



**USING GIS TO ASSESS THE BIOGEOGRAPHIC IMPACT OF
SPECIES INVASIONS ON NATIVE BRACHIOPODS
DURING THE RICHMONDIAN INVASION IN THE TYPE-CINCINNATIAN
(LATE ORDOVICIAN, CINCINNATI REGION)**

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ABSTRACT

The Late Ordovician age strata in the Cincinnati, Ohio, region record a dramatic immigration of extra-basinal taxa into the region, termed the Richmondian Invasion, at the Maysvillian/Richmondian Stage boundary. The effects of the species invasion on genus-level paleoecology and biodiversity are well characterized; however, no prior analyses have examined biogeographic patterns in terms of areal extent of geographic ranges at the level of individual species at fine spatial or temporal scales. Geographic ranges of rhynchonelliform brachiopod species and genera were reconstructed using GIS-generated bounding polygons for each of the six depositional sequences delineated within Cincinnati strata in order to assess biogeographic patterns before, during, and after the Richmondian Invasion. Taxa were divided into four groups for analyses: native species that become extinct in the Maysvillian, native species that persist into the Richmondian, new species evolving in the Richmondian from native ancestors, and interbasinal invaders. Several statistical patterns emerge: native species with larger ranges preferentially survive compared to those with smaller ranges; carryover taxa exhibit no significant change in range size following invasion; both carryover and invader taxa exhibit large geographic ranges characteristic of eurytopic taxa, whereas new species have small ranges and are ecological specialists. Invasive species, therefore, most profoundly impacted narrowly adapted, specialist species during the early stages of invasion. Ecosystem response to the invasion continued for at least one million years. Native generalist taxa occupied larger geographic ranges than invader taxa for the first million years of the invasion, indicating a limited role for competition in driving ecosystem change.

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INTRODUCTION

The highly fossiliferous Upper Ordovician

units exposed along the Cincinnati Arch in southwestern Ohio, northern Kentucky, and southeastern Indiana comprise the type strata for the

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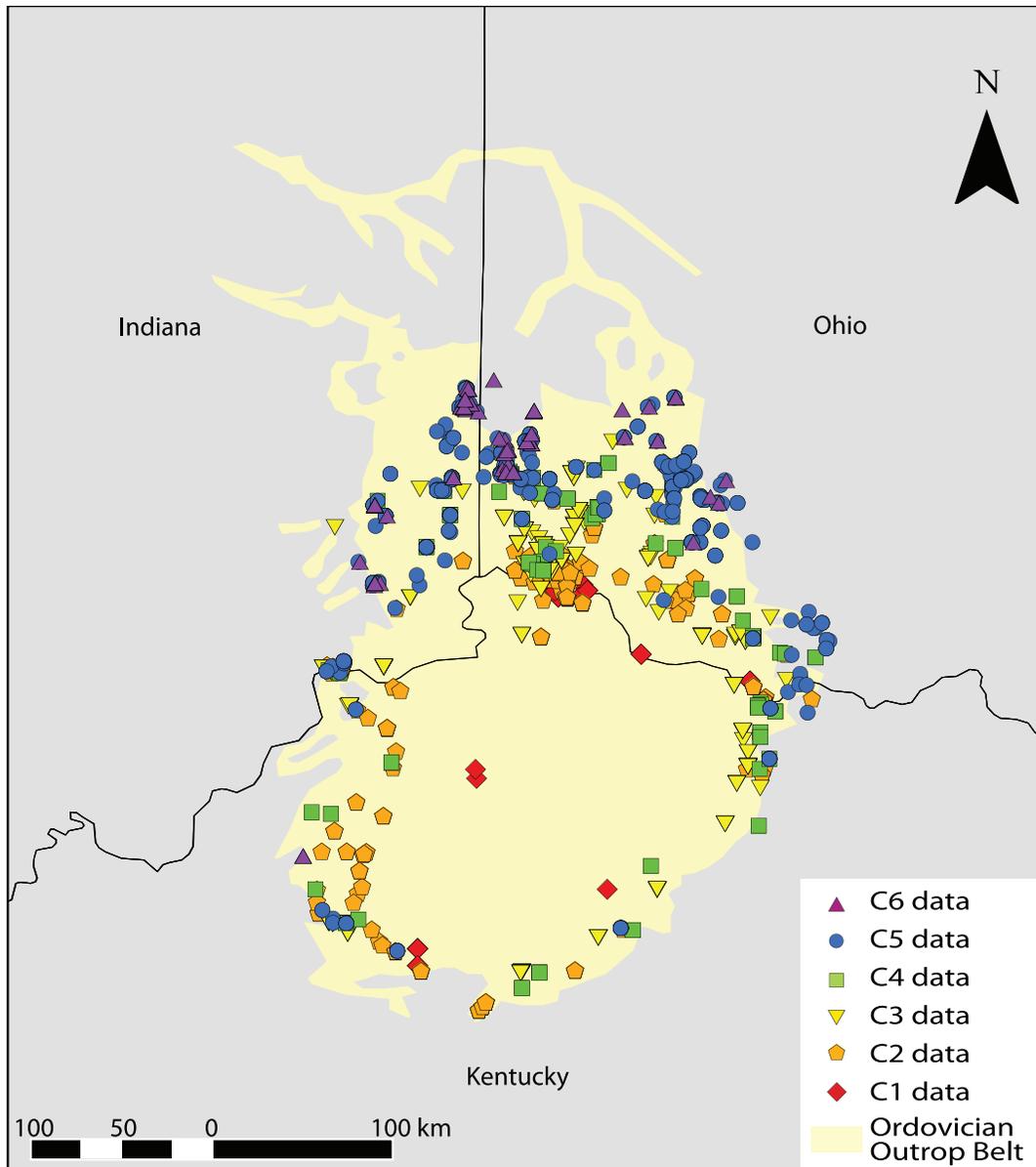


