

Rapid recovery from the Late Ordovician mass extinction

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Understanding the evolutionary role of mass extinctions requires detailed knowledge of postextinction recoveries. However, most models of recovery hinge on a direct reading of the fossil record, and several recent studies have suggested that the fossil record is especially incomplete for recovery intervals immediately after mass extinctions. Here, we analyze a database of genus occurrences for the paleocontinent of Laurentia to determine the effects of regional processes on recovery and the effects of variations in preservation and sampling intensity on perceived diversity trends and taxonomic rates during the Late Ordovician mass extinction and Early Silurian recovery. After accounting for variation in sampling intensity, we find that marine benthic diversity in Laurentia recovered to preextinction levels within 5 million years, which is nearly 15 million years sooner than suggested by global compilations. The rapid turnover in Laurentia suggests that processes such as immigration may have been particularly important in the recovery of regional ecosystems from environmental perturbations. However, additional regional studies and a global analysis of the Late Ordovician mass extinction that accounts for variations in sampling intensity are necessary to confirm this pattern. Because the record of Phanerozoic mass extinctions and postextinction recoveries may be compromised by variations in preservation and sampling intensity, all should be reevaluated with sampling-standardized analyses if the evolutionary role of mass extinctions is to be fully understood.

diversity | Silurian

The pace of diversification after mass extinction reveals much about the ecological and evolutionary processes that govern global biodiversity. Diversification may lag, owing to a slow response of the global environment to the perturbation that caused the mass extinction (1). Diversification may be logistic with the shape and duration of the rebound dependent on the magnitude and duration of the extinction and whether or not the system was at equilibrium immediately before the mass extinction (2). Diversification of some taxonomic groups may jump dramatically in the wake of mass extinctions if other groups that inhibited diversification during background times are dramatically reduced in species numbers (3). Diversification may be synergistic as new species facilitate the formation of more new species, causing per-taxon origination rates to increase continually for several million years (Myr) after the mass extinction (4, 5). Finally, diversification may vary geographically, with each region having different diversity trajectories and varying proportions of bloom taxa and invaders (6).

The models of postextinction diversity recovery above all are based at least in part on a direct reading of the fossil record with the assumption that the fossil record is an accurate and unbiased record of diversity. However, it has long been known that variability of sampling through time may exert a strong control on perceptions of Phanerozoic diversity trends (7). Recent studies have begun to evaluate in greater detail sampling biases on diversity by using a variety of methods and databases (8–10). Some intervals of mass extinction have come under close scrutiny because they tend to have a close association with sea-level

changes and drops in rock volume that bias the preserved record of diversity, extinction, and origination (10–15).

Here, we examine diversity and taxonomic rates through the Late Ordovician mass extinction and Early Silurian recovery in Laurentia based on genus occurrence data for articulate and inarticulate brachiopods, trilobites, bivalve mollusks, and corals. Laurentia contains some of the best-documented Upper Ordovician and Lower Silurian tropical marine benthic faunas known from this time interval. The occurrence data permitted us to perform a sampling-standardized analysis of extinction and recovery in this region and compare it to the global picture based on the Sepkoski compendium (16). A much more rapid rebound of diversity in Laurentia compared to globally suggests that the ecological processes of recovery were different between these two geographic scales. Our results also point to the need for sampling-standardized analyses on other paleocontinents and for the whole globe to determine how regional and global patterns relate. This analytical approach should be extended to other Phanerozoic mass extinctions where variations in sampling intensity are of concern.[†]

Data

There are many sources of bias inherent in measuring diversity through time, including variations in sampling intensity (8, 17–19), variations in sampling across environmental gradients (10, 20, 21), and variations in sampling among geographic regions (22, 23). We attempted to minimize these biases in compiling the data for this study. The database for Laurentia was constructed by using lists of genus occurrences. A total of 5,762 occurrences from 746 lists were downloaded from the Paleobiology Database (24) and supplemented through an independent literature search. Most supplemental lists have since been entered into the Paleobiology Database (see *Supporting Text*, which is published as supporting information on the PNAS web site). Taxonomic lists were placed into one of seven time intervals (see below). Each of the time intervals is well sampled from offshore through the shallow subtidal environmental zones with the exception of the Aeronian, where the deep subtidal environment is undersampled (Table 1). All of the time intervals also show a fairly broad geographic distribution of lists (Table 2). Despite attempts to obtain even sampling intensities, however, variability exists in the number of occurrences per time interval (Fig. 1). Particularly important is a large drop in sampling intensity from the Ashgill (Late Ordovician) to the Rhuddanian (Early Silurian), strengthening the need for sample standardization (see *Methods*).

