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Testing for faunal stability across a regional biotic transition: quantifying stasis and variation among recurring coral-rich biofacies in the Middle Devonian Appalachian Basin

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Abstract.—Previous observations about the stable nature of coral-rich assemblages from the Middle Devonian Hamilton Group have led some researchers to invoke the primacy of ecological controls in maintaining biofacies structure through time. However, few analyses have examined the degree to which recurring biofacies vary quantitatively, and none have assessed lateral variability as a benchmark for testing the significance of temporal variability. Thus, the extent to which Hamilton biofacies persist and the mechanism(s) responsible for their hypothesized stability remain contentious. In this study, recurring coral-rich biofacies were evaluated from two stratigraphic horizons within the Middle Devonian Appalachian Basin to examine (1) the extent to which species assemblages persisted within the basin through space and time, and (2) whether ecological interactions may be a plausible mechanism for generating the degree of stasis observed in this case.

Variations in species composition and abundance were examined across multiple spatial scales within both sampled coral-rich horizons. This permitted the establishment of a baseline against which temporal differences in biofacies composition and structure could be evaluated. Although successive coral-rich horizons remained taxonomically stable, their dominance structures changed significantly through the 1.5 Myr study interval. Moreover, additional comparisons among older Hamilton coral-rich horizons corroborate our primary results. These findings support a model in which species respond individually to fluctuations in the physical environment, as indicated by the fluidity of their relative abundances geographically and temporally.

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Introduction

One of the major goals of evolutionary paleoecology is to identify the processes governing the structure and stability of fossil assemblages over spatial and temporal scales. Previously, marine invertebrate fossil assemblages have been shown to vary over local and regional spatial scales in response to changing environmental conditions (e.g., Springer and Bambach 1985; Miller 1988; Lafferty et al. 1994; Patzkowsky 1995). Additionally, predictable, recurring species associations, termed biofacies, have been observed in repeated sedimentary cycles throughout the fossil record (e.g., Cisne and Rabe 1978; Brett et al. 1990), yet to what extent do recurring biofacies persist in space and time? Do they persist as cohesive units or are they more loosely structured, changing continually with habitat variations? These questions have sparked debate among neoecologists and paleoecologists alike. Some argue that communities are composed of highly interdependent species that assemble in consistent associations even in the face of environmental perturbation (Elton 1933; Pandolfi 1996; Gardiner 2001). Alternatively, others favor a more individualistic model of species assembly under fluctuating physical conditions, with species associations structured primarily by the habitat tolerances of each member of the available pool of species (Gleason 1926; Bennington and Bambach 1996; Jablonski and Sepkoski 1996; Miller 1997a; Patzkowsky and Holland 1997; Olszewski and Patzkowsky 2001; Holland and Patzkowsky 2004).

The Middle Devonian of the northern Appalachian Basin was characterized by extended periods of low species turnover, punctuated by abrupt intervals of biotic change—a pattern referred to as ''coordinated stasis'' (Brett

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and Baird 1995; Brett et al. 1996). To illustrate this phenomenon, Brett and Baird presented a case study of the oldest and youngest coral-rich beds then known from the Hamilton Group. In this case the taxonomic composition and even the ecologic structuring (dominance rankings of common and abundant taxa) of the biofacies showed little variability among samples separated by 5–6 Myr (Brett and Baird 1995). These observations led Morris et al. (1995) to suggest that biofacies were maintained by strong ecologic interactions among coexisting species in communities. However, before one can invoke potential mechanisms to explain purported ecologic stability in the fossil record, it is necessary to determine more precisely the extent of this stability.

Of the few recent studies attempting to quantitatively compare recurring Hamilton biofacies (see Baird and Brett 1983; Brower and Nye 1991; Newman et al. 1992; Bonuso et al. 2002), none have accounted sufficiently for lateral variability in species abundances within sampling horizons (however, see Lafferty et al. 1994). Without this lateral control, it is not possible to assess confidently whether species abundances vary significantly among sampling horizons through time, because the baseline variability expected within any one horizon has not been established. Ultimately both aspects of variation are crucial to understanding whether Hamilton biofacies maintain a high degree of consistency in composition and structure and enough stability therefore exists in Hamilton biofacies to posit ecological interactions as a mechanism for generating stasis.

In this study the highest two coral-rich beds from the Middle Devonian deposits of the Appalachian Basin were sampled and analyzed quantitatively to permit an evaluation of stability across an interval of biotic and environmental transition known as the *lower Tully bioevent* (Baird and Brett 2003). Faunal samples were collected at nine localities across the northern Appalachian Basin from two stratigraphic levels: the South Lansing bed (Moscow Formation, Hamilton Group) and the West Brook bed (upper Tully Formation). Variability in species abundance was analyzed within each bed among replicate samples (meters apart), localities (tens to hundreds of meters apart), and regions (hundreds of kilometers apart), providing an overview of spatial and geographic variability at several lateral scales.

Our results show that, despite being separated by an intervening period of physical and biotic disturbance, a very similar species pool persisted through the study interval. However, species abundances and dominance relationships varied significantly across the lower Tully bioevent.

Geologic Setting

Regional Background.—The study interval includes the South Lansing bed of the upper Moscow Formation (Givetian Stage) and the West Brook bed from the overlying Tully Formation (Taghanic Stage) of central New York and Pennsylvania (Fig. 1). The South Lansing bed (Brett et al. 1983) represents the highest widespread Hamilton occurrence of an inner-shelf coral-rich biofacies within the northern Appalachian Basin. It extends laterally over 90,000 km^2 across New York State and into Pennsylvania and was deposited under shallow-water, well-oxygenated conditions (Baird and Brett 2003). The Tully coral-rich biofacies in the West Brook bed (Cooper and Williams 1935) is thought to represent a close analog to the South Lansing and other Hamilton coral-rich units, in terms of both its constituent fauna and depositional setting. It occurs as a 0.5–1.0 m thick, fossiliferous, dark-gray, thinly bedded shale and stands out in marked contrast to the thick underlying succession of lower Tully shaly-limestones in the study area. The existing sequence stratigraphic framework for Hamilton and Tully deposits in the northern Appalachian Basin (see Brett and Baird 1985, 1986, 1994, 1996; Baird and Brett 2003) indicates that the duration of time between these two coral beds spans four fourth-order depositional cycles, or approximately 1.5 Myr, using estimates of the duration of Hamilton conodont zones (House 1992, 1995).

