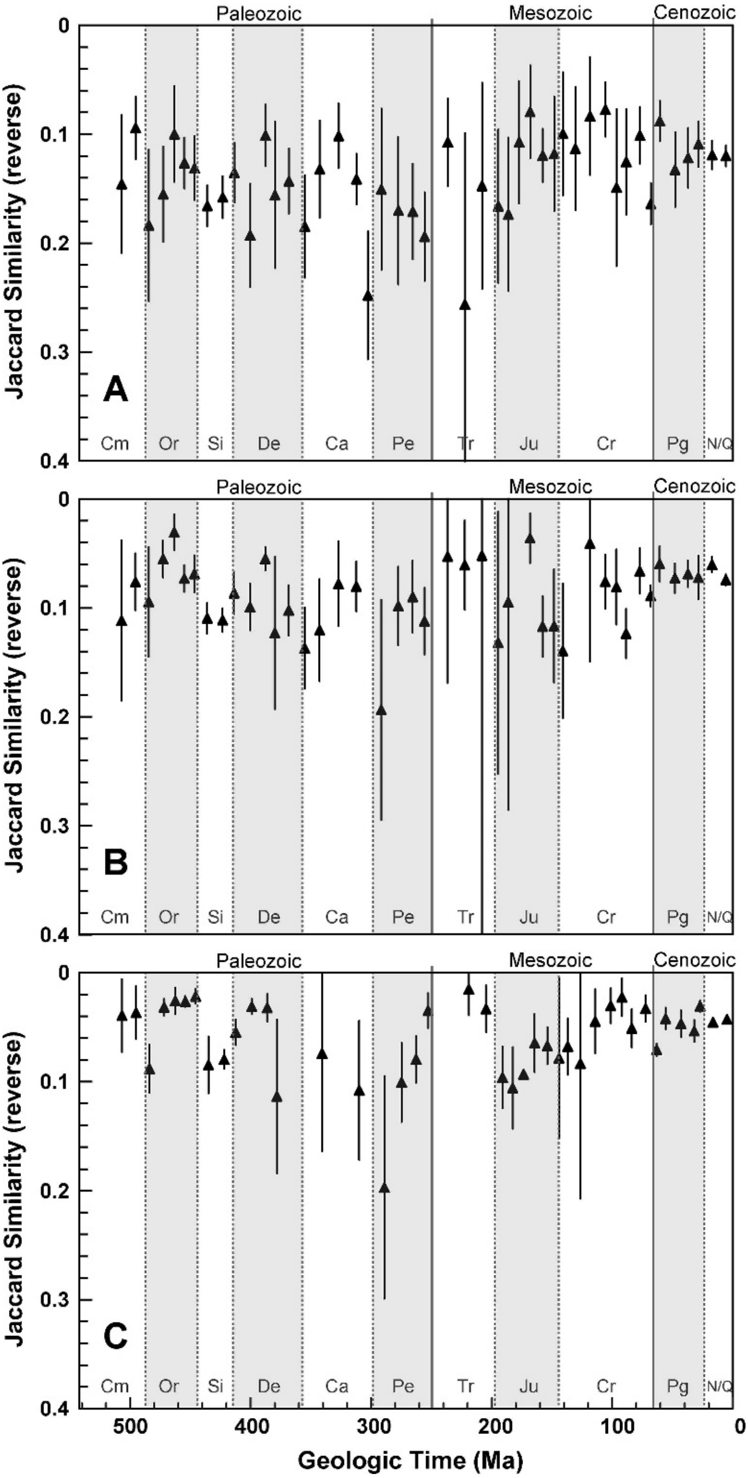

FIGURE 8. Time-series depictions, based on the Jaccard (presence-absence) similarity coefficient, of mean geo-disparity through the Phanerozoic among 5° × 5° cells for the same three distance bins as in Figure 7 (see the caption to Figure 7 for additional specifications).

other Paleozoic and Mesozoic intervals, and do not exhibit a unique set of values.

Remaining Issues and Future Work

Although several tantalizing patterns have been observed in our analyses to date, our main goal in this paper was to convey the importance of investigating and dissecting secular trends in geo-disparity, and to present an analytical protocol that we will continue to refine in the future. In this spirit, it is important to consider a number of issues that will be addressed as our investigations unfold. Furthermore, many of these issues are broadly relevant to a range of potential future investigations of the geographic and environmental textures of Phanerozoic diversity, and, so, are worth reviewing in detail.