Taxonomic assignments were updated where applicable through examination of the recent literature. To assess the effects of any remaining taxonomic problems, we also eliminated from our analyses very old lists, lists from references that

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Abbreviation: Myr, million years.

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Table 1. Environmental distribution of lists

Time interval	Environment						
	Basin	Offshore	Deep subtidal	Shallow subtidal	Peritidal	Reefs	Undefined
Wenlock	1	50	23	10	18	10	
Telychian	10	18	27	29	1	3	18
Aeronian	0	38	7	25	1		1
Rhuddanian	2	15	23	5	2		16
Ashgill	1	33	21	31	2		22
Upper Caradoc	4	54	43	48	3		7
Lower Caradoc	4	62	35	17	4		2

Numbers designate the number of lists entered for each environment in each time interval.

appeared otherwise especially problematic, and singletons (see below). Culling the data in these ways did not alter the overall diversity trends significantly, suggesting that the patterns are robust and that any remaining taxonomic problems are distributed randomly and do not obscure the underlying diversity patterns (25).

Global diversity was calculated from Sepkoski's compendium of genus first and last appearances (16). The compendium data can be ranged through to determine diversity, proportional origination, and proportional extinction. Because of the structure of the data (a record of first and last appearances rather than a list of all occurrences), it cannot be standardized for sample size, as can the Laurentian data. However, it does serve as a basis for comparison for the Laurentian diversity and turnover metrics.

Varying durations of time intervals can affect both diversity and turnover calculations (17). For example, as the duration of a time interval increases, diversity within that interval rises, while proportional extinction and origination metrics asymptotically approach one. To reduce the effects of this bias, the Laurentian time scale was divided into seven time intervals of roughly equal duration. The Caradoc series was divided into upper and lower intervals at the base of the Rocklandian stage, the Ashgill and Wenlock were left intact, and the Llandovery was divided into its three stages, the Rhuddanian, Aeronian, and Telychian. Correlation between North American and global series and stages are based on Webby (26), Ross *et al.* (27), Barnes *et al.* (28), Berry and Boucot (29), and Norford (30). Dates for the base of each Ordovician and Silurian series were taken from Tucker and McKerrow (31), and the dates for the intervening stages were determined by linear interpolation. The average duration of each Laurentian time interval is 5 Myr, with a SD of 0.5 Myr. We note that the radiometric dates used by Tucker and McKerrow (31) contain uncertainties in the range of plus or minus 2 Myr. However, when we exclude singletons, which

are sensitive to interval duration, the resulting diversity curve is minimally affected (see *Methods*).

Time intervals used for the calculation of global diversity were taken from Sepkoski's compendium (16) and were combined where possible to match time intervals used for the Laurentian data set. For example, although Sepkoski's two Ashgillian bins were combined to match the Laurentian, his three Caradoc subdivisions could not easily be combined into the two used for the Laurentian data.

Taxonomic groups analyzed were articulate and inarticulate brachiopods, bivalves, trilobites, and anthozoans. These taxa are generally well preserved and consistently reported and provide a good range of sampling of the three evolutionary faunas (32), accounting for 37% of Sepkoski's global Ordovician and Silurian data.

Methods

Total diversity in a time interval was calculated as the sum of the genera ranging into the interval, the genera that ranged through the interval, and the genera existing only in that interval (singletons). Proportional origination and extinction metrics were calculated as the number of originations or extinctions in a time interval divided by the total diversity in that interval.

Singletons are particularly sensitive to temporal variations in sampling and can produce misleadingly high turnover rates in such cases (17). However, because our time intervals have approximately equal durations, and because we standardize sample size in each interval (see below), much of the bias that singletons introduce was removed from our analysis. Also, singletons are expected to make up a greater proportion of diversity in the time interval containing a mass extinction, as a large proportion of the lineages originating in that stage are eliminated prematurely. Indeed, when singletons are removed