Biotic Events in the Study Area.—A significant biotic transition occurred at the onset of lower Tully deposition (see Fig. 1) coinciding with a phase of tectonic quiescence and increased carbonate production within the northern Ap-

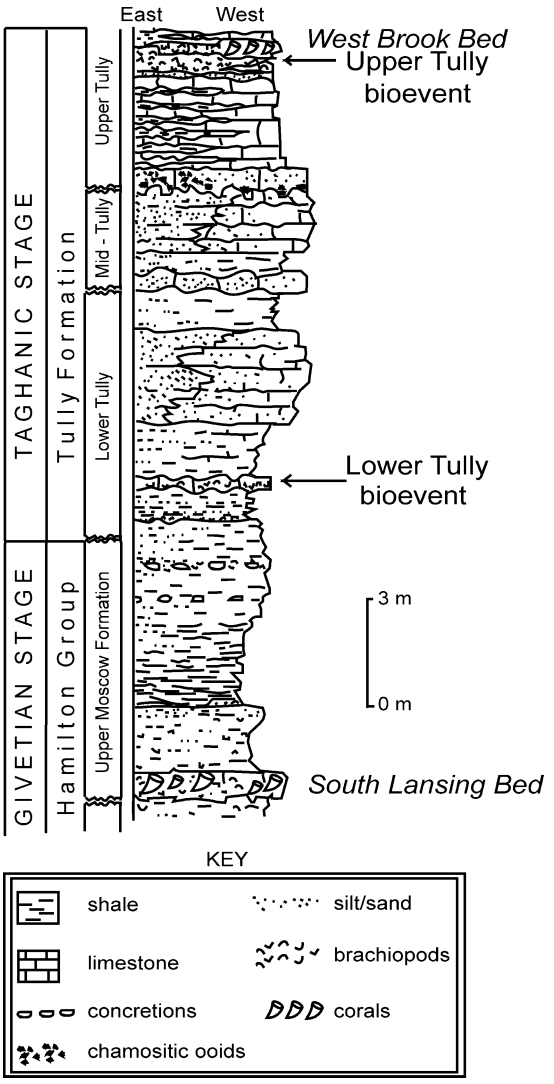

FIGURE 1. Generalized stratigraphic section of the study area indicating the two coral-rich units examined in this study. Modified from Baird and Brett (2003).

palachian Basin (Baird and Brett 2003). This event, recently termed the ''lower Tully bioevent'' (Baird and Brett 2003), displays a complex pattern of faunal turnover, which differs in timing among facies (Sessa et al. 2002). In the aftermath of this transition, typical Hamilton biofacies were conspicuously absent from the environments preserved in the lower and middle Tully sequences and were replaced by a low-diversity assemblage of brachiopod species that were rare or absent from the Hamilton Group (Cooper and Williams 1935; Willard 1937; Heckel 1973). However, at

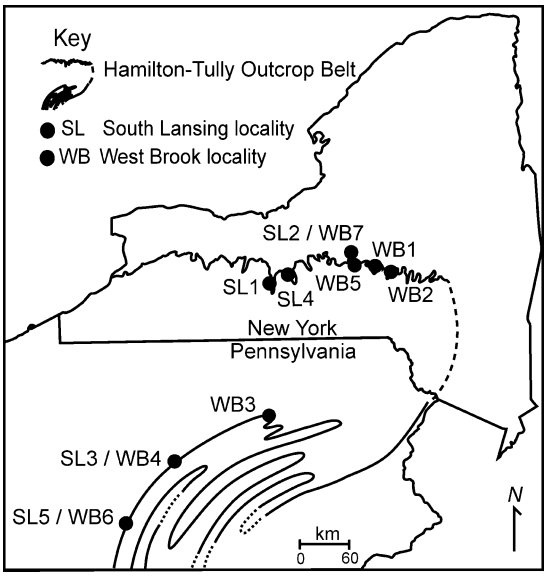

FIGURE 2. Locality map of sampled South Lansing (SL) and West Brook (WB) localities.

the base of the upper Tully, in the West Brook bed, a diverse assemblage of Hamilton brachiopod, coral, and bryozoan species returns. This regional faunal transition is known as the ''upper Tully bioevent'' (Baird and Brett 2003) and marks the final recurrence of the diverse coral-rich Hamilton biofacies in the northern Appalachian Basin (Cooper and Williams 1935; Heckel 1973; Baird and Brett 2003).

Field Methods and Data Analyses

Sampling and Laboratory Methods

To facilitate quantitative comparisons of species abundance and composition within and among recurring coral-rich facies, samples were collected from fossiliferous horizons at each of nine localities throughout central New York and Pennsylvania (Fig. 2). Because both modern and fossil benthic marine organisms have been shown to be distributed heterogeneously (in patches) across the seafloor (Buzas 1968; Cummins et al. 1986; Lafferty et al. 1994; Bennington and Bambach 1996; Miller 1997b; Bennington 2003; Webber 2005), a single bulk sample is unlikely to provide a reliable estimate of species abundances within any given outcrop (Hayek and Buzas 1997; Bennington 2003). To more dependably quantify species abundances within each bed at ev-

ery locality, we collected three to seven laterally distributed, replicate samples from each fossiliferous horizon. Dispersing samples in this way reduces the potential bias of spatial heterogeneity and allows for an assessment of variability at the scale of the local outcrop due to patchiness. This provides the baseline against which larger-scale variability can be assessed statistically (Hayek and Buzas 1997; Bennington and Rutherford 1999). Replicate samples were collected approximately one to three meters apart and consisted of enough bulk rock to fill a four-liter plastic storage bag.

Samples were cleaned and disaggregated in the lab and all fossiliferous material was examined and identified to the species level whenever possible. We used illustrations and descriptions from Linsley (1994) to make species identifications and the Minimum Number of Individuals method (MNI) (Gilinsky and Bennington 1994) to tally the densities of brachiopod, bivalve, and trilobite taxa. This method adds the larger number of brachial-pedicle/left-right valves and unique valve fragments for bivalved organisms, or cephalon-pygidium counts for trilobites, to the number of articulated specimens in each sample. Typically, gastropod and noncolonial coral species were preserved as whole specimens and counted accordingly. The presence of bryozoan and crinoid taxa and non-unique shell fragments was noted but not counted, yielding a conservatively low estimate of fossil density per sample.

Quantitative Methods

An initial data matrix of 54 samples by 124 taxa was produced from the fossil counts. Following recommendations in Clarke and Warwick (1994) rare taxa (those comprising less than 3%of all individuals) were removed prior to analyses because their presence or absence in a fossil sample may be due to chance alone—a quality that makes them unreliable for statistical comparison (Costanzo and Kaesler 1987; McKinney et al. 1996). Increasing the cutoff for rare taxa to 10% did not change significantly the outcome of any of the analyses presented in this paper. In addition, three samples were removed from the data set after preliminary multivariate analyses indicated that they were outliers. These samples contained unusually low numbers of specimens and provided estimates of species abundances that deviated greatly from those of other replicate samples collected at their respective localities. The resulting matrix analyzed in this study consists of 51 samples and 81 taxa (see Appendix online at http://dx.doi.org/10.1666/05009.s1). Prior to analyses, species abundances were transformed to percentages of the total number of individuals in each sample. This transformation was performed because differences in sample size can potentially influence the calculated similarities among samples (Gower 1987; Miller 1988; Shi 1993).