FIGURE 1. Data distribution by sequence mapped onto the Cincinnati outcrop belt. The outcrop belt is a structural arch; therefore, the central region exposes Middle Ordovician units and strata become progressively younger away from the central region.

Figure 1

Cincinnatian Series (Figure 1; Davis and Cuffey 1998). These strata are well known for their tremendous abundance of fossils, faunal diversity, and high quality of preservation. The fossils of the Cincinnati region have been studied for over 150 years, and major patterns of faunal turnover, community structure, and paleoecological gradients have been well characterized. Large-scale paleobiogeographic patterns, particularly as they pertain to either origination of the Cincinnatian fauna or

paleoecological gradients, have been examined. However, no quantitative analyses of paleobiogeographic patterns at the species level have yet been published. In this paper, the paleobiogeographic ranges of rhynchonelliform brachiopod species and genera of the type Cincinnatian strata are reconstructed and quantified.

Quantitative paleobiogeographic analyses have the potential to provide new insights into patterns of faunal turnover by facilitating statistical

analysis and hypothesis testing (Stigall Rode 2005). Biogeographic patterns are controlled by a combination of both evolutionary and ecological factors (Lomolino et al. 2006). Consequently, biogeographic assessments can provide detailed information about the impact of environmental changes (both biotic and abiotic) on faunal dynamics (Stigall 2008). Within the Cincinnati strata, a significant interval of faunal immigration, termed the Richmondian Invasion, is associated with the transition between the Maysvillian and Richmondian Stages (Holland 1997). In this study, the biogeographic impact of the introduction of the invader taxa on native brachiopods is analyzed. Specifically, the long-term effects of community restructuring previously identified during this interval (Holland and Patzkowsky 2007) are assessed as they pertain to biogeographic patterns and niche breadth.