Table 2. Geographic distribution of lists

Lower Caradoc: Tennessee (59), British Columbia (27), Virginia (22), Tennessee and Virginia (6), Minnesota (2), Mississippi (2), New York (2), Wisconsin (2), Nevada (1), Ontario (1).
Upper Caradoc: Tennessee (74), Virginia (19), British Columbia (18), Ohio (15), Kentucky (12), Ohio and Kentucky (3), Northwest Territories/Arctic Canada (3), Virginia and Kentucky (3), Indiana (2), Minnesota (2), Nevada (2), Oklahoma (2), New York (1), Ontario (1), Pennsylvania (1), Quebec (1).
Ashgill: Quebec (32), Tennessee (19), Indiana (18), Ohio (16), Kentucky (5), Illinois (4), Missouri (4), Virginia (4), Iowa (2), Oklahoma (2), British Columbia (1), Michigan (1), Minnesota (1), Northwest Territories/Arctic Canada (1).
Rhuddanian: Quebec (22), Ontario (11), British Columbia (10), Northwest Territories/Arctic Canada (10), Missouri (5), New York and Ontario (4), Iowa (3), Greenland (2), Illinois (1), New Brunswick (1), Ohio (1), Yukon (1).
Aeronian: Northwest Territories (28), Iowa (12), Ohio (7), Kentucky (5), Wisconsin (5), Michigan (2), Quebec (7), British Columbia (2), Illinois (1), Indiana (2), Ontario (1).
Telychian: Iowa (29), British Columbia (17), Quebec (17), New York (10), Northwest Territories (10), Wisconsin (10), Ontario (2), New York and Ontario (2), Michigan (3), Illinois and Michigan and Iowa (1), Indiana (1), Nevada (1), Virginia (1), Ohio (1), Pennsylvania (1).
Wenlock: New York (22), Wisconsin (32), Northwest Territories/Arctic Canada (34), Iowa (6), Indiana (4), Quebec (3), Tennessee (7), New York and Ontario (2), Illinois (1).

Numbers designate the number of lists from each state or province in each time interval.

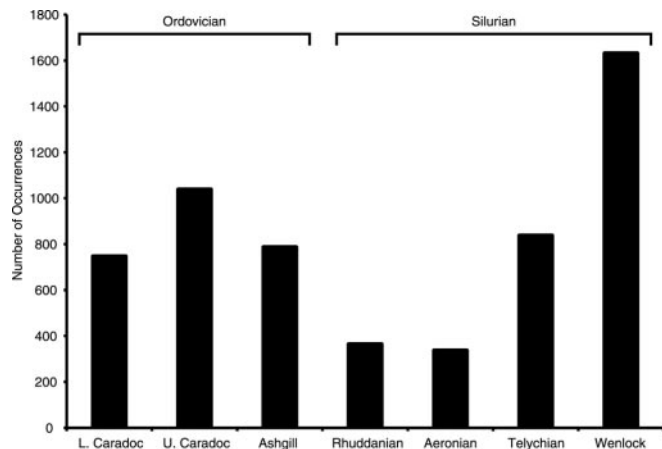


Fig. 1. Number of occurrences per time interval. Note the similarity between these data and the total diversity curve for Laurentia (see Fig. 3A). Particularly striking is the large drop in sampling intensity from the Ashgill (Upper Ordovician) to the Rhuddanian (Lower Silurian), coincident with the diversity drop that defines the mass extinction at this boundary.

from the analysis of the Laurentian data, the most notable difference is a reduction of Ashgillian diversity to Rhuddanian levels (data not shown). Although the curve is flatter overall, most other features of the diversity curve are retained, including the slight drop in diversity from the Upper Caradoc into the Ashgill, the relative lows in diversity in the Rhuddanian and Aeronian, and the increase in diversity in the Telychian (see Fig. 3A). Foote (17) discussed the issue of singletons in detail in the context of their effects on long-term variations in taxonomic rates through time. No discussion, however, is given to short time intervals such as around mass extinction events. We believe that the approximately equal duration of our time intervals and the use of sample standardization should remove most of the biases inherent in the use of singletons. Removing singletons would remove a large amount of legitimate data, especially within the interval containing the extinction event, and thus we retain singletons in our analyses presented here.

Data for the global curve included genera that were ranged through from older and younger intervals (i.e., older than the Caradoc and younger than the Wenlock). It was not possible to do the same for the Laurentian data, as no data from outside the interval were collected. Because of this, diversity near the edges of the study interval (Lower Caradoc and Wenlock) is reduced. These edge effects have minimal effect on diversity across the Ordovician–Silurian boundary.

