

Appendix for:
Response of beta diversity to pulses of Ordovician-Silurian extinction

Collection- and formation-based sampling biases within the original dataset

Both numbers of occurrences and numbers of collections (= localities) vary substantially from one stage to the next (Fig. A1-A). Numbers of formations also vary over time: but unlike occurrences and localities, there is not a particularly strong correlation between formations and either localities or occurrences (Fig. A1B).

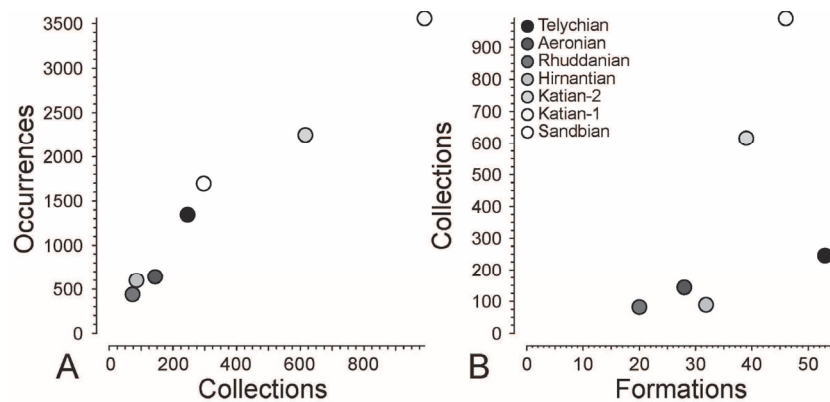


Fig. A1 – A. Occurrences vs. Collections (= unique fossiliferous localities) for the 7 intervals examined herein. B. Collections vs. Formations.

In terms of using our subsampling routines, global gamma diversity patterns are essentially the same for both analyses conducted with raw data, and those using the 6-by-10 or even 5-by-15 analyses. Thus, our analyses are not predisposed to showing radically different results simply because we are excluding major portions of the data.

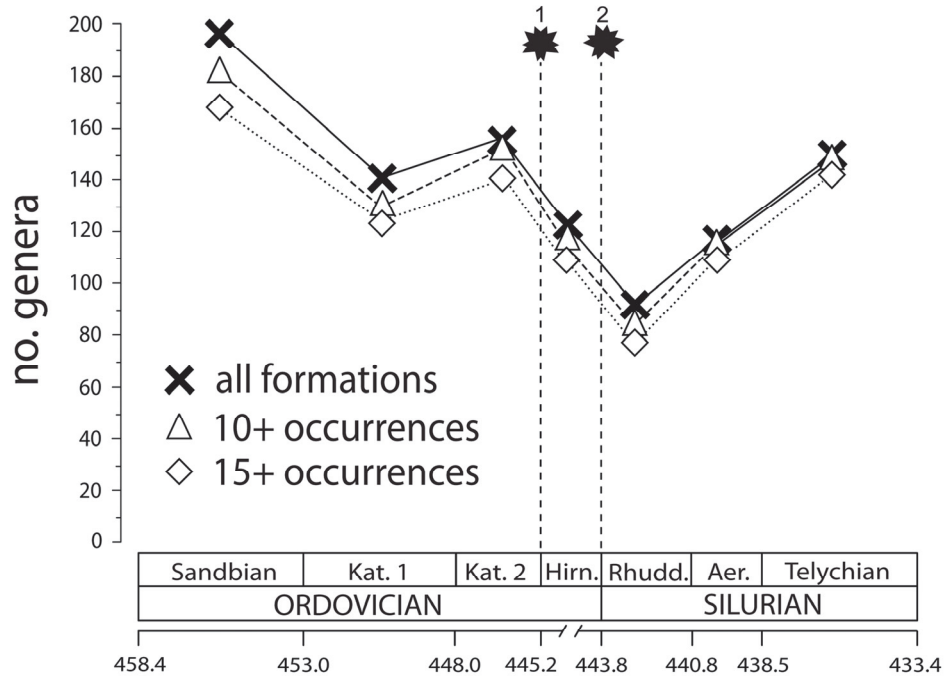


Figure A2 – Raw generic richness for all PaleoDB data (X), for those genera found in formations with 10+ occurrences (triangles) and for those genera found in formations with 15+ occurrences (diamonds). The strong similarity among these diversity curves indicates that examining only formations with 10+ or 15+ occurrences could replicate the basic patterns seen in the raw data.

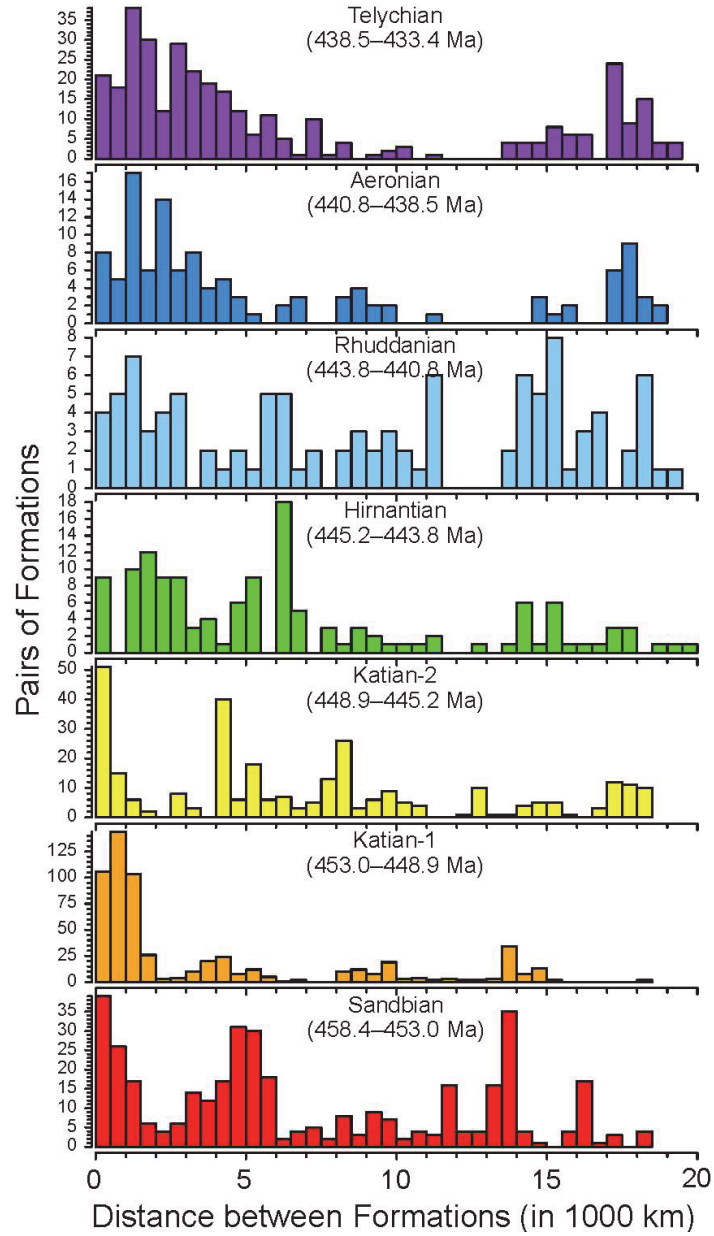


Fig. A3 - Pairwise distances between formations in each interval. Distances are between the centroid of localities within each formation.