Modern invasive species have been known to significantly disrupt ecosystems into which they are introduced. Most modern invasive species occur in new ecosystems due to human activity (Davis 2009), either through intentional introductions (such as song birds or cultivated plants that become naturalized) or inadvertently (such as stowaways on cargo ships). The term invasion has, however, also been used to describe any process of dispersal and establishment beyond a former range for modern species (Reise et al. 2006). Species invasions in the fossil record occur due to natural causes, for example a relative rise in sea level that leads to breaching of geographic barriers or removal of oceanographic barriers (Vermeij 2005). Therefore, for a fossil species to be considered analogous to a modern invader, it must have evolved in one geographic region or tectonic basin and then subsequently immigrated into a second region in which it did not evolve (Stigall 2010). These species have similar impacts to modern invasive species because they are newly introduced to ecosystems with which they did not evolve in concert.

The impact of these invaders (fossil or modern) is expected to include increased competition for resources and increased predation on native taxa (Lockwood et al. 2007; Davis 2009). The effect of increased predation is well characterized for modern invasive species: the introduction of novel predators often results in local extinction of prey species (Davis 2009). For example, the introduction of the Brown Tree Snake has decimated the endemic species of ground-nesting birds in Guam (Fritts and Rodda 1998). The long-term

effects of increased competition, however, are unclear. To date, no studies of modern invasive taxa have successfully demonstrated complete extinction of native species due to competition from invaders (Davis 2003). Studies of invasion biology, however, are limited in temporal duration. Field studies typically are conducted over several years, and even the best-studied historical invasions have an observational record of only decades. Longer term patterns inferred from invasion events in the fossil record, therefore, have the potential to provide insight into the long-term impacts of species introductions.

Cincinnati strata that preserve the geographic distribution of species before, during, and after the Richmondian Invasion provide a natural laboratory to test patterns of species level and ecosystem response to species invasions over geologic time. This paper expands on previous studies of community organization across the invasion interval (e.g., Holland and Patzkowsky 2007) by analyzing patterns of biogeographic distribution at the species level. In particular, the impact of the Richmondian invasion on native taxa is assessed by examining temporal shifts in geographic ranges of species within species groups. The differential response of native species that adapted successfully to the invasive regime versus those that did not can thus be ascertained. Furthermore, the timing of invasion impact is investigated by analyzing biogeographic patterns in each of six depositional sequences separately. This study, thereby, provides insight into the long-term effects of invasive species in modern ecosystems. This is particularly significant because the longer term effects of biotic invasions on these issues cannot be studied over ecological timescales.

GEOLOGIC SETTING AND STRATIGRAPHY

During the Late Ordovician, the Cincinnati region was located nearly 20 degrees south of the equator and rotated 45 degrees clockwise from its present orientation (Figure 2) (Scotese and McKerrow 1991). The Cincinnati region occupied a distal position in the Taconic foreland basin, developed from the collision of an island arc system with the eastern seaboard of Laurentia (Brett and Algeo 2001). The study area assumed a ramp structure which gently dipped from the modern southeast to northwest and was covered by a shallow epicritic sea up to 30 m deep (Holland 2008).

Strata of the type Cincinnati Series are divided into six depositional sequences, C1 to C6 (Figure 3) (Holland 1993; Holland and Patzkowsky