Rarefaction of genus occurrences was performed initially to determine the effects of variations in sampling intensity (Fig. 1) on diversity among time intervals. We used ANALYTICAL RAREFACTION 1.3 (www.uga.edu/~strata/software) (19, 33) to perform these analyses. Rarefaction uses the relationship between diversity and sample size (here, number of occurrences) to predict diversity at a smaller, standard sample size. This procedure allows diversity between collections of unequal sample size to be compared directly. However, standard rarefaction handles diversity only within a single sample (e.g., a time interval) and does not permit the calculation of range-through diversity or turnover metrics (18, 19, 33). To perform a sample standardization of range-through data, a subsampling program was written to expand the rarefaction analysis (8, 24). A standard number of occurrences were drawn at random from each of the time intervals, genera were ranged-through intermediate time intervals, and diversity and turnover metrics were calculated. This process was repeated 1,000 times, the results were averaged, and error bars were calculated.

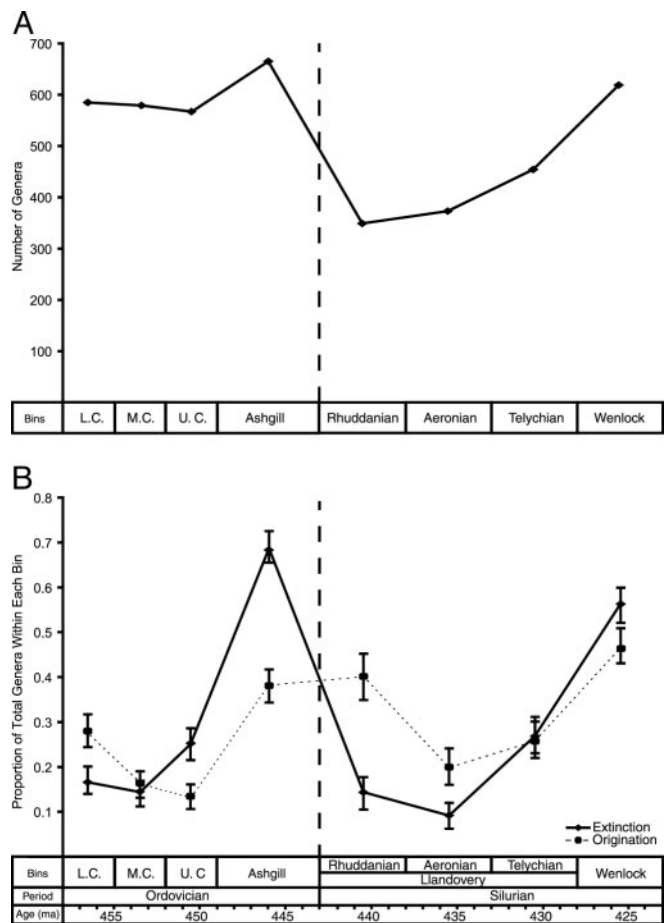


Fig. 2. Global diversity and turnover metrics. (A) Global diversity calculated from Sepkoski's compendium of generic first and last appearances (16). (B) Global proportional origination and extinction metrics. L.C., Lower Caradoc; M.C., Middle Caradoc; U.C., Upper Caradoc. Dashed line marks the Ordovician–Silurian boundary.

Results

Global diversity for articulate and inarticulate brachiopods, trilobites, anthozoans, and bivalves shows a slight dip through the Caradoc, a spike into the Ashgill, and then a sharp drop across the Ordovician–Silurian boundary (Fig. 2A), resulting in a diversity drop of 49%. Diversity was slow to rebound, achieving preextinction levels of diversity ≈ 15 Myr later in the Wenlock. The sharp drop in diversity across the Ordovician–Silurian boundary and slow rebound in the Silurian for this subset of Sepkoski's compendium is similar to that for the total Sepkoski data (5, 34).

Proportional extinction (Fig. 2B) based on Fig. 2A shows a significant spike in extinction in the Ashgill (69%) and then dropping in the Lower Llandovery (Rhuddanian) before a steady rise into the Wenlock. Proportional origination (Fig. 2B) is low in the Lower and Upper Caradoc, higher in the Ashgill and Lower Llandovery (Rhuddanian) spanning the Ordovician–Silurian boundary, and low again in the Middle Llandovery (Aeronian) before rising into the Wenlock. Although origination is elevated across the Ordovician–Silurian boundary, it does not spike in the Lower Llandovery (Rhuddanian). These patterns are generally similar to origination and extinction based on the total Sepkoski data (5) with the exception of elevated origination in the Ashgill and Lower Llandovery (Rhuddanian) seen in the subset of the Sepkoski data (Fig. 2B), which is not present in the global data.

The Laurentian diversity curve (Fig. 3A), although similar, contains some important differences from the global curve (Fig.