Following data transformation, samples were compared using the Bray-Curtis similarity coefficient (Bray and Curtis 1957). The equation for calculating the similarity between two samples, j and k, containing p species is

$$S_{jk} = 100\left[\frac{\sum_{i=1}^{p} |y_{ij} - y_{ik}|}{\sum_{i=1}^{p} (y_{ij} + y_{ik})}\right] = 100\,\frac{\sum_{i=1}^{p} 2\,\min(y_{ij} + y_{ik})}{\sum_{i=1}^{p} (y_{ij} + y_{ik})} \quad (1)$$

where S is the similarity between samples j and k; y_{ij} represents the percent abundance of the i^{th} species in the j^{th} sample; y_{ik} is the percent abundance of the i^{th} species in the k^{th} sample, and min (y_{ij}, y_{ik}) selects the minimum of the two values. The Bray-Curtis coefficient, also known as the Quantified Dice or Sorenson coefficient, is used commonly in ecological studies because the joint absence of a species from samples does not contribute to the overall calculated similarity between the samples being compared (Faith et al. 1987).

Analysis of Local, Regional, and Temporal Variability.—Multivariate analyses were performed on the data set using the PRIMER v. 5 statistical analysis package (Clarke and Warwick 1994). Nonmetric multidimensional scaling (NMS) was used to graphically display similarity relationships among samples,

based on the Bray-Curtis similarity coefficient. NMS is one of the most effective methods available for the ordination of ecological data because it (1) is a nonparametric technique and, therefore, does not assume a normal distribution of data; and (2) allows for flexibility in the choice of standardization, transformation, and similarity coefficient (Minchin 1987; Clarke 1993; Shi 1993). The NMS algorithm (see Kruskal 1964) is an iterative procedure; graphical plots are constructed by successively refining the plot points until they reflect, as closely as possible, the rank similarities or dissimilarities among samples in the original matrix (Clarke 1993). Differences between sample dissimilarities in the starting matrix and the graphed points in the NMS plot are reflected as a stress value; stress will be zero if agreement between the two is perfect. Although NMS ordinations were constructed in both two- and three-dimensional space, only two-dimensional plots are presented in this paper. The stress values associated with two-dimensional representations are sufficiently low (<2.5) and indicate that they reflect accurately the relationships among samples (Clarke and Warwick 1994).

The similarity percentages procedure (SIMPER; Clarke and Warwick 1994) was used to summarize the average contribution that individual species made to the overall dissimilarity of sample groupings. In this way it was easy to recognize species that were typical of a group and most responsible for between-group differences. Sample groupings were defined a priori and represent the localities, regions, and beds sampled in this study. First, the average dissimilarity between all pairs of intergroup samples (e.g., every sample in group 1 paired with every sample from group 2) is computed and then this average is parsed into the individual contributions of every species to the between-group dissimilarity. A good discriminating species will consistently contribute to the dissimilarity between pairs of intergroup samples and have a larger ratio of mean dissimilarity contribution to standard deviation than species common to both groups.

Analysis of Similarities (ANOSIM), a nonparametric test based upon the rank order of the Bray-Curtis values, was used to test for statistically significant differences: (1) among groups of samples within a single bed (where each group consists of the replicate samples collected from a locality), and (2) between beds. ANOSIM tests a null hypothesis of ''no significant differences among the groups of samples being compared'' by deriving a global test statistic (R), reflecting the observed differences between groups (Clarke and Warwick 1994). R will equal one if all samples within defined groups are more similar to each other than any samples between groups and zero if the ranks of similarities between and within groups are exactly the same. As part of this analysis, the set similarity values between samples are randomized and the R statistic is recomputed. This randomization was conducted 5000 times to produce a distribution of the R- values expected if similarity were distributed randomly. The observed value of R is compared with the null distribution from the randomization procedure. If the observed R-value is greater than at least 95% of the randomized R-values (i.e., $p < 0.05$), then the null hypothesis of random variation among samples is rejected.

Using the replicate samples collected at each locality, we calculated mean abundances with 95% cluster confidence intervals (CCIs) for each of the ten most common species from each bed to assess the statistical significance of differences among mean species abundances through time (Bennington 2003). CCIs were calculated using the equation:

$$\hat{\sigma} = \left[\sum \frac{n_j(p_j - p)}{n\bar{m}^2(m - 1)} \right]^{1/2} \qquad (2)$$

where $\hat{\sigma}$ is the standard error, n_j is the total number of individuals in sample j, p_j is the total individuals of a particular species in sample j divided by the total number of individuals, p is the total number of individuals of a particular species divided by the sum of all individuals, m is the number of replicate samples, and n is the total number of individuals divided by the total number of replicate samples (Buzas 1990). Confidence intervals are given by

$$d = \pm t\,\hat{\sigma} \qquad (3)$$

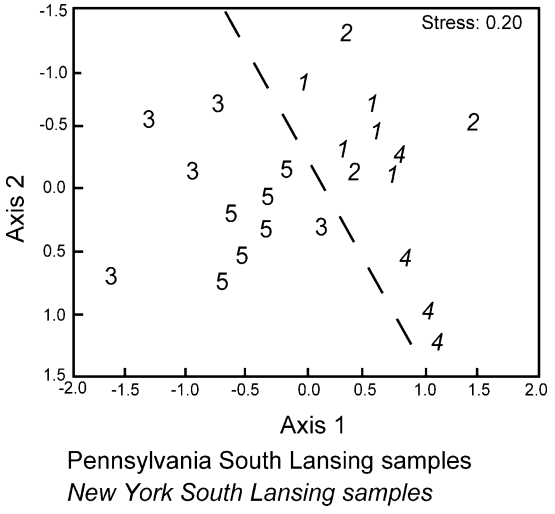

FIGURE 3. Two-dimensional results from NMS ordination of South Lansing replicate samples. Numbers on the ordination plot correspond to sampling localities shown in Figure 2. Dashed line indicates segregation of samples collected from New York and Pennsylvania along Axis 1.

where t is the normal deviate, equal to 1.96 for 95% confidence intervals (Buzas 1990). The cluster standard error is based on abundance variation between replicate samples and, therefore, can be used to make statistically meaningful comparisons of variation in species abundances through space and time. Calculations were performed using the program SpeciesCI v. 3.0 (Bennington 2003: available online at http://people.hofstra.edu/faculty/jbbennington/research/paleoecology/speciesci.html).

Finally, to compare our results directly with those presented by Brett and Baird (1995) on the stability of Hamilton coral-rich biofacies, we computed *percent carryover* and *holdover* metrics. In this study percent carryover refers to the total percentage of South Lansing taxa that were also found to occur in the West Brook bed; percent holdover indicates the total percentage of West Brook taxa that the South Lansing carryover taxa account for. Brett and Baird (1995) indicated that stable intervals are characterized by ranges of 60–80% for these measures.

Results and Discussion

Within-Bed Variability

South Lansing Samples.—The two-dimensional NMS ordination plot (Fig. 3) of the 23 South Lansing samples reveals a segregation of samples by geography along Axis 1. Samples from Pennsylvania localities tend to plot to the left on Axis 1 whereas New York samples plot to the right. The SIMPER analysis shown in Table 1 highlights species that are

TABLE 1. Contributions of the taxa that most distinguish the regional South Lansing assemblages. Taxa with large discrepancies in average abundance between the New York and Pennsylvania assemblages, and with a high dissimilarity to standard deviation ratio, are responsible for the observed differences among localities in the ordination of South Lansing samples. (SIMPER procedure from PRIMER, Clarke and Warwick 1994).