Distances among Formations

To estimate the distances between formations, we begin with inferred paleolatitude and paleolongitudes for individual collections. We then reduced these to individual localities. These often are redundant, but in some cases, collections represent individual beds from a particular locality (e.g., some well-studied outcrop). We then used the centroid of the coordinates for these localities as “the” position for each formation. We calculate distances between two formations as the distance between these two formations, which is just the angle between the two coordinates on a sphere multiplied by the Earth’s circumference.

The distances (Fig. A3) show a variety of distributions, with the Katian-1 and Katian-2 showing high proportions of closely spaced formations, whereas intervals such as the Hirnantian and (especially) Rhuddanian showing much more uniform distributions.

As seen among extant communities ((Belmaker et al. 2008); (Morlon et al. 2008)), there is a general correlation between how close two formations are and how similar the brachiopod faunas are (Fig. A4).

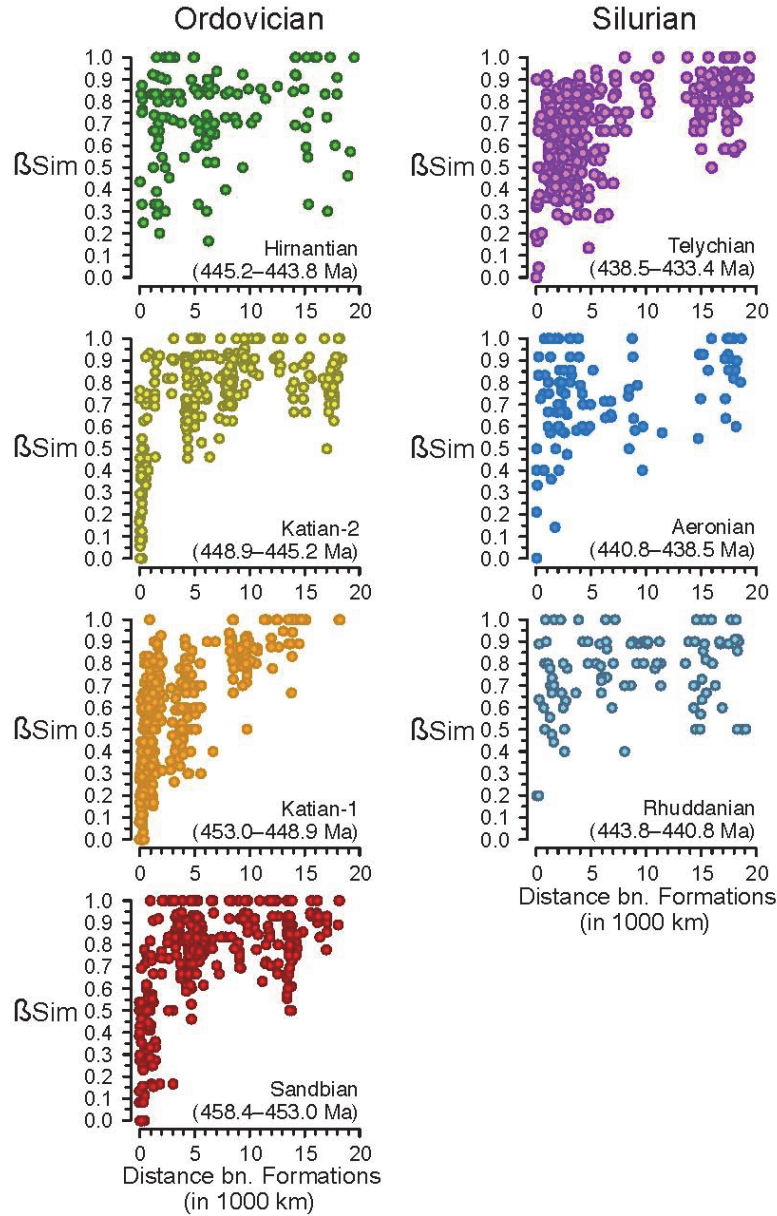


Fig. A4 - Faunal dissimilarity vs distance between formations. Dissimilarity here is Simpson's ((1960)) metric, which is $1 - (\text{shared} / \text{maximum possible shared})$.

We accommodate spatial autocorrelation by repeating these analyses so that formations were subsampled only if each of the 5 or 6 formations was 500 or 1000 kilometers apart from the other 4 or 5 subsampled formations (see Fig. A5).

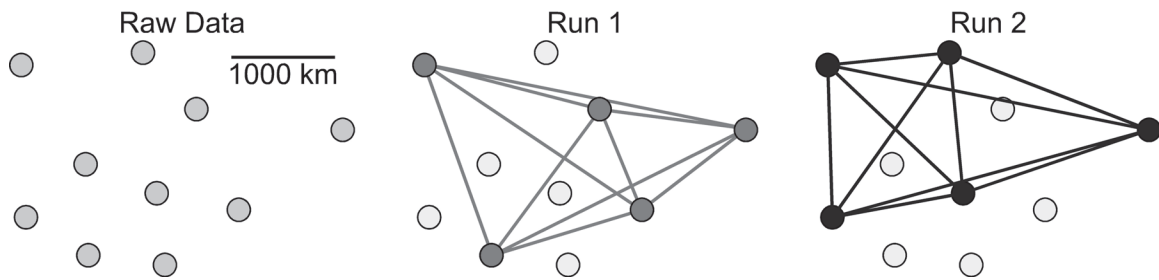


Fig. A5 – Subsampling five formations 1000 km apart. Starting with the initial distribution of formations (dark gray), we sample 5 formations that are 1000 km apart from each other (blue and purple). Subsampling routines keep the 2nd subsampled formation only if its centroid is 1000+ km from the 1st formation’s centroid; otherwise, it continues sampling until a 2nd formation meeting that criterion is found. The 3rd formation is kept only if its centroid is 1000+km from both the 1st and 2nd formations’ centroids. This is repeated until 5 formations 1000+ km apart (or 6 formations 500+ km apart) are found.

Extrapolated Diversity Patterns

Subsampling provides interpolated estimates of relative diversity at some measure of “common” sampling. We augmented this with extrapolated estimates of both overall richness (gamma diversity) and faunal dissimilarity (beta diversity). We stress that the extrapolations are made *after* we subsampled six formations with 10+ occurrences or five formations with 15+ occurrences. We then used the distributions of brachiopod with 1, 2, 3, etc. finds to extrapolate gamma or beta diversity for that sampling run. As different runs subsampled different formations, the estimates of gamma and beta diversity varied from run-to-run.