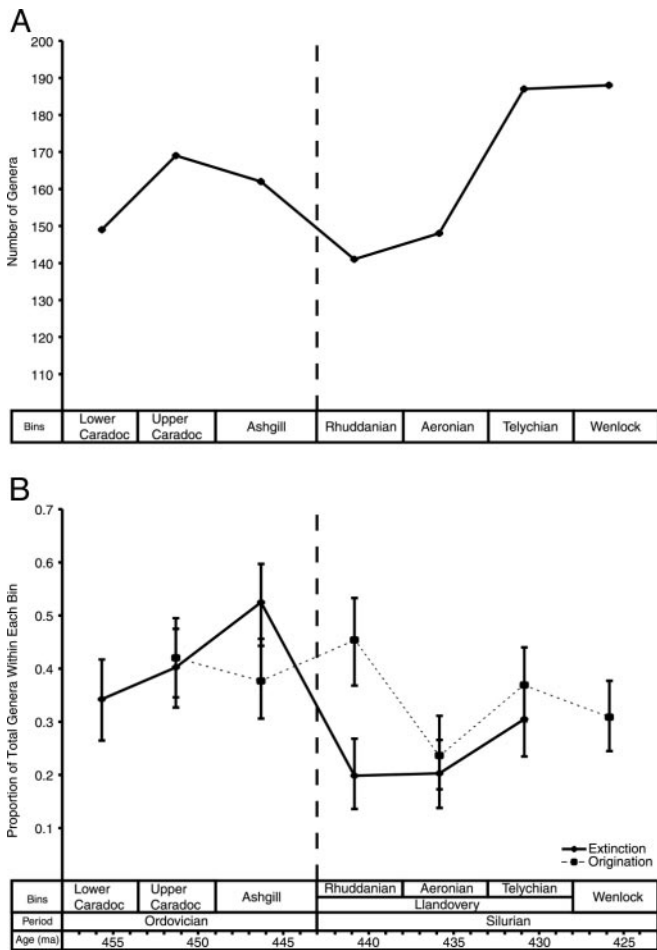


Fig. 3. Unstandardized diversity and turnover metrics for Laurentia. (A) Laurentian total generic diversity. The Caradoc is divided into two intervals here, with all others the same as in the global plot. Diversity is calculated as the total number of genera existing in Laurentia found within or ranged through a time interval. Because no data were collected from older or younger time periods, data could not be ranged through time intervals at the edges of this plot (i.e., the Lower Caradoc and the Wenlock). These edge effects do not significantly alter the trends across the extinction boundary. (B) Proportional origination and extinction metrics calculated for Laurentia. Unlike global rate metrics, regional rate metrics can incorporate factors such as immigration and local extinction in addition to taxonomic origination or extinctions. Dashed line marks the Ordovician-Silurian boundary.

2A). In the Laurentian curve, diversity rises from the Lower Caradoc to the Upper Caradoc, drops slightly in the Ashgill, and then drops more sharply into the Rhuddanian as a result of the extinction. Diversity drops by only 14% from the Ashgill to the Lower Llandoverly (Rhuddanian), significantly less than in the global data. The rebound to preextinction levels of diversity occurs by the Telychian, ≈ 5 Myr earlier than suggested by the global curve.

Proportional extinction (Fig. 3B) based on the Laurentian data (Fig. 3A) shows increasing extinction through the Lower and Upper Caradoc to a peak in the Ashgill of 53%, before dropping sharply in the Lower Llandoverly (Rhuddanian) and then rising slowly through the Middle and Upper Llandoverly (Telychian). The Laurentian extinction data (Fig. 3B) are generally similar to the Sepkoski global data (Fig. 2B) although the Ashgill extinction peak is lower (53% vs. 69%) in Laurentia, and extinction in the other time intervals is generally higher than the global data. Proportional origination is high in the Upper Caradoc and Ashgill and bumps up slightly in the Lower Llandoverly before dropping to lower levels in the Middle