Taxon	Mean[1] New York abundance	Mean[1] Pennsylvania abundance	Mean[2] dissimilarity	Dissimilarity/SD[3]
Amplexiphyllum hamiltoniae	0.50	3.17	2.68	1.38
Mediospirifer audaculus	11.50	3.08	6.82	1.26
Rhipidomella vanuxemi	0.58	2.17	1.69	1.24
Pseudoatrypa devoniana	2.83	0.75	2.05	1.23
Cyrtina hamiltonensis	1.33	1.25	1.41	1.19
Elita finbriata	0.83	0.83	0.86	1.11
Mucrospirifer mucronatus	2.50	1.08	2.58	1.08
Favosites cf. *milne-edwardsi**	0.00	1.83	1.83	0.82
*Heliophyllum halli**	0.25	1.50	1.53	0.76
Heterofrontus sp.*	0.00	0.92	0.68	0.60
Blothrophyllum sp.*	0.00	0.42	0.45	0.53
Coenites sp.*	0.00	0.67	0.62	0.50
*Cystiphylloides americanum**	0.00	0.50	0.43	0.48
*Pleurodictym dividuem**	0.00	1.00	0.91	0.33
Favosites cf. *arbuscula**	0.00	2.92	1.81	0.33

[1] The mean percent abundance for each species over all localities.
[2] The mean contribution of a particular species to the overall dissimilarity between the New York and Pennsylvania assemblages.
[3] Ratio of the mean contribution of each species to its standard deviation. Large values indicate good discriminator species between regional assemblages.
* Large coral taxa; although not sufficiently abundant to serve as good discriminating species, they occur only in Pennsylvania samples.

TABLE 2. Results of the ANOSIM test for the South Lansing bed. Results that are not statistically significant are shown in boldface type.

Global test	
Null Hypothesis:	No significant difference among South Lansing sampling localities
Sample statistic (Global *R*):	0.652
Significance level of sample statistic:	0.00%
Number of permutations:	5000
Number of permuted statistics greater than or equal to Global *R*:	0
Outcome:	Reject null hypothesis

Pairwise tests

Groups (locality comparisons)	*R*-value	Significance level % (*p*)	Possible permutations
SL1, SL2	0.692	0.018	56
SL1, SL3	0.552	0.008	126
SL1, SL4	0.606	0.016	126
SL1, SL5	0.690	0.001	792
SL2, SL3	0.733	0.018	56
SL2, SL4	**0.704**	**0.057**	**35**
SL2, SL5	0.817	0.008	120
SL3, SL4	0.744	0.016	126
SL3, SL5	0.454	0.001	792
SL4, SL5	0.905	0.003	330

characteristic of each of the two major sample groupings in the NMS ordination and those that are useful for distinguishing among groupings. Samples from New York localities were associated with higher mean abundances of the brachiopods *Mediospirifer audaculus*, *Pseudoatrypa devoniana*, *Cyrtina hamiltonensis*, and *Mucrospirifer mucronatus*. New York samples are distinguished from those of Pennsylvania by the near absence of the rugose coral *Amplexiphyllum hamiltoniae* and the brachiopod *Rhipidomella vanuxemi*, both of which were abundant faunal components in Pennsylvania. Additionally, eight other favositid and rugose coral species were found only in Pennsylvania samples.

Despite the tendency for geographically proximate South Lansing localities to plot closely in ordination space, ANOSIM detected statistically significant faunal variability overall ($R = 0.652$; $p = 0.00$; Table 2). Only one set of locality comparisons (SL2, SL4) displayed differences that were not statistically significant ($p = 0.057$). In any case, faunal differences among South Lansing localities tended to be significantly greater than that expected due to random chance. It's worth pointing out here that the discrepancy between NMS and ANOSIM results is not surprising because there are bound to be slight distortions of the ''true'' relationships among samples in ordination space even when stress is low. This is a consequence of attempting to represent high-dimensionality data in a smaller number of dimensions (McCune and Grace 2002).

West Brook Samples.—The two-dimensional NMS ordination of the 28 West Brook samples is shown in Figure 4. There is a greater degree of variability among samples from individual localities than there was among South Lansing samples (Fig. 3). However, despite this within-locality patchiness, geographically proximate localities again form separate regional groupings along Axis 1. Samples from Pennsylvania localities plot along the left of the axis; New York samples, on the other hand, plot to the right.

The SIMPER procedure (Table 3) reveals that, on average, New York samples contained greater abundances of the brachiopods *Longispina mucronata*, *Sinochonetes lepidus*, *Eoschuchertella* cf. *arctostriata*, *Elita fimbriata*, and *Mesoleptostrophia junia*, and lesser abundances of four of the most common Pennsylvania species: the brachiopods *Spinatrypa spinosa*, *R. vanuxemi*, and *Protodouvillina inequistriata*, and

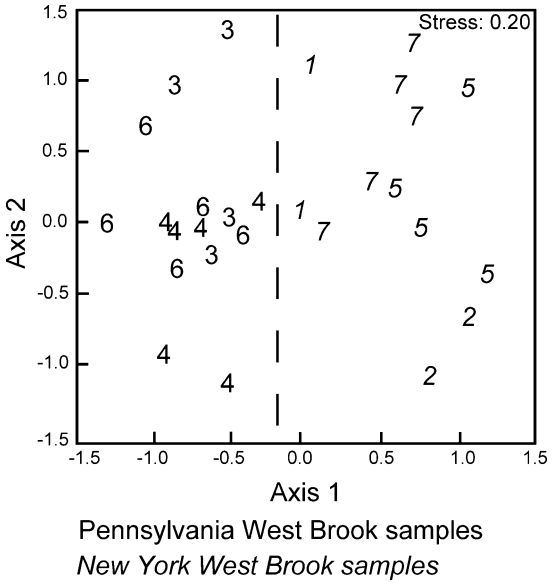

FIGURE 4. Two-dimensional results from NMS ordination of West Brook replicate samples. Numbers on the ordination plot correspond to sampling localities shown in Figure 2. Dashed line indicates segregation of samples collected from New York and Pennsylvania along Axis 1.

the rugose coral *A. hamiltoniae*. The ANOSIM global test detected statistically significant variability among West Brook assemblages overall ($R = 0.59$; $p = 0.00$; Table 4) even though more than half of the individual locality comparisons did not show clear significance. However, the significance values from individual comparisons often have so few permutations (because few replicate samples were available for comparison in some cases) that they cannot be tested at the $\alpha = 0.05$ level; thus some of these individual comparisons may not have enough power to detect significant differences between groups no matter how large the differences (reflected by the *R*-values) may actually be (Clarke and Warwick 1994).

Temporal Variability

Having established a baseline of the variability within each bed, we made comparisons among all 51 South Lansing and West Brook samples to determine whether statistically indistinguishable assemblages recurred through time. The ordination in Figure 5 shows a major division among South Lansing and West Brook samples along Axis 1. South Lansing samples group largely to the left and center of Axis 1, whereas those from the West Brook plot to the right. Within each of these major sample groupings, the regional distinctions discussed earlier can be observed easily. It is telling that even among individual replicate samples, which may represent incomplete or biased approximations of a bed's faunal content, there is only a single case of sample overlap between the two units (due to the increased abundance of *Amobcoelia umbonata*, a species

TABLE 3. Contributions of the taxa that most distinguish the regional West Brook assemblages. Taxa with large discrepancies in average abundance between the New York and Pennsylvania assemblages, and with a high dissimilarity to standard deviation ratio, are responsible for the differences observed among localities in the ordination of West Brook samples. (SIMPER procedure from PRIMER, Clarke and Warwick 1994).