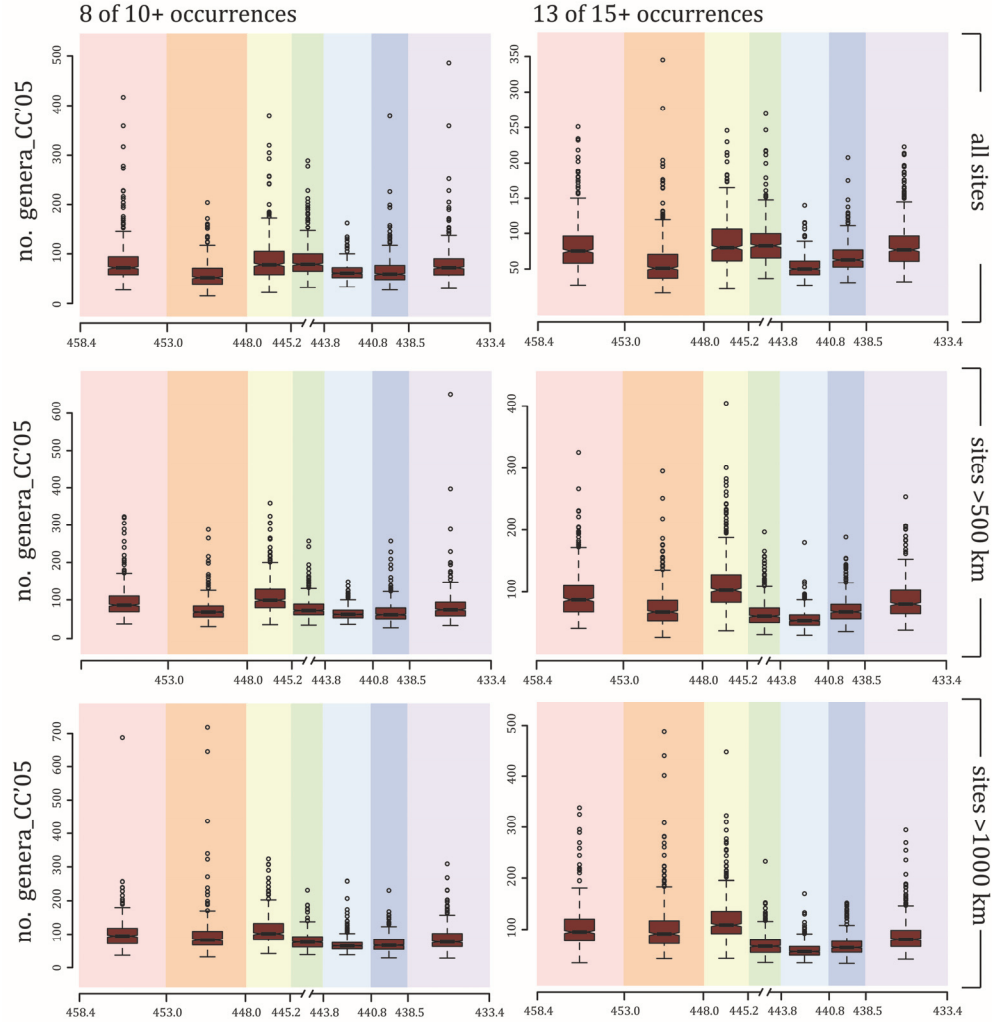


Fig. A6. Chao-2 ((Chao 1984)) estimates of generic richness based on all occurrences from five or six formations with 10+ or 15+ occurrences each. Error bars show 95% of formation subsamplings.

We extrapolate richness, S_{est} , using the Chao-2 metric. When using occurrence data, this is:

$$S_{est} = S_{obs} + \left(\frac{C-1}{C} \right) \left(\frac{q_1[q_1-1]}{2[q_2-1]} \right)$$

where S_{obs} is the observed richness given 5 or 6 subsampled formations, C is the number of collections in the five or six formations, q_1 is the number of genera with one

occurrence in those 5 or 6 formations, and q_2 is the number of genera with two occurrences in those 5 or 6 formations (see (Chao 1987); (Chao and Lee 1992)). Note that we derive similar patterns using Jackknife estimators of richness (see, e.g., (Burnham and Overton 1978, 1979)). These capture the general patterns shown by subsampling, especially when we look at the effects of constraining sampling to distant formations. The one major difference is that extrapolated richness suggests that generic diversity was slightly lower in the Rhuddanian (right after the second major extinction pulse) than it was in the Hirnantian (between the first and second extinction pulses). In contrast, subsampled richness interpolates slightly higher richness in the Rhuddanian than in the Hirnantian (see main text).

The basic principles of extrapolated richness can be extended to shared richness between two biotas ((Chao et al. 2000), (2005); (Pan et al. 2009)). Here, we modify the approach developed by Chao et al. ((2005)) to estimate Simpson's ((1960)) dissimilarity. Chao et al. used Jaccard and Sorensen's similarity metrics in their examples; however, the core components to each similarity (or dissimilarity) metric is the same: shared richness (S_{AB}), richness in Formation A (S_A) and richness in Formation B (S_B). The Simpson Dissimilarity metric is:

$$\beta_{Sim} = 1 - \frac{S_{AB}}{\min(S_A, S_B)}.$$

In other words, it is the compliment of the proportion of possible shared taxa that are shared. Thus, this goes to zero if all of the taxa in the less diverse formation are seen in the more diverse formation. Chao et al.'s extrapolated dissimilarity (or similarity) metrics replace S_{AB} with UV , S_A with $U(1-V)$ and S_B with $V(1-U)$, where:

$$U = \sum_{i=1}^{S_{AB}} \left(\left[\frac{a_i}{N_A} \right] + \left[\frac{C_B - 1}{C_B} \times \frac{m_{B1}}{2m_{B2}} \times \sum_{j=1}^{S_{AB}} \left(\frac{a_j}{N_A} \mid b_j = 1 \right) \right] \right)$$

And

$$V = \sum_{i=1}^{S_{AB}} \left(\left[\frac{b_i}{N_B} \right] + \left[\frac{C_A - 1}{C_A} \times \frac{m_{A1}}{2m_{A2}} \times \sum_{j=1}^{S_{AB}} \left(\frac{b_j}{N_B} \mid a_j = 1 \right) \right] \right)$$

where:

a_i = number of occurrences for species i in Formation A;

b_i = number of occurrences for genus i in Formation B;

N_X = number of occurrences in Formation X;

C_X = number of collections in Formation X;

m_{X1} = proportion of mutually shared taxa known from one collection in Formation X;

m_{X2} = proportion of mutually shared taxa known from two collections in Formation X (this is replaced with 1.0 if $f_{X2} = 0$).

Note also that the second summation sums the proportion of occurrences in Formation A (or B) only for those species with single occurrences in Formation B (or A). In other words, it gives the proportion of occurrences in one formation from taxa that are singletons in the other formation. Finally, note that the second term is adjusted by the number of collections rather than the number of occurrences, as it is collections that sets the limit on how many occurrences a genus might have. (That is, if there are 10 collections, then all taxa can have at most 10 occurrences, regardless of how many specimens we collect.)