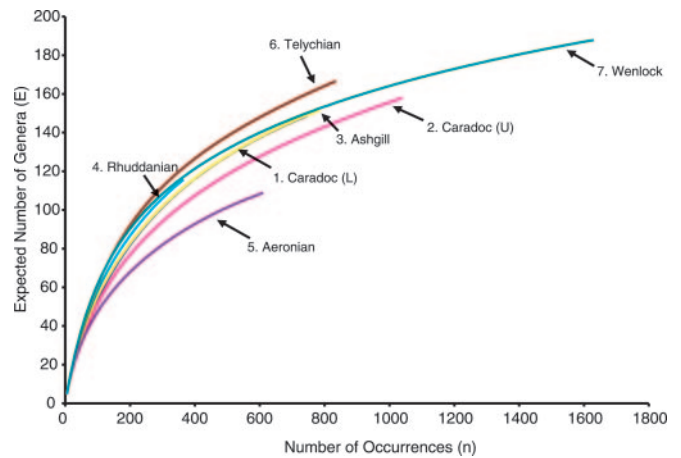


Fig. 4. Rarefaction curves for the seven time intervals used in this project. Rarefaction curves show the expected diversity for smaller sample sizes. Curves demonstrate that variations in sampling intensity have affected diversity trends across the Ordovician-Silurian boundary. Numbers before the time bins represent the order of the bins in time from oldest to youngest.

Llandoverly through Wenlock. The Laurentian origination data (Fig. 3B) differ from the global data (Fig. 2B) in that origination was generally high beginning in the Upper Caradoc and then bumped up slightly in the Lower Llandoverly, before attaining a lower level in the Middle Llandoverly through Wenlock.

Rarefaction curves for each time interval (Fig. 4) show the effect of variations in sampling intensity on perceived diversity trends for the paleocontinent of Laurentia. For example, with the exception of the Middle Llandoverly (Aeronian) curve, all other Silurian time intervals (Rhuddanian, Telychian, and Wenlock) lie above the Ordovician curves (Lower and Upper Caradoc and Ashgill). This result suggests that for a standard level of sampling, diversity is similar to or slightly higher in the Silurian compared to the Ordovician. The Middle Llandoverly (Aeronian) may be lower because of the poorer sampling in deep subtidal environments compared to other time intervals (Table 1).

Rarefaction with range-through produced a diversity trend across the Late Ordovician mass extinction that was markedly different from both the global and Laurentian total diversity curves (Fig. 5A). Diversity remains generally flat from the Lower Caradoc through Middle Llandoverly (Aeronian), including across the extinction boundary. Lower Llandoverly (Rhuddanian) diversity falls within the 95% confidence interval for the Ashgill, suggesting that, after the mass extinction, diversity rebounded to preextinction levels within 5 Myr, ≈ 15 Myr sooner than implied by the global curve. Diversity rises slightly in the Upper Llandoverly (Telychian) before dropping in the Wenlock, which most likely results from edge effects rather than an actual diversity decline.

Although Ashgillian diversity equaled Lower Llandoverly diversity (Fig. 5A), proportional extinction on the subsampled data still shows that 55% of Laurentian genera go extinct in the Ashgill (Fig. 5B). The Rhuddanian, however, sees a significant drop in extinction while origination peaks, bringing diversity back to preextinction levels. Both origination and extinction metrics drop below Ordovician levels by the Middle Llandoverly. These data therefore suggest that diversity changes in Laurentia are being driven by fluctuations in both extinction and origination. Importantly, these standardized data show a significant peak in origination in the first 5 Myr of the Silurian (Rhuddanian), which the unstandardized data at both the regional scale (Laurentia) and the global scale do not show.