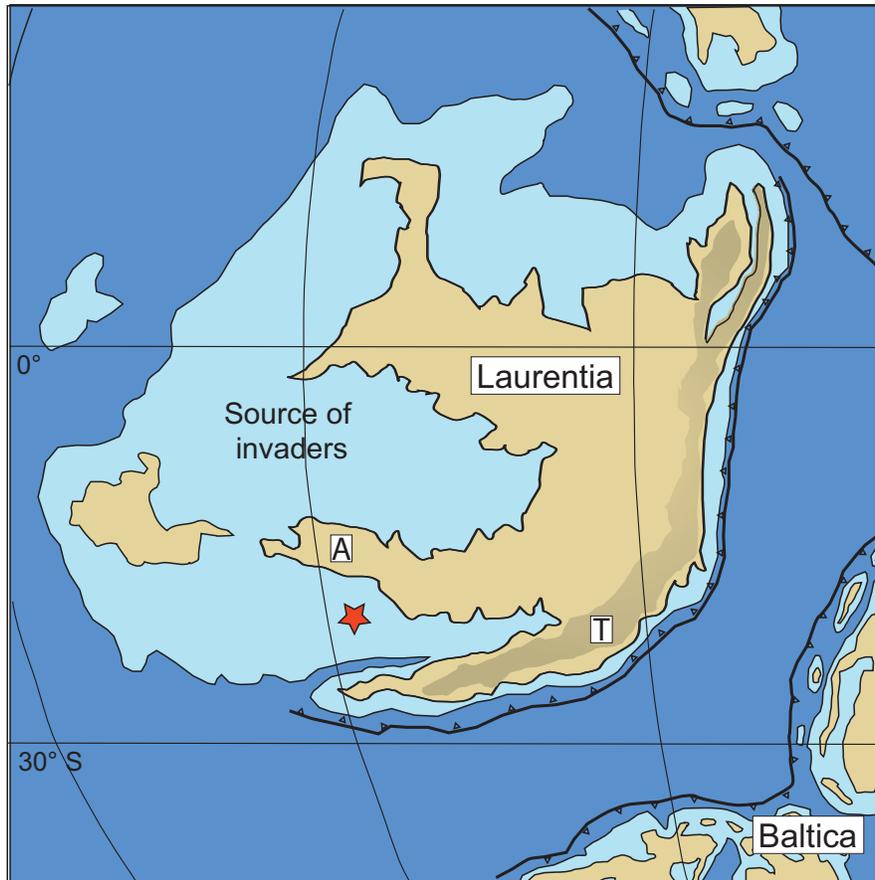


FIGURE 2. Paleogeographic reconstruction of Laurentia in the Late Ordovician. The star indicates the Cincinnatian region. Most of Laurentia is covered by a shallow epicontinental sea. The Taconic foreland basin extends to the south of the study region. A: Transcontinental Arch, T: Taconic Highlands.

1996). Each sequence spans between approximately three quarters of a million years to two million years. Thin transgressive systems track deposits occur at the base of the sequences, but the majority of the sequences represent highstand deposition. Each sequence records an overall shallowing upward progression, and the sequences shallow upward overall due to infilling of the basin.

Four primary depositional environments were arrayed along the ramp: offshore, deep subtidal, shallow subtidal, and peritidal (Holland 1993, 2001). Sedimentology varies with paleoenvironment, but in general, Cincinnatian sediments represent storm-derived deposition (Brett and Algeo 2001). Layers alternate between terrigenous mudstones comprising sediments sourced from the weathering Taconic highlands and bioclastic packstones to grainstones, which represent the shelly storm lag (Jennette and Pryor 1993). In deeper-water paleoenvironments, mudstones comprise a high percentage of the section as only the largest

storms were able to disturb the seafloor sediments, whereas shallower water deposits are dominated by limestone layers because the fine-grained particles were almost entirely winnowed away by storms or waves (Jennette and Pryor 1993; Holland 2001). Although storm processes were pervasive in the Cincinnatian system, lateral transport of skeletal debris was limited (several meters) as evidenced by the ability to resolve detailed paleoecological changes within limestone units at the outcrop scale (Frey 1987; Barbour 2001).

In general, Cincinnatian limestones lack features associated with tropical deposition (e.g., ooids, peloids, and significant micrite) and exhibit characteristics of cool-water carbonates. Because these layers were deposited in the paleotropics, they are interpreted to represent a high-nutrient system rather than truly cool-water deposition (Holland and Patzkowsky 1996). This is particularly the case for the C1 to C4 units. These units contain phosphate grains and crusts indicative of high-