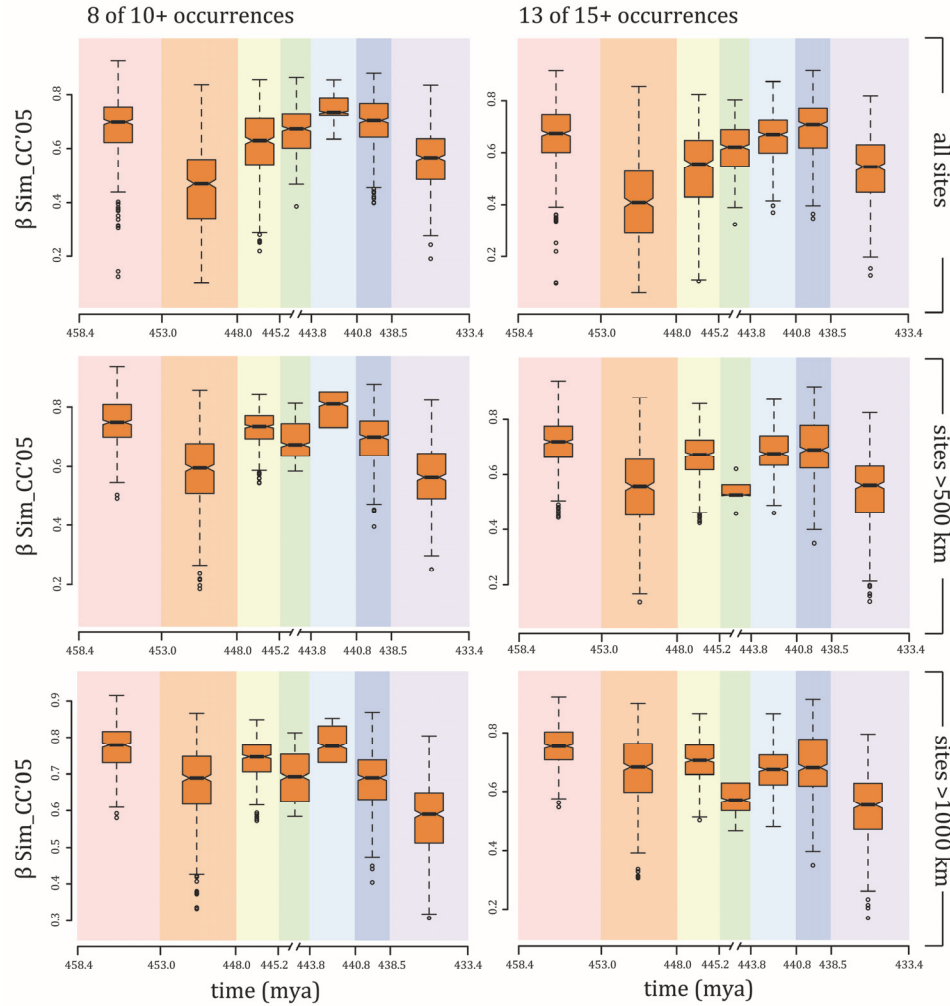


Fig. A7. Faunal dissimilarity among formations after using Chao et al.'s (2005) corrections for unsampled shared richness and unsampled true richnesses.

As with the Chao2 estimate of true generic richness, we extrapolated Simpson's dissimilarity after subsampling six formations of 10+ occurrences or five formations of 15+ occurrences. As with the richness estimate, we used all occurrences from each subsampled formation: the variation in results reflects different runs sampling different combinations of formations.

Extrapolated beta diversity patterns generally resemble those of subsampled beta diversity patterns (Fig. A7). In particular, Hirnantian beta diversity is very low,

particularly when we examine only well-sampled formations that are distantly separated. This reflects the tendency for shared Hirnantian genera to be found infrequently in one formation or the other, despite a general lack of singletons in the overall samples. Thus, extrapolated shared diversity rises faster than extrapolated total richness. Other patterns remain similar, such as the tendency for geographically constrained sampling to greatly elevate Katian beta diversity. The one major difference is that Telychian beta diversity drops much more markedly relative to other intervals when using extrapolated beta diversity.

Occupied Formations

One simple summary of faunal dissimilarity can be gleaned visually from the average number of formations from which genera are known. Here, we show this after the 6-by-10 and 5-by-15 subsampling routines. We show only the 20 most commonly sampled taxa given 500 subsamplings (Fig. A8). The results correspond well with the beta diversity analyses. Given no geographic constraints on subsampling, the highest average subsampled formations are for genera in the Katian-1. However, once geographic restrictions are imposed, Katian-1 looks much like other intervals. The opposite happens for the Hirnantian: after geographic constraints are imposed, and especially given denser sampling, there we see a large number of genera frequently found in multiple formations. Interestingly, the pattern in Telychian is largely unaffected by geographic constraints.

Extinction & Geographic ranges

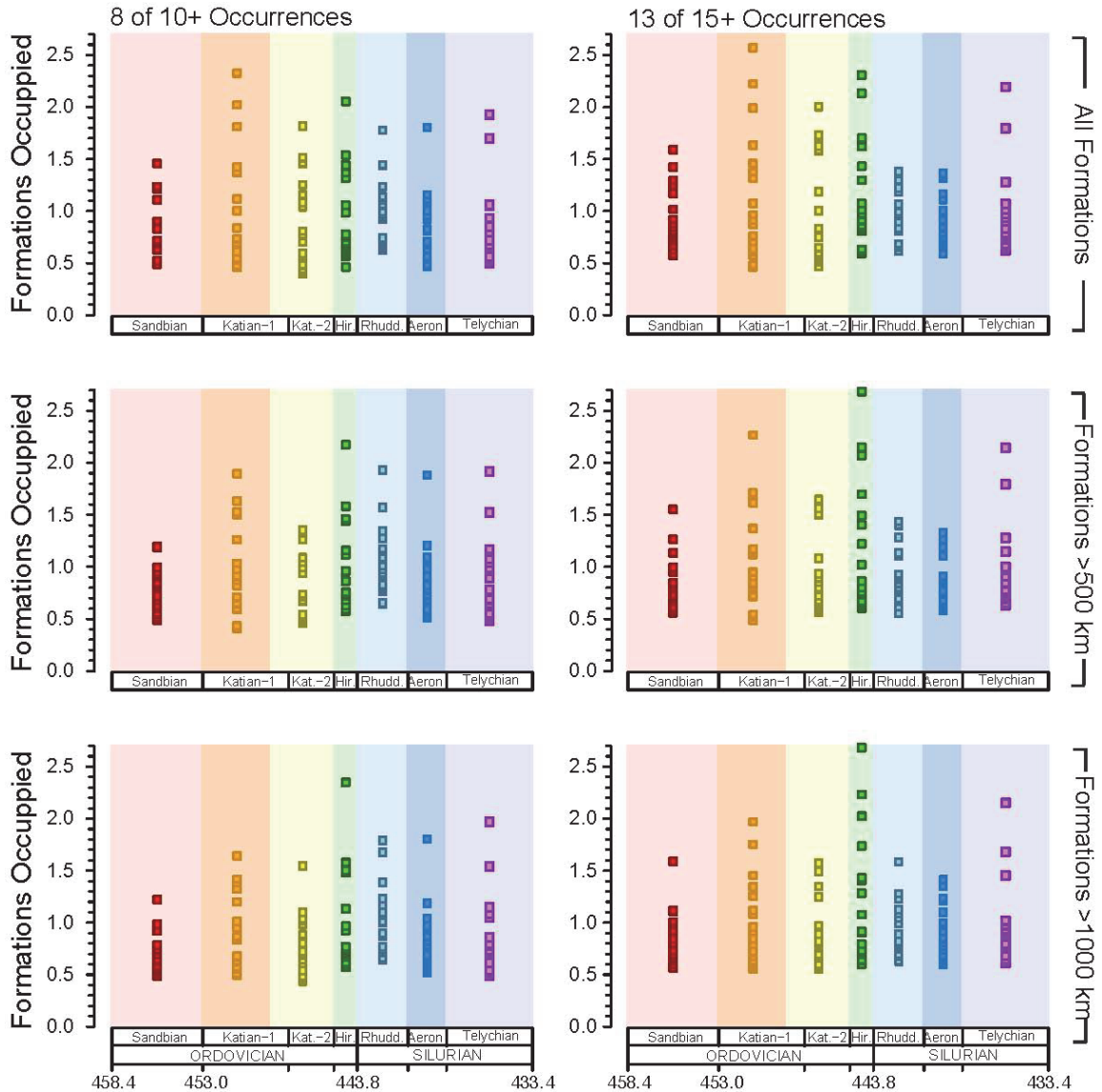


Fig. A8. Average numbers of formations in which the 20 widest-spread genera are found given 500 subsampling replications and different subsampling routines.