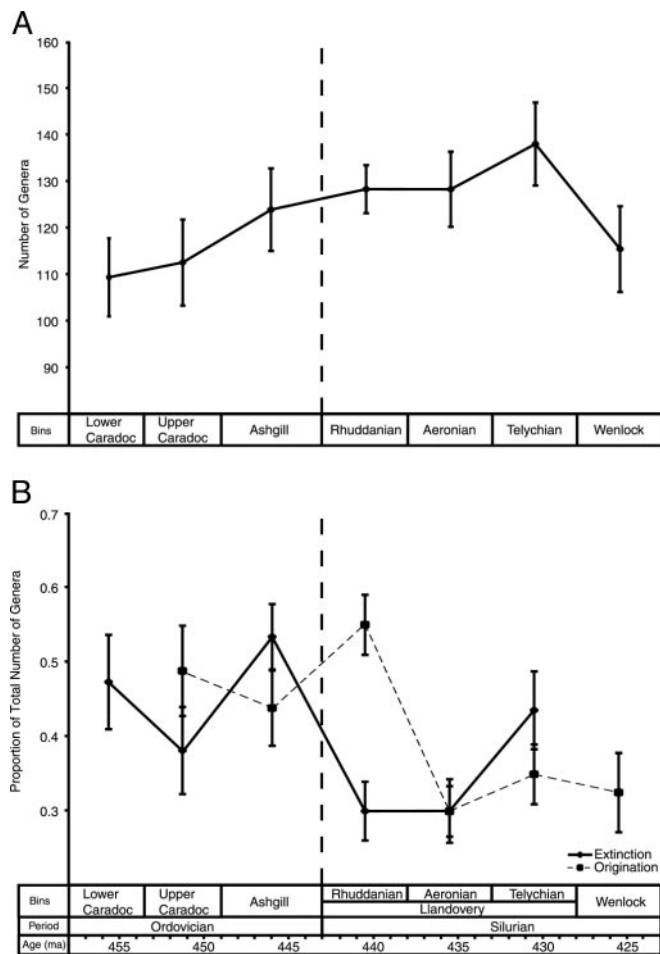


Fig. 5. Sampling-standardized diversity and turnover metrics for Laurentia. (A) Standardized diversity curve generated by using rarefaction with range-through (see text for explanation). (B) Proportional extinction and origination metrics based on the standardized data. Dashed line marks the Ordovician-Silurian boundary.

Discussion

Analysis of the Laurentian data indicates that the recovery from the Late Ordovician mass extinction occurred within 5 Myr in Laurentia (Fig. 5A) compared with between 15 Myr and 20 Myr globally (Fig. 2A). Adjusting for sample size had a significant effect on the Laurentian diversity patterns. The unstandardized diversity curve for Laurentia (Fig. 3A) changed dramatically after sample standardization with the peaks and valleys of diversity smoothed out across the Ordovician-Silurian boundary (Fig. 5A). Likewise, the patterns and absolute magnitudes of taxonomic rates change after adjustments for sample size (Figs. 3B and 5B). Because global diversity is built from many regional patterns, the current study points to the need for similar analyses on other paleocontinents to gain a more complete understanding of how global and regional patterns relate. Nonetheless, comparison of Laurentian diversity with global diversity has implications for the nature of the postextinction recovery.

Evidence for a rapid rebound of diversity after the Late Ordovician mass extinction also comes from studies of local community structure. Sheehan *et al.* (35) have suggested that reassembly of community structure after mass extinctions throughout the Phanerozoic and including the Early Silurian occurred within 3–8 Myr. In the Great Basin, Lower Silurian benthic communities are depauperate in the recovery interval, but rebound in diversity by the upper Aeronian (36, 37). Several studies indicate that graptolites

and conodonts rebounded by the middle Llandovery (38–41). Adrain *et al.* (42) looked at Ordovician and Silurian alpha diversity of trilobites across a range of depositional environments and on several paleocontinents and found little or no impact of the Late Ordovician mass extinction on the number of trilobite species that occupied local habitats, despite a nearly 50% drop in clade diversity globally. They argued that the processes that govern alpha diversity exert little control on global diversity, at least in this context, and that the processes that govern between-habitat (beta) or geographic (gamma) diversity may exert the overriding control on global diversity. Our results suggest that diversity in Laurentia fluctuated little at the 5-Myr time scale, suggesting a cap on gamma diversity. Thus, higher-resolution studies are needed (37) from multiple paleocontinents to tease apart how diversity was partitioned among alpha, beta, and gamma diversity across the Ordovician-Silurian boundary.

The disparity in rates of recovery in Laurentia compared with the whole globe suggests the processes that govern regional ecosystem recovery were somehow different or decoupled from processes operating at the global level. Indeed, recovery of global diversity is limited by taxonomic diversification rates, whereas diversity of regional ecosystems, such as paleocontinents, can recover much more quickly because taxonomic diversification can be augmented by immigration. There is evidence to suggest that immigration played an important role in the recovery of diversity in the early Silurian of Laurentia (43, 44). After a glacioeustatic sea-level fall that drained epicontinental seas and disrupted marine habitats, sea levels rose, permitting brachiopod taxa to migrate into Laurentia from Baltica (northern Europe) and causing a rapid turnover in brachiopod faunas and a switch to more cosmopolitan taxa (44). The early Llandovery peak of origination in Laurentia reflects at least in part this influx of Baltic genera (Fig. 5B). Globally, origination does not peak in the early Llandovery, rather extinction rates drop below origination rates and then origination rates begin a slow rise (Fig. 2B and ref. 5). Thus, regional diversity can remain constant while global diversity drops if regional diversity is replenished by immigration from other paleocontinents, causing a shift from highly endemic to cosmopolitan distributions of taxa. Additional studies from other paleocontinents are needed to test this general hypothesis.