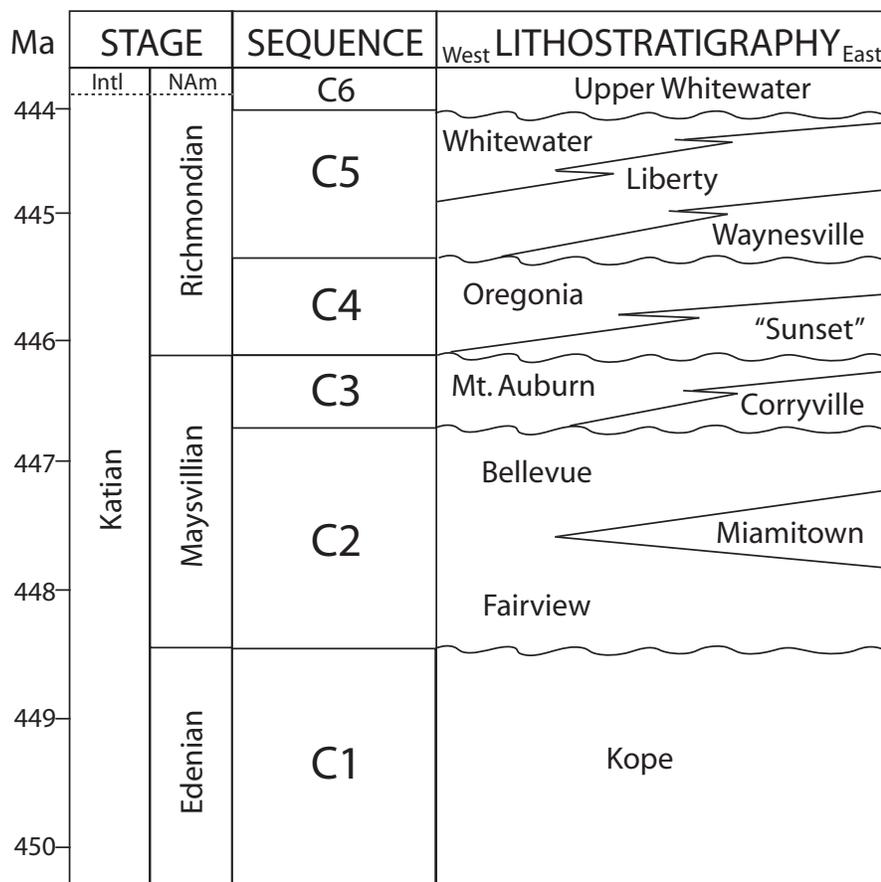


FIGURE 3. Cincinnati stratigraphy. Modified from Holland and Patzkowsky (1996).

nutrient conditions (Holland 2008). In the C5 and C6 sequences, phosphate deposition decreases, nutrient levels appear to drop, and micrite becomes more abundant. This shift in nutrient load has been interpreted as a shift in paleoceanographic conditions (Holland and Patzkowsky 1996). This shift appears to coincide with the Richmondian transgression and the influx of invader taxa into the basin, as discussed more fully below.

PALEOECOLOGICAL FRAMEWORK

Cincinnati strata preserve a rich and diverse fauna. Even though graptolites, conodonts, and nautiloids occur, the preserved fauna is primarily benthic and is dominated by brachiopods and bryozoa with associated echinoderms, trilobites, gastropods, bivalves, and corals (Feldmann 1996; Davis 1998; Meyer and Davis 2009). Numerous recent analyses have elucidated aspects of Cincinnati paleontology including studies of diversity structure (Novack-Gotshall and Miller 2003), autecology of specific taxa (Leighton 1998;

Datillo 2004), biofacies (Anstey et al. 1987; Barbour 2001; Holland et al. 2001; Holland and Patzkowsky 2007; Patzkowsky and Holland 2007), characterization of ecological and faunal gradients (Miller et al. 2001; Holland et al. 2001; Holland 2005; Holland and Patzkowsky 2007), microevolutionary patterns (Webber and Hunda 2007), and taphonomy (Meyer 1990; Brandt-Velbel 1985).

The most dramatic shift in paleoecological patterns occurs across the Maysvillian-Richmondian (C3-C4) boundary. The onset of the Richmondian Invasion occurs in the C4 sequence when a suite of taxa from the paleoequatorial region immigrated into the Cincinnati region (Foerste 1917; Holland 1997). Significant faunal reorganization occurred during the C4 sequence. Detailed gradient ecology and biofacies analyses of genus-level community composition by Holland and Patzkowsky (2007) indicated that the C1 to C3 pre-invasion communities exhibited high levels of similarity in community structure. The C4 sequence preserves a fundamental breakdown/restructuring

of biofacies. Clearly differentiated biofacies are reestablished during the C5 sequence, although the C5 community structure differs significantly from those of the Maysvillian due to the ecological dominance of many invader taxa (Holland and Patzkowsky 2007).