Many studies document that taxa with broad geographic ranges have lower extinction rates during “normal” intervals. A similar pattern is apparent here. If we look only at genera known from 2+ formations, we see that the two pulses (affecting Katian-2 and Hirnantian genera) both stand out for having unusual numbers of wide-ranging genera go

extinct (Fig. A9). However, in other intervals, extinctions are concentrated among narrowly ranging genera. We stress that these actually show “last appearance” frequencies, which are a combination of extinction and sampling in younger intervals ((Sepkoski 1975); (Foote and Raup 1996)). However, analyses accounting for sampling corroborate the general patterns shown here (e.g., (Krug and Patzkowsky 2004)). This stands in marked contrast with patterns among genera known from single formations (Fig. A10).

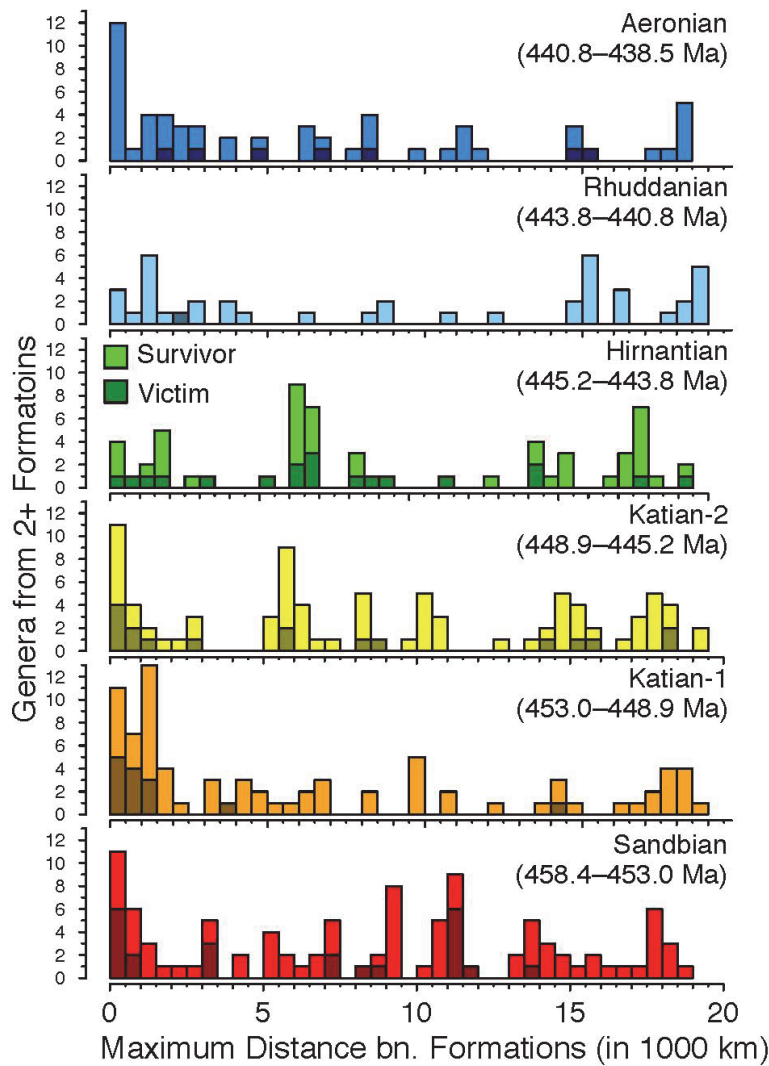


Figure A9. Maximum distances between formations for those taxa known from 2+ formations. Dark shades represent taxa last observed in that interval.

Among these genera, the two pulses (again affecting Katian-2 and Hirnantian genera) have elevated last appearance frequencies. However, the 1-unit support bars for all six intervals overlap, which means that we cannot reject a null hypothesis of constant extinction rates for endemic genera given these data (see (Edwards 1992)).

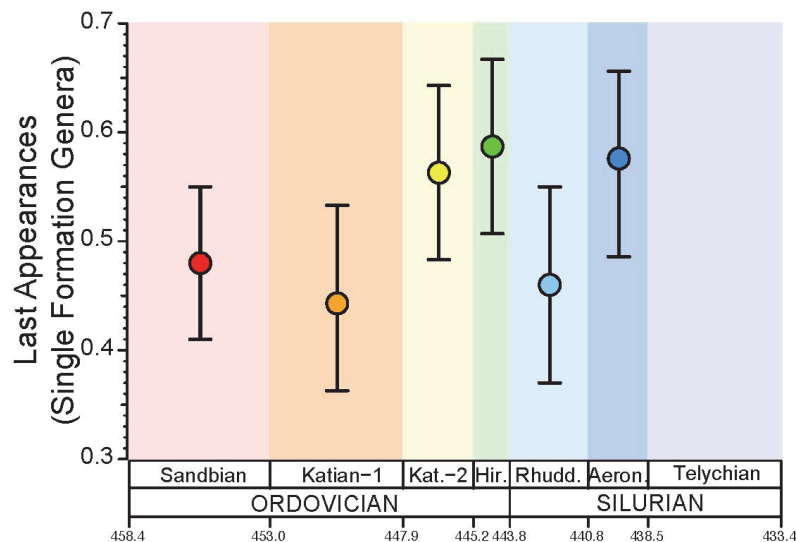


Figure A10. Last appearance frequencies for genera observed in only one formation. Bars represent one unit support on hypothesized frequencies greater or less than the observed. These reflect a combination of extinction and sampling of later time intervals.

Indeed, disappearance rates for Aeronian endemics match those of the Katian-2 and Hirnantian: the chief difference is the much higher survivorship among the few broadly ranging genera. (Also, many more of these “last appearances” are artifacts of sampling, as these genera are known from post-Telychian formations; this is not true for any of the genera last appearing in the Katian or Hirnantian.) Regardless of the dynamics in the Silurian, these patterns do emphasize that what stands out about the two pulses of extinction is the elimination of brachiopod genera with wide ranges.

Geographic range shifts

In addition to extinction, taxa might suffer decreased ranges during turnover events.

Correspondingly, some “opportunists” might greatly expand their geographic ranges. Also, major shifts in beta diversity might accompany large decreases in typical ranges (increasing endemism and elevating beta diversity) or large increases in typical ranges (increasing ubiquity and decreasing beta diversity). The end-Katian pulse not only sees numerous wide-ranging genera disappear (red lines in Fig. A11), but it also sees many widely-ranging genera suffer major decreases in their range sizes. Subsequently, the wide-ranging Hirnantian do include several genera that widely expand their ranges (including some genera appearing for the first time, denoted by blue lines in Fig. A12). However, many of the wide-ranging genera actually have diminished ranges from the Katian-2. Moreover, if we look at the distribution of range shifts (Fig. A13), the Hirnantian does not show an unusually large number of genera with major increases in maximum distances between occurrences. In contrast, the major decrease in beta diversity in the Telychian accompanies numerous major increases in geographic range.

The pattern across the second pulse is even more exaggerated. Very few wide-ranging Hirnantian genera contribute to the (small) population of wide-ranging Rhuddanian genera.