The results of our analyses also have implications for diversity studies throughout the Phanerozoic. Based on high-resolution (epoch level) analyses of the number of sedimentary formations (a proxy for quantity of sedimentary rock) and global diversity, Peters and Foote (14) found that much of the short-term variation in global diversity depends on the amount of sedimentary rock available for sampling. Notably, mass extinctions tend to occur at times when the quality of the record, as estimated by the amount of sedimentary rock available for sampling, changes from high in the extinction interval to low in the recovery interval. This pattern of record quality is related to major drops in sea level that are coeval with a large number of mass extinctions in the Phanerozoic (45). Indeed, the Late Ordovician mass extinction has been linked directly to a significant fall and rise in eustatic sea level associated with the waxing and waning of a large Gondwanan ice sheet (46), and this record of sea-level change is directly associated with fluctuations in the quantity of sedimentary rock available for study (14). Our results are consistent with a number of recent modeling (47, 48) and empirical studies (9, 10, 13, 14) that suggest the need for a reassessment of stratigraphic bias on perceived trends in diversity and taxonomic rates across all mass extinction horizons. Such studies are critical for understanding the full impact of environmental perturbations on biodiversity and the processes of postextinction recovery. In a study of rates of speciation in the fossil record, Sepkoski (5) described the recovery from the Late Ordovician extinction as typical of a postextinction recovery

period, with a protracted increase in origination rates beginning in the Lower Llandovery and continuing through the Wenlock. The protracted increase in origination rates at the global scale may reflect a biased record (12). Although the study presented here is based on only a single paleocontinent, it does point out the importance of sample standardization in diversity studies. Thus, any model of recovery that hinges on the timing of origination (1–5) must be reevaluated in light of analyses that account for variation in sampling intensity among paleocontinents and for the whole globe.

Although sampling bias is one of the most important issues affecting diversity trajectories through time, there are other issues that must be resolved to fully understand the nature of postextinction recovery. First, the degree to which pseudoextinction affects turnover metrics must be addressed. Although inconsistent taxonomic assignments do not seem to affect the total or subsampled curves for Laurentia, the phylogenetic relationships of these taxa can add insight into the nature of the recovery. If a portion of the Early Silurian taxa had sister taxa in the Ordovician that survived the event, then the Ashgillian extinction and Rhuddanian origination rates both would be overestimated (50). Such data would not only provide independent support for the effects of sampling biases on diversity curves (51) for this time period, but may aid in our understanding of the diminished ecological and evolutionary effects of the Late Ordovician mass extinction (52–54). Second, diversification events have been shown to display a high degree of geographic heterogeneity (6, 49, 55–57), and including other paleocontinents in the current analysis is necessary to understand the influence of regional processes on the recovery as well as how regional patterns relate to global patterns.

Conclusions

After adjusting for variations in sampling intensity through time, Late Ordovician (Ashgill) diversity in Laurentia equals diversity in

the Early Silurian (Rhuddanian). This finding indicates that diversity in Laurentia rebounded to preextinction levels within the first 5 Myr of the Silurian, ≈ 15 Myr sooner than suggested by global compilations. A peak in extinction in the Ashgill is followed immediately by a peak in origination in the Lower Llandovery, suggesting a relatively rapid turnover of taxa in Laurentia. The difference in the rate of recovery of Laurentian diversity compared with global diversity suggests that processes different from those affecting global diversity governed recovery of diversity in Laurentia. For example, immigration of taxa from other paleocontinents, such as Baltica, may have replenished local and regional biotas, but had no effect on global diversity, leading to a more cosmopolitan global fauna. Data from other paleocontinents are necessary to confirm this hypothesis, as well as to gain a better understanding of how regional patterns relate to the global picture.

Because the sampling-standardized diversity and taxonomic rate curves for Laurentia differ substantially from the curves based on the unstandardized data, it raises the question of whether the global curves need similar adjustments. Indeed, several recent studies point to the incompleteness of the rock record that distort estimates of diversity and taxonomic rates associated with mass extinctions and postextinction recoveries throughout the Phanerozoic (10, 12–14). Although no definite conclusions on this issue can be drawn from the analysis of only one paleocontinent, our results suggest that future studies of Phanerozoic mass extinctions should attempt to remove the distorting effects of incompleteness and variation in sampling intensity if the macroevolutionary and ecological processes of mass extinctions and postextinction recoveries are to be fully understood.

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