Taxa	Mean[1] New York abundance	Mean[1] Pennsylvania abundance	Mean[2] dissimilarity	Dissimilarity/SD[3]
Spinatrypa spinosa	0.38	5.73	7.95	1.46
Eoschuchertella cf. *arctostriata*	0.92	0.27	1.38	1.37
Longispina mucronata	1.08	0.53	1.49	1.32
Sinochonetes lepidus	3.00	0.60	2.80	1.30
Amplexiphyllum hamiltoniae	2.08	10.73	10.75	1.22
Elita fimbriata	0.92	0.27	1.79	1.19
Phacops rana	4.00	1.47	4.28	1.16
Protodouvillina inequistriata	0.92	1.73	1.62	0.11
Rhipidomella vanuxemi	0.69	2.60	3.31	1.08
Mesoleptostrophia junia	0.62	0.33	0.98	1.02
Cyrtina hamiltonensis	1.00	0.47	1.58	0.98
Tropidoleptus carinatus	0.62	0.33	1.51	0.96
Stereolasma rectum	3.46	0.53	4.15	0.85

[1] The mean percent abundance for each species over all localities.
[2] The mean contribution of a particular species to the overall dissimilarity between the New York and Pennsylvania assemblages.
[3] Ratio of the mean contribution of each species to its standard deviation. Large values indicate good discriminator species between regional assemblages.

TABLE 4. Results of the ANOSIM test for the West Brook bed. Results that are not statistically significant are shown in boldface type.

Global test	
Null Hypothesis:	No significant difference among West Brook sampling localities
Sample statistic (Global *R*):	0.590
Significance level of sample statistic:	0.00%
Number of permutations:	5000
Number of permuted statistics greater than or equal to Global *R*:	0
Outcome:	Reject null hypothesis

Pairwise tests			
Groups (locality comparisons)	*R*-value	Significance level % (*p*)	Possible permutations
WB1, WB2	**1.000**	**0.333**	**3**
WB1, WB3	**0.464**	**0.133**	**15**
WB1, WB4	**0.542**	**0.071**	**28**
WB1, WB5	**0.250**	**0.333**	**15**
WB1, WB6	**0.491**	**0.095**	**21**
WB1, WB7	**0.364**	**0.143**	**21**
WB2, WB3	**1.000**	**0.067**	**15**
WB2, WB4	1.000	0.036	28
WB2, WB5	**0.500**	**0.067**	**15**
WB2, WB6	1.000	0.048	21
WB2, WB7	0.873	0.048	21
WB3, WB4	**0.190**	**0.110**	**210**
WB3, WB5	0.719	0.029	35
WB3, WB6	0.344	0.016	126
WB3, WB7	0.838	0.008	126
WB4, WB5	0.810	0.005	210
WB4, WB6	**0.095**	**0.171**	**462**
WB4, WB7	0.747	0.002	462
WB5, WB6	0.831	0.008	126
WB5, WB7	**0.188**	**0.087**	**126**
WB6, WB7	0.816	0.008	126

that is more common in the West Brook bed, within a South Lansing sample). This robust pattern shows that each of these beds contains compositionally and/or structurally unique faunas.

Compositional Variability.—The extent to which the South Lansing and West Brook faunas were compositionally distinct was analyzed by examining the proportion of taxa shared among beds, the fraction of South Lansing taxa that carry over into the West Brook, and the percentage of West Brook taxa that represent holdovers from the South Lansing (Table 5). Of the 124 taxa collected in this study, about 61% (76 taxa) are shared among the two beds. For brachiopod taxa, the most prominent members of both beds, this number is even greater at 84% (46/55 taxa). Only 30% (33/109 taxa) of South Lansing taxa were not collected within the West Brook bed. Although some of these taxa may have experienced regional extinction during the lower Tully bioevent, most of the apparent losses are likely due to incomplete sampling. Species range data in Linsley (1994) reveals that only two of the 33 taxa, the brachiopods *Cupularostrum dotis* and *Schuchertella chemungensis*, became extinct across this event.

In total, 70% (76/109 taxa) of all South Lansing taxa reappear within the upper Tully and comprise 84% (76/91 taxa) of the total sampled West Brook fauna. Of the remaining 16% of West Brook taxa, only one, the brachiopod *Leptaena rhomboidalis* is not common to the Hamilton Group and may represent a genuine ''addition'' to the coral-rich biofacies (Linsley 1994; C. Brett personal communication 2003). Furthermore, the overall carryover and holdover percentages shown in Table 6 fall within the 60–80% range established by Brett and

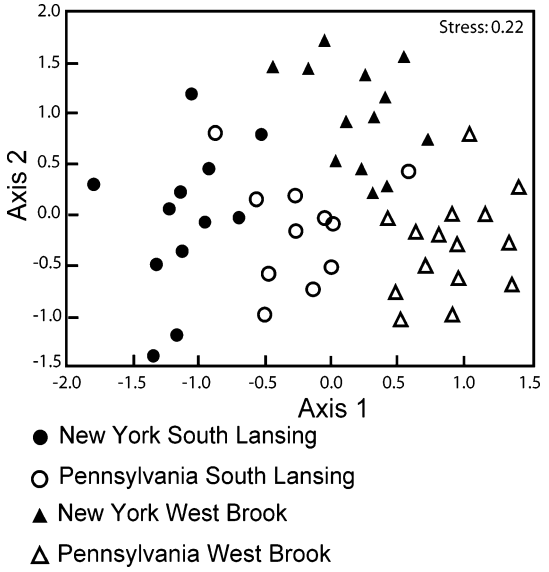

FIGURE 5. Two-dimensional results from NMS ordination of all replicate samples collected. Notice the strong distinction between South Lansing and West Brook samples along Axis 1.

Baird (1995) to classify intervals of taxonomic stability. This suggests a strong recurrence of Hamilton taxa despite their documented absence in the lower Tully interval (Baird and Brett 2003).

Structural Variability.—Figure 5 shows such a distinct division among South Lansing and West Brook samples because these units have considerably different abundance structures, despite their overall similar faunal compositions. Table 6 displays, in rank order, lists of the most abundant taxa (defined here as those that comprise 75% of the individuals in each bed) collected from each bed. Of the taxa constituting these two lists only 31% (10/31) occur among the most abundant taxa in both beds; moreover, the rank orders and mean percent abundances of these taxa appear to vary greatly between lists. Thus, although a similar species pool persisted through the study interval, species abundance relationships appear to have changed dramatically through time.

To assess the significance of variation in the percent abundances of the most common South Lansing and West Brook taxa, we calculated and compared mean relative abundances and 95% cluster confidence intervals (Fig. 6). Note that mean abundances of only the top ten most abundant taxa from each bed are displayed. For many of these species, mean abundances are similar and cluster confidence intervals show some degree of overlap between beds. However, this is not true of the three *most abundant* West Brook species, *A. hamiltoniae*, *S. spinosa*, and *P. rana*, or for *M. audaculus*, the most abundant South Lansing species. These species display nonoverlapping confidence intervals and therefore differ significantly in mean relative abundance between sampled horizons.