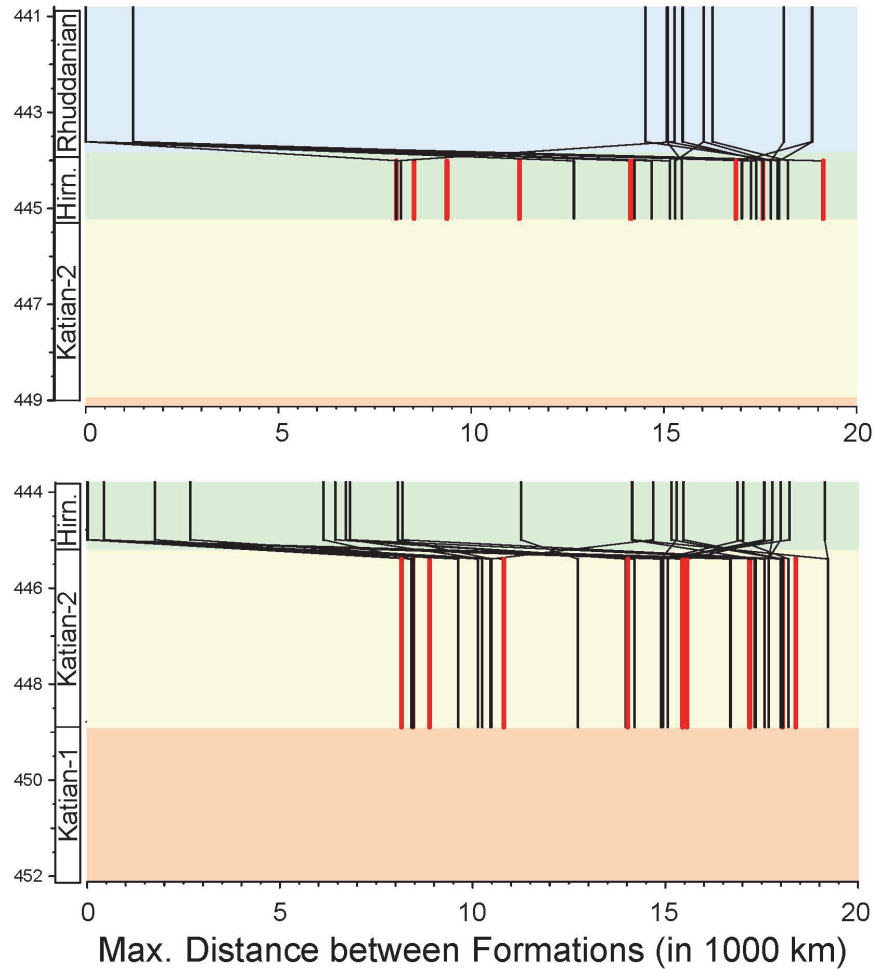


Fig. A11. Fates of Katian-2 and Hirnantian genera known with maximum range distances of 7500+ kilometers. Red lines denote genera that last appear in that interval. Shifts link earlier and later members of genera that survive pulses.

Wide-ranging Hirnantian genera suffer both high extinction rates and high decreased range frequencies (Fig. A11, A13). Thus, it seems that many of the survivors suffered considerable extirpation. The few wide-ranging Rhuddanian genera represent a mix of wide-ranging Hirnantian genera with decreased ranges, Hirnantian survivors with greatly increased ranges, and first appearing genera.

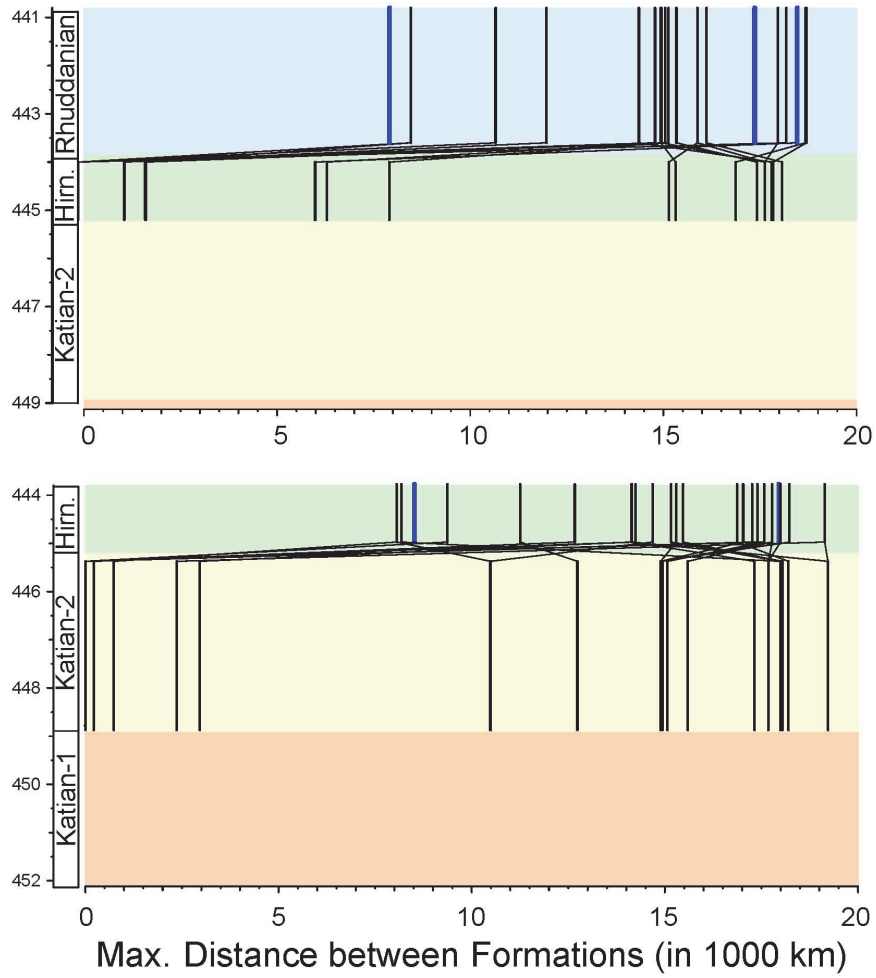


Fig. A12. Origins of Katian-2 and Hirnantian genera known with maximum range distances of 7500+ kilometers. Blue lines denote genera that first appear in that interval. Shifts link earlier and later members of genera that survive pulses.