The Richmondian Invasion was a cross-faunal immigration event. Taxa new to the Cincinnati region included species from all trophic levels including tabulate and rugose corals, nautiloid cephalopods, gastropods, bivalves, trilobites, and brachiopods (see Holland 1997 for a complete list of invader taxa). The influx of invaders appears to have been largely unidirectional from the paleoequatorial region of the western United States and Canada (Figure 3) and thus was originally referred to as an invasion of the “Arctic Fauna” (Foerste 1917). Significantly, the influx of invaders did not result in an appreciable increase in extinction rate. Instead, many native species persisted across the invasion interval, resulting in higher diversity levels in Richmondian units compared to Maysvillian strata of the Cincinnati region (Patzkowsky and Holland 2007). Particularly notable were the introductions of taxa such as rugose corals and rhynchonellid brachiopods. Member of these orders—and in some cases the same genus (i.e., *Rhynchotrema*)—were present in the Cincinnati Arch during the Mohawkian Stage, but were absent for at least five million years prior to their reintroduction (Elias 1983; Holland 1997). During the interval of their absence, members of the invader genera occurred in paleoequatorial waters and are preserved in strata in Canada and the Western United States. For example, *Grewingia*, *Streptolesma*, and *Rhynchotrema* occur in the Steamboat Point Member of the Bighorn Dolomite of Wyoming, which is correlative with the C2 sequence (Holland and Patzkowsky 2009). Furthermore, certain invader species, such as *Thaerodonta clarksvillensis* and *Hiscobeccus capax*, occur in the Maysvillian portions of the Red River Formation of Southern Manitoba (Jin and Zhan 2001). Holland and Patzkowsky (1996) have linked the invasion with paleo-oceanographic changes that resulted in warm, low nutrient waters replacing the former nutrient-rich temperate conditions in the Cincinnati region, thereby facilitating the migration of paleoequatorial taxa into the area.

METHODS

Data Acquisition

For this analysis, biogeographic ranges of taxa were reconstructed at both the species and genus level at the temporal resolution of stratigraphic sequence of Holland and Patzkowsky (1996) using Geographic Information Systems (GIS). The geographic ranges of rhynchonelliform brachiopods were reconstructed because analyses of these organisms are expected to produce the most accurate range reconstructions for Cincinnati taxa. Brachiopod fossils are among the most diverse and abundant fossils that are present in all Cincinnati depositional environments, and most can be identified to species based on external skeletal morphology (Meyer and Davis 2009). High sampling density and accurate species identifications reduces undersampling and other errors potentially associated with range reconstruction (see Rode and Lieberman 2004). Brachiopods lived on or borrowed shallowly within the seafloor, thus their fossils distribution likely reflects their actual living distribution accurately on the outcrop scale (Kidwell and Flessa 1996), the scale at which these analyses are conducted. As noted above, storm processes, which affected Cincinnati benthos, did not result in significant lateral transport of skeletal material (Frey 1987; Barbour 2001). Moreover, Finnegan and Droser (2008) noted that storm deposits have a higher proportion of local taxa than unworked beds because they concentrate rare taxa in the resulting lag. Consequently, although these storms impacted the sediment, storm reworking produced biodiversity data that are more complete than non-reworked deposits.