Geo-Disparity versus Beta Diversity.—Although environmental gradients inevitably incorporate a geographic dimension, geo-disparity should not be viewed as synonymous with beta (''between-community'') diversity. From a theoretical standpoint, compositional partitioning along environmental gradients may occur for reasons (e.g., biotic interactions) that are entirely different than those responsible for geo-disparity (e.g., biogeographic barriers). From an operational standpoint, the finest geographic scale analyzed herein, the distance between centroids of adjacent $5^\circ \times 5^\circ$ cells, may be too coarse to capture disparity associated with a typical environmental gradient. To analyze beta diversity trends, it would be appropriate to focus on portions of the world for a given stratigraphic interval where paleoenvironmental data and density of sampling are adequate to assess compositional disparity directly along the gradients. This could be accomplished by adapting the numerical methods presented here, or, if sampling is adequate and appropriate, by applying additive-partitioning methods (Layou 2007; Patzkowsky and Holland 2007).

Geographic and Secular Variations in Paleoenvironment.—Dovetailing on the issue of geo-disparity versus beta diversity, it is important to recognize that differences in composition among cells need not simply reflect their distances from one another, but could also reflect differences in their aggregate environmental characteristics. Some cells, for example, might encompass a larger proportion of carbonate-rich settings, whereas others might be more siliciclastic-rich, factors that are now thought to significantly influence biodiversity on a global scale (Miller and Connolly 2001; Foote 2006; Kiessling and Aberhan 2007). If these differences are distributed nonrandomly within and among cells, they could ''disrupt'' an otherwise straightforward relationship between disparity and distance, which, among other things, may explain the unusual patterns exhibited in our analyses of the Mesozoic to date. It is now well understood that there was a secular Phanerozoic decline in the availability of carbonate environments and a concomitant increase in siliciclastic settings (Walker et al. 2002; Peters 2008), with what was likely a unique mixture of both settings in the Mesozoic Era. With this in mind, it will be important to map the geographic distributions of carbonate-rich and siliciclastic-rich settings, as well as other environmental attributes throughout the Phanerozoic, to assess the extent to which they affect geo-disparity or impart their own, unique signatures on the history of Phanerozoic diversity.

Secular Variations in the Availability of Data from Shallow, Ocean-Facing Settings.—Earlier, we considered the possible importance to geo-disparity of the secular transition from epicontinental-sea to ocean-facing settings. Although a large proportion of ocean-facing shallow-water settings associated with Paleozoic paleocontinents ultimately succumbed to subduction, there *were* several noteworthy early- to mid-Paleozoic areas separated from paleocontinents that contained open-ocean-facing fossil biotas. Many of these were small terranes that sometimes contained faunas compositionally distinct from their epicontinental counterparts (e.g., Harper 1992; Owen et al. 1992; Harper et al. 1996). Additional examples, which are also relatively small in area, include the Mediterranean Province, a set of islands at high southern latitude marginal to the Paleozoic supercontinent of Gondwana, which today constitute large portions of central and southern Europe and northern Africa; and Avalonia, which included much of present-day England and Wales. There is evidence of significant terrane accretion during the Paleozoic onto large continental platforms (Cocks and Torsvik 2007), suggesting a secular loss in the availability of unique terrane biotas as the Paleozoic progressed. In any case, although the collective areal coverage of these regions may not have been as extensive as coeval continental areas, they often contain abundant fossil biotas. At present, although there is good coverage in the PaleoDB for parts of Avalonia and the Mediterranean Province, some terranes are not well represented, and a concerted effort will be undertaken in the future to augment their coverage.

Geographic Patchiness during the Mesozoic.— As with the global secular transition from carbonates to siliciclastics, the Mesozoic era was characterized by a relatively equitable mix of epicontinental-sea and ocean-facing settings, as opposed to the epicontinental-sea-dominated record of the Paleozoic, or the increasingly ocean-facing-dominated record of the Cenozoic. Not only might this in itself have contributed to the unique patterns observed for the Mesozoic (e.g., Fig. 3), but the comparatively patchy interspersion of epicontinental seas, ocean-facing environments, and landmasses evident on Mesozoic global paleogeographic maps might also have affected the relationship between disparity and distance. Landmasses intermittently located throughout the faunally rich Tethyan realm, for example, may have served as regional barriers to dispersal, thereby reducing similarity between geographically proximate regions. This possibility can be investigated by focusing on the nature of compositional variation within these regions.

Data Quality.—There have long been concerns that large databases such as Sepkoski's compendia (Sepkoski 1982, 1992, 2002) and the PaleoDB contain numerous taxonomic inconsistencies and that these, in turn, compromise analyses based on these data. Although this might ultimately prove to be the case for studies conducted at relatively fine spatial or temporal scales, comparative analyses to date of standardized and vetted data corrected by taxonomic specialists versus the ''raw'' data contained in the aforementioned sources (e.g., Adrain and Westrop 2000; Wagner et al. 2007) indicate, that, for the analysis of broad-scale Phanerozoic patterns, the corrected data do not yield signals appreciably different from the uncorrected data. This may not be the case for studies investigating spatial variations in coverage, however, and the effect of taxonomic data quality on the analysis of geo-disparity will be investigated further in the future.