Not surprisingly, the ANOSIM global test detected statistically significant variability among samples from the two beds ($R = 0.749$; $p = 0.00$; Table 7). Only six individual comparisons yielded nonsignificant p-values; however, four of these were not testable at the $\alpha = 0.05$ level and have R-values at or approaching one. Regardless, by this measure, assemblages in the South Lansing bed are statistically distinct from that of the West Brook. Support for this conclusion remains even after transforming the original species abundance data matrix to one of presence-absence and

TABLE 5. Total counts of taxa collected within the South Lansing and West Brook beds. Percent holdover/carryover metrics are displayed to compare the taxonomic compositions of each bed.

Total	South Lansing	West Brook	Study totals	Percent shared	Percent carryover	Percent holdover
Taxa	109	91	124	61	70	84
Brachiopods	52	49	55	84	88	94
Bivalves	26	17	31	39	46	71
Corals	13	5	13	38	38	100
Gastropods	4	7	8	38	75	43
Cephalopods	3	3	4	50	67	67
Trilobites	4	6	6	67	100	67
Bryozoans	7	4	7	57	57	100

TABLE 6. Ranked lists of the taxa comprising 75% of the total individuals within each of the South Lansing and West Brook beds. Boldface taxa appear as one of the most abundant taxa in both lists.

South Lansing species	Percent abundance	West Brook species	Percent abundance
Mediospirifer audaculus	12	***Amplexiphyllum hamiltoniae***	19
Mesoleptostrophia junia	9	*Spinatrypa spinosa*	9
Protodouvillina inequistriata	6	***Phacops rana***	7
Athyris spiriferoides	5	***Stereolasma rectum***	5
Tropidoleptus carinatus	3	***Sinochonetes lepidus***	5
Amplexiphyllum hamiltoniae	3	***Rhipidomella vanuxemi***	5
Pseudoatrypa devoniana	3	***Protodouvillina inequistriata***	4
Mucrospirifer mucronatus	3	***Ambocoelia umbonata***	3
Sinochonetes lepidus	3	***Longispina mucronata***	2
Pustulatia pustulosa	3	*Platyceras* spp.	2
Favosites cf. *arbuscula*	2	***Cyrtina hamiltonensis***	2
Rhipidomella vanuxemi	2	*Greenops* cf. *boothi*	2
Eoschuchertella* cf. *arctostriata	2	*Orthis lepidus*	2
Cyrtina hamiltonensis	2	***Eoschuchertella* cf. *arctostriata***	2
Megakozlowskiella sculptilis	2	*Cupularostrum prolifica*	2
Stereolasma rectum	2	*Protoleptostrophia perplana*	2
Paleonielo constricta	2	*Pentamerella pavillionensis*	2
Ambocoelia umbonata	2		
Longispina mucronata	2		
Favosites cf. *milne-edwardsi*	2		
Nucleospira concinna	1		
Heliophyllum halli	1		
Devonochonetes scitulus	1		
Elita fimbriata	1		
Phacops rana	1		

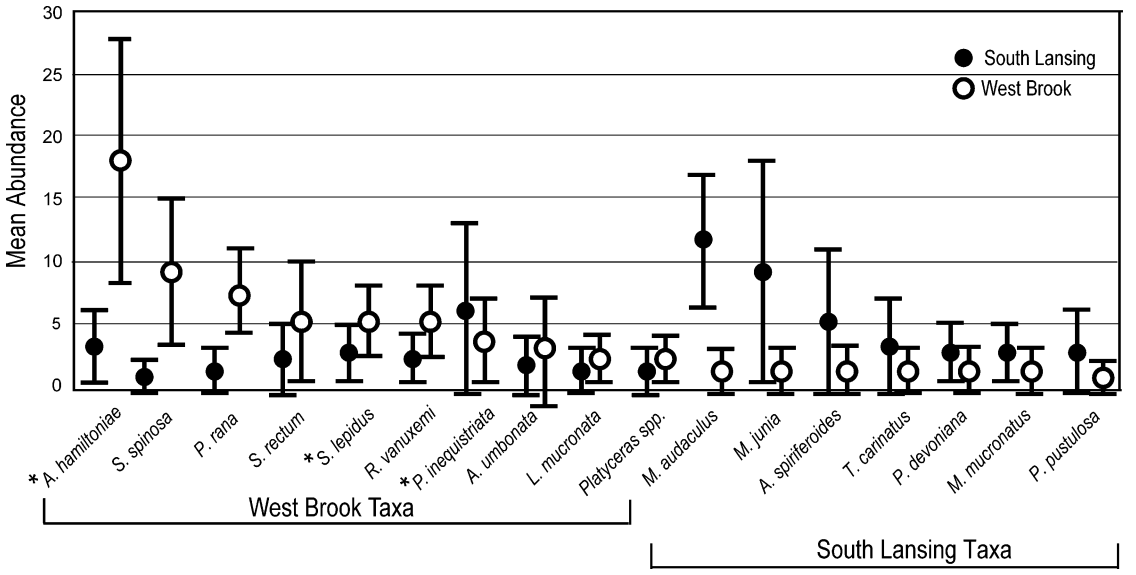

FIGURE 6. Plots of mean abundance with 95% cluster confidence intervals for the ten most abundant taxa collected from each bed. Taxa are listed in rank order by bed. Notice that the mean abundances of the three most abundant West Brook species (*A. hamiltoniae*, *S. spinosa*, and *P. rana*) and the most abundant South Lansing species (*M. audaculus*) vary significantly through time. Taxa with an asterisk occur as one of the most abundant species in both beds.

TABLE 7. Results of the ANOSIM test between beds. Results that are not statistically significant are shown in boldface type.

Global test	
Null hypothesis:	No significant differences among the South Lansing and West Brook
Sample statistic (Global *R*):	0.749
Significance level of sample statistic:	0.00%
Number of permutations:	5000
Number of permuted statistics greater than or equal to Global *R*:	0
Outcome:	Reject null hypothesis

Pairwise tests			
Groups (locality comparisons)	*R*-value	Significance level % (*p*)	Possible permutations
WB1, SL1	0.873	0.048	21
WB1, SL2	**1.000**	**0.100**	**10**
WB1, SL3	**0.364**	**0.190**	**21**
WB1, SL4	**1.000**	**0.067**	**15**
WB1, SL5	0.714	0.028	36
WB2, SL1	1.000	0.048	21
WB2, SL2	**1.000**	**0.100**	**10**
WB2, SL3	0.927	0.048	21
WB2, SL4	**1.000**	**0.067**	**15**
WB2, SL5	0.935	0.028	36
WB3, SL1	1.000	0.008	126
WB3, SL2	1.000	0.029	35
WB3, SL3	0.681	0.008	126
WB3, SL4	1.000	0.029	35
WB3, SL5	0.828	0.003	330
WB4, SL1	0.987	0.002	462
WB4, SL2	0.988	0.012	84
WB4, SL3	0.704	0.002	462
WB4, SL4	1.000	0.005	210
WB4, SL5	0.873	0.001	1716
WB5, SL1	0.800	0.008	126
WB5, SL2	**0.833**	**0.057**	**35**
WB5, SL3	0.600	0.008	126
WB5, SL4	0.948	0.029	35
WB5, SL5	0.693	0.003	330
WB6, SL1	1.000	0.008	126
WB6, SL2	1.000	0.018	56
WB6, SL3	0.818	0.008	126
WB6, SL4	1.000	0.008	126
WB6, SL5	0.926	0.001	792
WB7, SL1	0.860	0.008	126
WB7, SL2	0.990	0.018	56
WB7, SL3	0.588	0.008	126
WB7, SL4	1.994	0.008	126
WB7, SL5	0.617	0.001	792

performing the ANOSIM test again (R = 0.600; p = 0.00). Thus, a wholesale change in the most commonly occurring taxa takes place across the lower Tully event, resulting in a different set of dominance relationships.