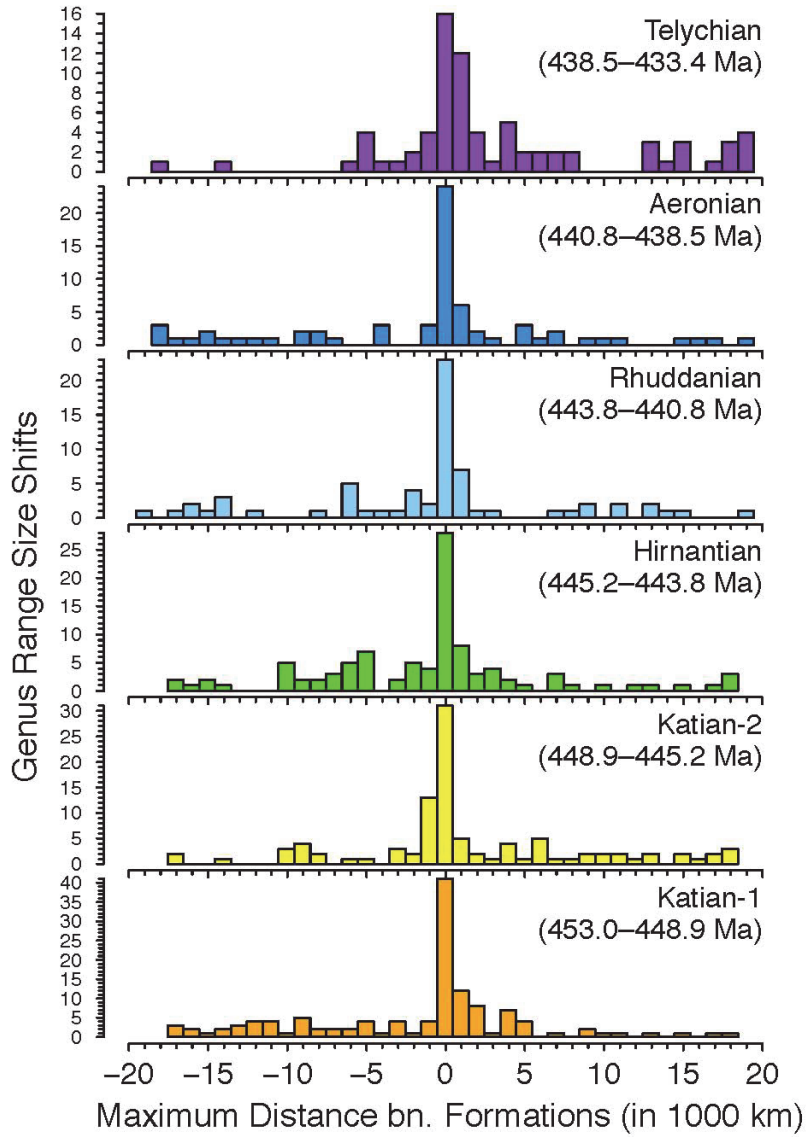


Fig. A13. Changes in geographic range size for genera surviving from the prior interval. Thus, each point in the Katian-1 ranges reflects the difference between that genus' range in the Katian-1 and the preceding Sandbian.

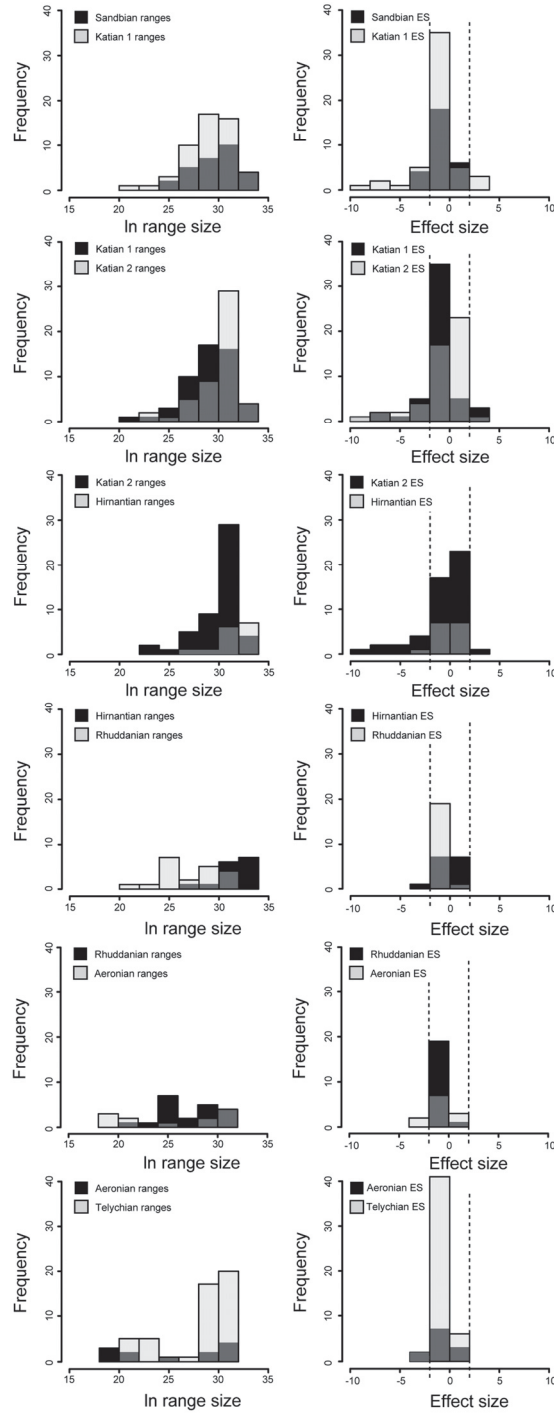


Fig. A14 - Range size and effect size frequency plots for studied interval; in each case genus ranges/effect sizes in preceding stage (dark grey) are plotted behind those of succeeding stage (light grey) in order to highlight transitions. In effect size plots 2 sigma significance levels are given by dashed lines

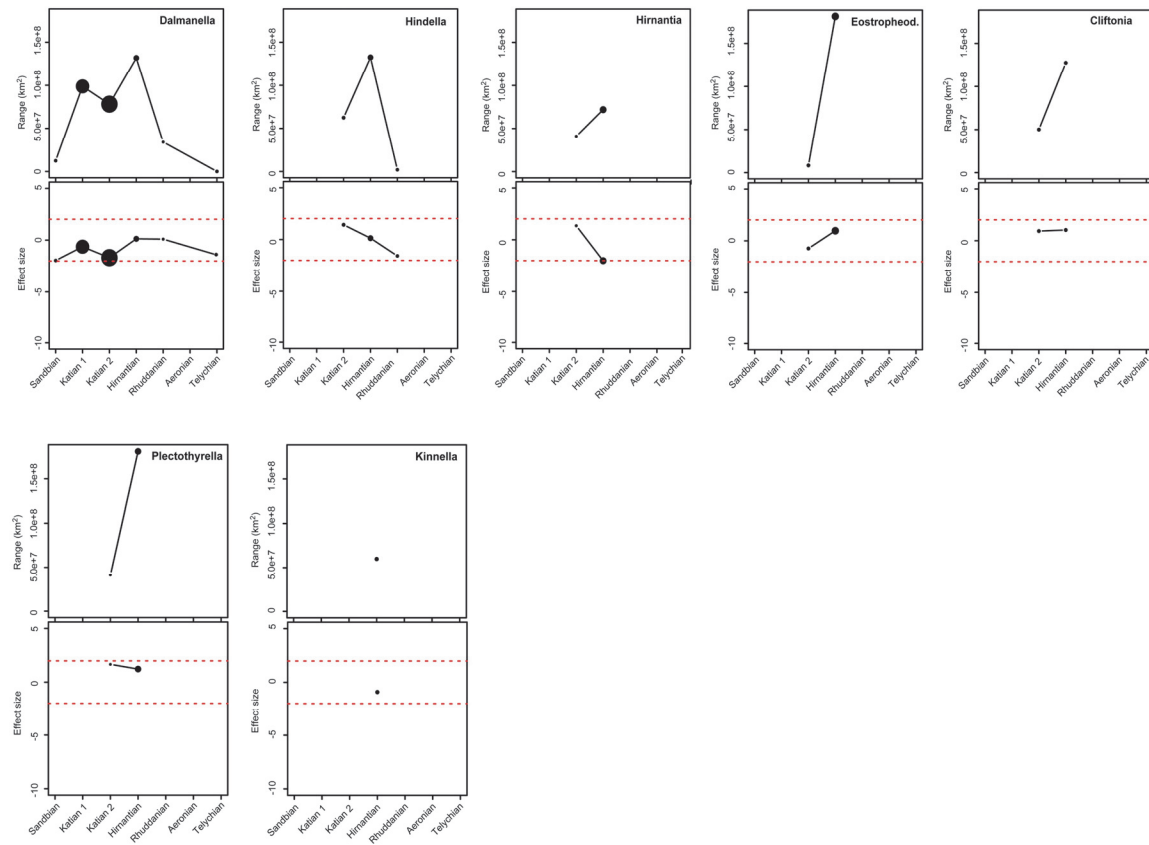


Fig. A15 - Individual range size/effect size trajectories for genera belonging to the archetypical 'Hirnantia fauna' (as defined by Rong and Harper, 1988); point size is proportional to the total number of sites occupied.