Genus versus Species-Level Patterns.—Because Valentine's hypothesis of a relationship between increased Cenozoic diversity and provinciality focused on the species level (Valentine 1970; Valentine et al. 1978), it might reasonably be asked whether the hypothesized Cenozoic increase in endemism might *only* be expressed at the species level, and therefore would not be recognizable in the genus-level analyses conducted here. If the data permit it in the future, it would be worthwhile to conduct species-level analyses. Nevertheless, Valentine himself conveyed two reasons why the genus, and perhaps even the family, level should afford sufficient acuity to diagnose a Cenozoic increase in geo-disparity, if it occurred. First, there is evidence that the basic, underlying structure of provinciality in the present day diagnosed at the species level can also be recognized at the genus and family levels (Campbell and Valentine 1977). Second, as Valentine (1969) recognized in his earliest analyses of Phanerozoic diversity trends, the pattern of diversification observed changes fundamentally between the taxonomic levels of order and family. At the family level and below, a post-Paleozoic diversity increase is recognized that is not apparent at the order level and above. Valentine suggested that the increases observed at the family through species levels, though inevitably accentuated as one moves down the taxonomic hierarchy, were all products of the same underlying dynamic.

The Taxonomic Spectrum.—The focus in this initial analysis was on the members of a limited, but representative, cross-section of major higher taxa from each of Sepkoski's three Phanerozoic evolutionary faunas. Although we might expect the marine biota as a whole to exhibit Phanerozoic-scale patterns similar to those observed here, it is possible that this would not be the case. Furthermore, it is important to compare and contrast geo-disparity among different higher taxa, particularly in cases where there is reason to believe that the taxa in question have different paleoecological or paleogeographic attributes, have not been adequately sampled in some regions included in the PaleoDB, or are known to have occupied different environmental regimes throughout all or most of the Phanerozoic. Obvious examples of this last case are the corals; as major representatives of reef and other hard-substrate environments since the Paleozoic, corals provide an opportunity to compare and contrast level-bottom and reef associations. Following on the analyses of Kiessling and Aberhan (2007), it will also be fruitful to parse the data with respect to a variety of paleoenvironmental and paleogeographic parameters, as suggested earlier, or fundamental differences in the biological properties of taxa, such as their life habits (e.g., benthonic versus nektonic groups) or, for taxa among which these properties are known, the nature of their developmental stages (e.g., planktotrophic versus non-planktotrophic larvae), which are now thought to be among the important macroevolutionary attributes of taxa (Jablonski 1986; Peterson 2005).

Stratigraphic Acuity.—Given the limited data available for some Phanerozoic stages and substages, we adopted the somewhat coarser PaleoDB binning scheme, as described earlier. Because geo-disparity should, by definition, be viewed as a property of biotic distributions at a given point in time, it would obviously be desirable to work with time slices that are as constrained as possible, and we look forward to working at a finer stratigraphic scale in the future. There is little reason to believe, however, that the secular patterns observed in the present study, in particular the *lack* of a significant increase in geo-disparity during the Cenozoic relative to the Paleozoic, would change appreciably with a different stratigraphic-binning scheme. All else being equal, if a stratigraphic bin encompasses a longer temporal interval, we would expect the *apparent* level of geo-disparity to be artificially increased because the interval would incorporate a greater degree of evolutionary turnover; the opposite would be the case with a shorter-duration bin. In our study, the average temporal durations of the Cenozoic bins were not appreciably different from those of the Paleozoic, so any such overprint should be minimal.

At the same time, we might expect a similar effect related to the well-documented secular decline in turnover rates through the Phanerozoic (e.g., Raup and Sepkoski 1982; Alroy 2008; among many others): all else being equal, a Paleozoic bin might encompass a greater degree of taxonomic turnover than a Cenozoic bin of roughly equal duration, and this might artifactually inflate the measured geo-disparity of Paleozoic bins relative to the Cenozoic. This possibility will have to be investigated further.

We presented this extended discussion of outstanding issues not only because they need to be addressed to fully come to grips with Phanerozoic diversity trends, but also because they convey the underlying complexity of global diversity trends over the sweep of the Phanerozoic. We are confident that these issues can be addressed in future work, allowing for the routine incorporation of a paleogeographic component into quantitative assessments of global diversity trends. With the continued growth of databases and analytical tools to underpin these investigations, we look forward to the very real possibility of understanding the relationship among Phanerozoic diversity trends at several levels of the geographic and ecological hierarchies.

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