Potential Biases.—It must be acknowledged that some of the variation between the South Lansing and West Brook horizons could reflect sampling bias rather than true biological signal, although we believe this is unlikely. Even though the two beds were sampled at the same, or nearby localities, and no discernable differences were apparent in their gross lithology and sedimentology, we cannot be certain that temporal samples represent the exact same position along environmental gradients through time. Moreover, despite distributing our sampling effort across a broad geographic

area it is unlikely that entire gradients have been sampled from either bed because relevant portions of gradients at both levels may have been buried in the subsurface or eroded away. For example, no populations of large rugose or tabulate corals, such as those recovered at South Lansing localities in Pennsylvania, were recorded at any of the West Brook exposures in this study (the effects of this bias were examined by performing an additional ANOSIM test in which Pennsylvania South Lansing samples were excluded. No appreciable change in outcome was evident [$R = 0.774$; $p = 0.00$]). In any case, at least some of the differences registered between these two horizons may represent the comparison of samples from subtly different portions of environmental gradients.

Despite these potential biases, however, we argue that the differences observed between beds in this study are meaningful. First, as documented, the taxonomic composition of both beds is quite similar and highly different from the makeup of other Hamilton and Tully biofacies (see Brett et al. 1990; Baird and Brett 2003), in that all samples contain a high proportion of species that are restricted to inner-shelf, high-diversity assemblages. We therefore infer that the samples from both the South Lansing and West Brook beds record a similar, narrow portion of the total Hamilton-Tully biofacies spectrum and that they are at least broadly comparable.

Second, despite differences between beds, there is considerable *consistency* in the relative abundance of common species among samples *within* a bed over the broad study area. Moreover, these differences are more pervasive than is documented here. Assemblages from the South Lansing and West Brook bed have each been examined at nearly 50 localities in New York and Pennsylvania (see Baird and Brett 2003) and show consistent differences in their most common species. For example, in nearly every outcrop of the West Brook bed the brachiopod *S. spinosa* was found to be common and *M. audaculus* was invariably rare. As noted in this paper, the opposite is true in the South Lansing bed. These differences exist within both beds throughout the study area, despite noted lateral variation in overall species composition among localities. Indeed, this phenomenon is well known in Hamilton beds and the unique abundances of certain species at particular levels has long proven useful in recognizing distinct horizons, as was well documented over 100 years ago by Grabau (1898), Cleland (1903), and many others. The older names of many widespread Hamilton horizons (e.g., *Pleurodictyum* bed, *Rhipidomella-Centronella* bed) reflect this uniqueness of species abundances despite documented similarities in taxonomic composition. These observations indicate that the differences in dominance of certain species among stratigraphic units are a biologically real phenomenon that is not merely driven by chance comparison of differing portions of two highly similar gradients.

Implications of These Patterns.—Two qualitative models have been proposed to account for patterns of biofacies persistence and change in the fossil record (Ivany 1996). In the first model persistence of environmental factors such as temperature, water depth, or sedimentation rate promotes the maintenance of taxa with coincident environmental preferences. As long as an environment remains relatively stable, and taxa are well adapted to the prevailing physical conditions, then these taxa should persist together until the physical habitat changes drastically (Bambach 1994; Miller 1997a; Brett 1998). Slight shifts in physical parameters might be accompanied by changes to species dominance structures, but there would be a pattern of broad persistence through time. In this model the geographic and temporal distributions of taxa shift independently according to their own physical tolerances.

Under the second model intrinsic (ecological) controls on organisms, such as biotic interactions, provide resistance to physical disturbances that might otherwise induce turnover (Morris et al. 1995). This would promote the persistence of biofacies through time, even in the face of minor environmental perturbations. In this model, ecologic stasis would be the norm; community restructuring would only occur given major physical disruptions.

The results of this study provide evidence in favor of the first model. At the onset of a

major physical transition during the upper Moscow/lower Tully interval, members of the South Lansing coral-rich biofacies must either have migrated to, or persisted in, areas outside of the northern Appalachian Basin, presumably where their preferred habitats continued to exist. Indeed, it is clear that many stenotopic species must have been periodically displaced from the foreland basin during deposition of the Hamilton Group. For example, many species typical of coral-rich beds (including nearly all coral species) have never been found in any of the much thicker intervening beds, despite the careful examination by the authors and earlier workers (Cleland 1903; Cooper 1933, 1934) in nearly all available exposures across New York and Pennsylvania. However, the ability of these species to recur indicates persistence of tolerable environments somewhere throughout this time span. When favorable physical conditions returned to the study area, most members of this biofacies were able to successfully recolonize via migration or larval dispersal and become established again. However the entire faunal assemblage does *not* appear to have tracked the returning environments in lockstep as evidenced by the significant changes in abundance structure. Although it is not clear why these changes occurred, the basin-wide consistency of these changes is clear: despite the persistence of most taxa from the South Lansing into the West Brook, abundances of component taxa vary markedly. Moreover, as evidenced by the analyses of each interval individually, there was significant compositional variation among coeval localities as well. This pattern would likely not have been generated if the faunal changes were controlled by strong ecological interactions and/or community dynamics.

Given that this study was conducted in the ''type interval'' of the coordinated stasis hypothesis, it is appropriate to ask whether variation between the South Lansing and West Brook assemblages is any greater than that among other coral-rich biofacies occurring lower in the Hamilton Group. One could speculate that more ''mainstream'' Hamilton coral-rich biofacies should persist to a greater degree than those examined here and that the lower Tully biotic event was responsible for the biofacies restructuring we observed.