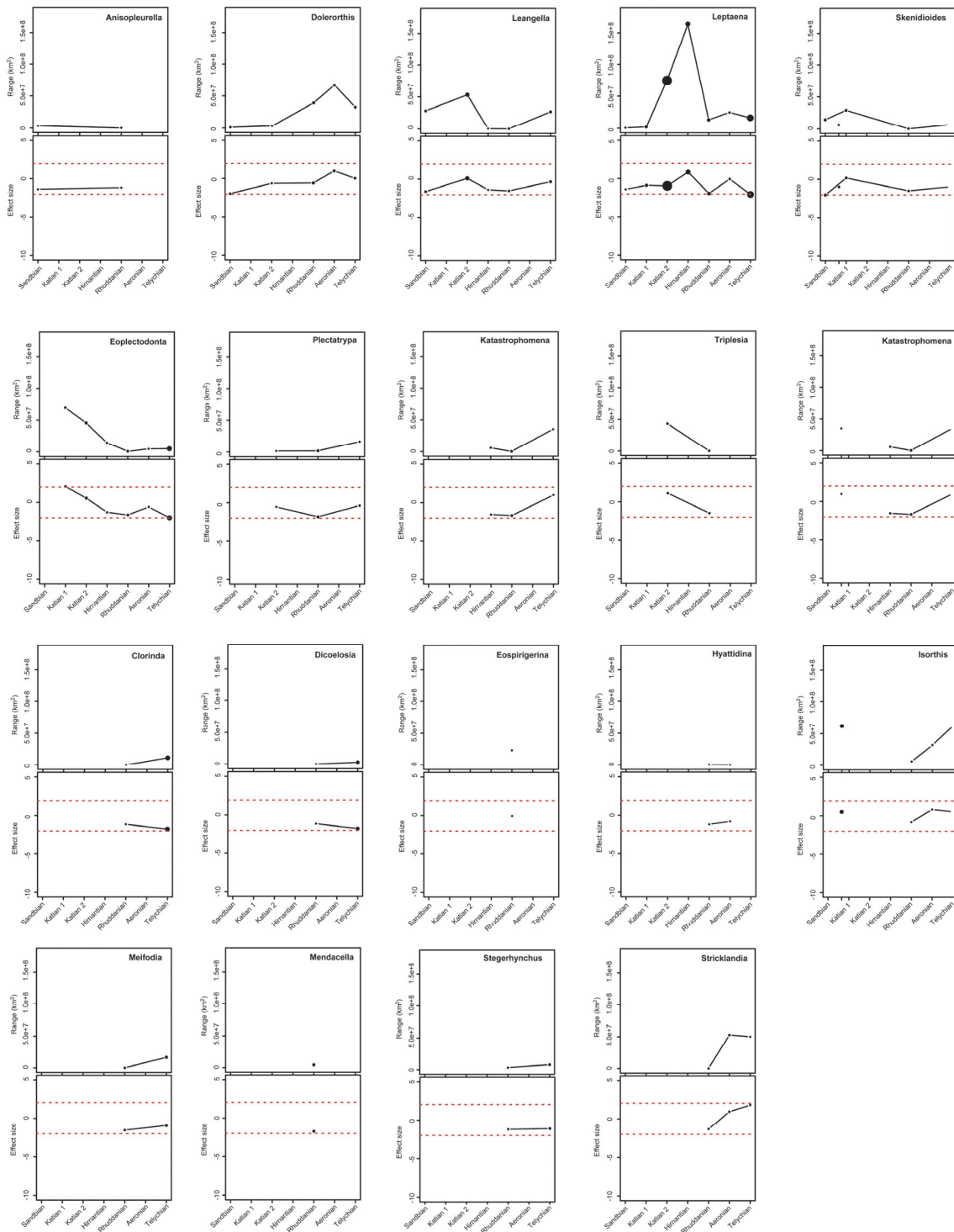


Fig. A16 - Individual range size/effect size trajectories for genera present in the Rhuddanian; note that Rhuddanian communities comprise Ordovician 'lazarus' taxa, holdovers belonging to the 'Hirnantia fauna', and newly evolved members of the Silurian fauna. Point size is proportional to the total number of sites occupied.

Analysis	8-by-10					
Gamma	Sand.-Kat.1	Kat.1-Kat.2	Kat.2-Hirn.	Hirn.-Rhudd.	Rhudd.-Aer.	Aer.-Tely.
All Sites	-5.688	4.590	2.584	-1.220	-1.862	2.388
500 km	-3.538	4.682	-3.748	0.444	-1.234	1.910
1000 km	-1.050	1.752	-3.918	0.344	-1.218	1.690
Gam. CC'05						
All Sites	-24.068	29.830	-0.160	-24.202	2.428	13.624
500 km	-20.520	35.474	-31.972	-12.694	2.360	14.978
1000 km	-4.624	17.650	-36.526	-10.060	-0.176	16.762
Alpha						
All Sites	-0.426	0.420	0.351	-0.267	-0.411	0.668
500 km	-0.160	0.404	-0.383	-0.002	-0.308	0.635
1000 km	0.119	0.130	-0.432	0.012	-0.369	0.619
Beta						
All Sites	-0.094	0.063	0.025	0.020	-0.010	-0.013
500 km	-0.055	0.051	-0.041	0.031	-0.003	-0.022
1000 km	-0.031	0.020	-0.038	0.027	0.002	-0.025
Beta CC'05						
All Sites	-0.225	0.158	0.050	0.078	-0.046	-0.138
500 km	-0.165	0.147	-0.040	0.104	-0.100	-0.129
1000 km	-0.096	0.064	-0.051	0.102	-0.111	-0.099
Analysis	13-by-15					
Gamma	Sand.-Kat.1	Kat.1-Kat.2	Kat.2-Hirn.	Hirn.-Rhudd.	Rhudd.-Aer.	Aer.-Tely.
All Sites	-8.786	5.514	3.280	-4.446	3.182	2.690
500 km	-5.340	6.926	-9.012	0.704	3.352	2.534
1000 km	-1.192	2.422	-10.030	1.196	2.288	2.990
Gam. CC'05						
All Sites	-23.504	25.268	-0.424	-31.464	12.632	19.326
500 km	-20.960	35.898	-43.474	-13.772	15.132	16.524
1000 km	-0.368	16.464	-49.764	-13.944	11.590	19.394
Alpha						
All Sites	-1.070	0.769	0.654	-1.352	0.362	1.284
500 km	-0.455	0.956	-1.272	-0.558	0.379	1.389
1000 km	0.131	0.238	-1.263	-0.434	0.257	1.448
Beta						
All Sites	-0.144	0.072	0.031	0.049	0.027	-0.052
500 km	-0.084	0.072	-0.115	0.117	0.026	-0.057
1000 km	-0.040	0.026	-0.133	0.120	0.019	-0.051
Beta CC'05						
All Sites	-0.248	0.120	0.078	0.049	0.034	-0.158
500 km	-0.170	0.122	-0.127	0.144	0.009	-0.151
1000 km	-0.086	0.037	-0.158	0.126	0.014	-0.148

Table A1 – First differences between mean values of alpha, beta, and gamma diversity in each geological stage, for the two subsampling routines (compare with Figures 7-9 in main text). For ease of reading, increases between stages are in black, while decreases are highlighted in blue.

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