To address this issue, we made additional comparisons between Hamilton coral-rich beds, using abundance data available in the literature for the Bay View and Fall Brook beds of the Moscow Formation (Baird and Brett 1983: Appendices A, B). These beds underlie the South Lansing and contain the sequentially next oldest occurrences of coral-rich biofacies in the Hamilton Group. Because these three units are not separated by pronounced environmental or biotic perturbations, one might expect them to display a higher degree of faunal similarity to one another than any one does to the West Brook fauna. However, the dominance structures of these coral units vary greatly (Table 8). In fact, only 5% (2/39 taxa) of the most dominant taxa co-occur in all three lists. Furthermore, individual comparisons among these horizons (e.g., the Bay View versus Fall Brook; Bay View versus South Lansing; and Fall Brook versus South Lansing) show that on average, only 18% of the most common taxa are shared between lists. Perhaps the most compelling evidence that variation among the South Lansing and West Brook faunas is indeed typical of other Hamilton coral-rich biofacies comes from a comparison of the oldest fauna analyzed here (the Bay View) with that of the youngest (the West Brook): 25% (5/20 taxa) of the most abundant Bay View and West Brook taxa co-occur in the most abundant lists of these beds. This percentage is as great as, if not greater than, that displayed in comparisons among only the three ''mainstream'' Hamilton coral-rich units. These observations provide evidence that minor disruptions of habitats between ''mainstream'' Hamilton coral-rich beds produce just as much change in the biofacies as the presumably more significant disruption associated with the Tully bioevents. Therefore, the ''type examples'' of faunal stability for coordinated stasis are perhaps more loosely structured than originally thought. This strongly suggests that the pattern termed coordinated stasis is only one of taxonomic stability; species abundance relationships are not conserved through time. Thus, because minor and major disruptions

TABLE 8. Ranked lists of the taxa comprising 75% of the total individuals within each of the Hamilton coral-rich beds (Bay View, Fall Brook, and South Lansing). Boldface taxa occur in the most-abundant lists of all beds.

Bay View	Percent abundance	Fall Brook	Percent abundance	South Lansing	Percent abundance
A. umbonata	20	*A. hamiltoniae*	12	*M. audaculus*	12
P. devoniana	17	*M. audaculus*	6	*M. junia*	9
Cystiphylloides sp.	10	***P. devoniana***	6	*P. inequistriata*	6
S. spinosa	9	*R. vanuxemi*	5	*A. spiriferoides*	5
Mucrospirifer consobrinus	7	*C. hamiltonensis*	5	*T. carinatus*	3
L. mucronata	6	***P. rana***	5	*A. hamiltoniae*	3
P. rana	5	*Rhipidothyris lepida*	5	***P. devoniana***	3
E. cf. *arctostriata*	5	*Cystiphylloides conifollis*	4	*M. mucronatus*	3
		P. inequistriata	4	*S. lepidus*	3
		Mucrospirifer consobrinus	3	*P. pustulosa*	3
				F. cf. *arbuscula*	2
				R. vanuxemi	2
				E. cf. *arctostriata*	2
				C. hamiltonensis	2
				M. sculptilis	2
				S. rectum	2
				P. constricta	2
				A. umbonata	2
				L. mucronata	2
				F. cf. *milne-edwardsi*	2
				N. concinna	1
				H. halli	1
				D. scitulus	1
				E. fimbriata	1
				P. rana	1

produce restructuring of the biofacies, biotic interactions cannot be driving the coordinated stasis pattern.

This study demonstrates that even amid significant fluctuations in the dominance of component species, biofacies can still appear to be stable entities when compared by using only simple holdover/carryover metrics. Underlying ecological patterns related to coordinated stasis concerning the nature of long-term faunal dynamics and community coherence can be addressed only if faunas are examined with abundance data. To present a convincing argument for ecologic stability, it is necessary to show that variations in abundance among fossiliferous horizons are no greater than that exhibited within a time horizon (see Bennington and Bambach 1996; Ivany 1999; Bonuso et al. 2002).

Comparisons with Other Paleozoic Studies of Stability.—Our results are consistent with those from other quantitative examinations of recurring faunas throughout the Paleozoic. For example, in their study of Pennsylvanian soft-bottom, marine assemblages, Bennington and Bambach (1996) showed that fossil assemblages from comparable environments in successive marine cycles could be distinguished by their overall species abundance structures. This led Bennington and Bambach to conclude that compositional stability was due simply to species recruitment into similar habitats from a persistent species pool. Likewise, similar observations on the independent nature of species responses to physical perturbation have been drawn from studies of the structure and stability of crinoid biofacies from the upper Pennsylvanian (Holterhoff 1996), Pennsylvanian and Permian brachiopod and bivalve biofacies from the Midcontinent (Olszewski and Patzkowsky 2001), Middle Devonian outer-shelf assemblages from New York (Bonuso et al. 2002), and Middle and Upper Ordovician assemblages from Kentucky (Holland and Patzkowsky 2004). Interestingly, both Bonuso et al. (2002) and Holland and Patzkowsky (2004) suggest that much of the perceived stability in recurring assemblages is driven by conservation of the abundances of the most common taxa. Our observations do not entire-

ly contradict this conclusion, as many of the most common species encountered had statistically indistinguishable abundances through time. However, of the ten most abundant species overall, four differed significantly in mean abundance from the South Lansing to the West Brook coral-rich assemblages, including the two most common species in our study. This demonstrates that the differences detected in our analysis are generated not only by changes in abundances of the less numerous species.

Conclusions

The major findings of this study can be summarized as follows:

1. The composition and structure of most local assemblages within the South Lansing and West Brook coral-rich beds varied significantly over local (hundreds of meters) and regional (hundreds of kilometers) spatial scales. South Lansing assemblages were dominated in Pennsylvania by the brachiopod *R. vanuxemi* and large rugose and favositid corals, and in New York by the brachiopods *M. audaculus*, *P. devoniana*, *C. hamiltonensis*, and *M. mucronatus*. West Brook assemblages were dominated by the brachiopods *L. mucronata*, *S. lepidus*, *E.* cf. *arctostriata*, *E. fimbriata*, and *M. junia* in New York and the coral *A. hamiltoniae*, the brachiopods *S. spinosa*, *R. vanuxemi*, and *P. inequistriata*, and the trilobite *P. rana* in Pennsylvania.
2. The data presented here suggest that taxonomic composition within biofacies can be maintained with considerable fidelity over extended periods of time and even across periods of biotic crisis in which a biota is largely or completely displaced from a depositional basin. Indeed, over 60% of all taxa collected from the South Lansing bed reappeared within the West Brook, indicating that a relatively stable species pool persisted throughout the 1.5 Myr study interval.
3. Despite this evidence for compositional stability, the overall dominance structures of these coral-rich biofacies were not conserved. Ranked lists of the most abundant taxa collected from successive coral-rich horizons are markedly different and mean abundances of the most common species overall varied significantly through time. Moreover, ANOSIM tests indicate that faunal variation between the South Lansing and West Brook coral-rich horizons was significantly greater than that expected from a random sampling of the within-horizon species pool. Taken together, these results indicate that species assemblages were only loosely organized and likely generated by a shared set of physical tolerances through time; thus it appears unlikely that biotic interactions played a major role in generating the degree of taxonomic stability observed.
4. Comparisons among additional, coral-rich units from lower in the Hamilton Group suggest that a more dynamic view of ecosystem structure and assembly is warranted within the type area of the coordinated stasis hypothesis. Furthermore, results of this study argue for a stronger role for quantitative sampling and analysis techniques in order to examine intervals of purported stability adequately. Analyses based upon simple holdover/carryover metrics can capture only limited aspects of ecological assemblages (species membership), and may also mask important structural variation that can be observed only by examining abundance data.

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