Data required to reconstruct geographic ranges consist of geographically and temporally restricted species occurrence data. These data include species identification, precise latitude and longitude coordinates of the collection locality, and stratigraphic information to place the species occurrence within the correct stratigraphic sequence. Species occurrence data were collected from museum collections, targeted field work, and the Paleobiology Database (paleodb.org). Collections at the Cincinnati Museum Center, Miami University Limper Museum, and the Ohio State University Orton Geological Museum were examined. At each museum, specimens were inspected by the author in order to verify (or correct) species identifications. Species identifications followed published identification keys (Davis 1998, Feldmann 1996) and published synonymies (e.g.,

Walker 1982). Taxa known to be problematic or for which current consensus opinion questions their taxonomic validity (e.g., *Platystrophia unicostata* and *Rafinesquina fracta*) were excluded from the database. Specimens with stratigraphic or geographic information that could not be resolved to sequence or precise location (e.g., Late Ordovician, Cincinnati Region) were necessarily excluded from the dataset. Museum data were supplemented by a download of data, primarily the dataset of Holland and Patzkowsky (2007), from the Paleobiology Database and field work targeted to fill in gaps in data coverage. The final species occurrence database includes 1490 unique species occurrence data points for 49 brachiopod species in 21 genera across all six depositional sequences (Figure 1, Tables 1, 2, Appendix 1, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html).

Range Reconstruction

Geographic ranges were calculated in two ways using GIS. The first method estimates the area of a geographic range by creating a minimum spanning convex hull to enclose all known occurrence points for a taxon (see examples in Figure 4). Using this method, all known taxon occurrence sites are enclosed by a polygon with the fewest possible number of sides, then the area of that polygon is calculated in ArcGIS (ESRI 2008). This method has been successfully employed with Devonian brachiopods and bivalves (Rode and Lieberman 2004), Devonian phyllocarids (Rode and Lieberman 2005), and Cambrian arthropods (Hendricks et al. 2008). Step-by-step instructions for this method are presented in Stigall Rode (2005) and Stigall (2006). Although the polygon method provides the most parsimonious estimate of a taxon's geographic range, it is potentially sensitive to underestimation of a taxon's range due to under-sampling or overestimation of geographic ranges that were not laterally continuous (see Stigall Rode and Lieberman 2005). Therefore, geographic ranges were also estimated using a distance method based on the maximum linear extent between two points of known taxon occurrence, a method previously employed by Hendricks et al. (2008). To further reduce the sensitivity of the results to sampling bias, analyses were calculated at both the species and genus levels. The 49 species analyzed comprised 21 genera. Of these, twelve invasive genera and one Maysvillian restricted genus were monotypic within the study.

There are currently no published phylogenetic analyses for relationships of Cincinnati brachiopods. The monophyly of some genera, such as *Strophomena* and *Platystrophia*, have been questioned (Zuykov and Harper 2007; Leighton, personal comun., 2009), while some species, such as *Dalmenella meeki*, are known to be assigned to genera to which they do not belong (Jin, personal comun., 2009). As species are a primary unit of evolutionary innovation, whereas genera represent systematists's opinions of related but potentially non-monophyletic groups of species, the discussion below will focus primarily on species-level patterns. Generic level data will be used to assess and support the relative strength of the pattern at multiple taxonomic levels.

The areal extent of the outcrop belt shifts significantly in both size and location among sequences. As discussed above, Cincinnati strata were deposited along a depositional ramp, which prograded northward through time. Furthermore, strata are now exposed along a structural arch. Therefore, the oldest sequences outcrop more centrally along the arch whereas the younger sequences occur both toward the northern and more distal regions of the arch (Figure 1). In order to meaningfully compare temporal patterns among sequences, these variations in outcrop availability must be accommodated. Therefore, calculated geographic ranges were normalized by outcrop extent for each time slice. Areal ranges were normalized by dividing the observed range by the area of the minimum convex hull digitized for all species occurrence data in the database for a single sequence (Tables 1, 2, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html). Maximum linear extents were similarly normalized by dividing by the maximum linear extent between any pair of species occurrences within a single sequence (Tables 3, 4, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html).

A second standardizing procedure, dividing the raw geographic range estimate by the number of species occurrence points used in the range estimation, was also undertaken (Appendix 2). Results of statistical analyses conducted with data normalized by occurrence points were congruent with those of the area standardized data. (Appendices 3-4, 6-9). Normalizing by outcrop extent is less heavily influenced by sampling bias or sampling intensity. Therefore, results of analyses conducted

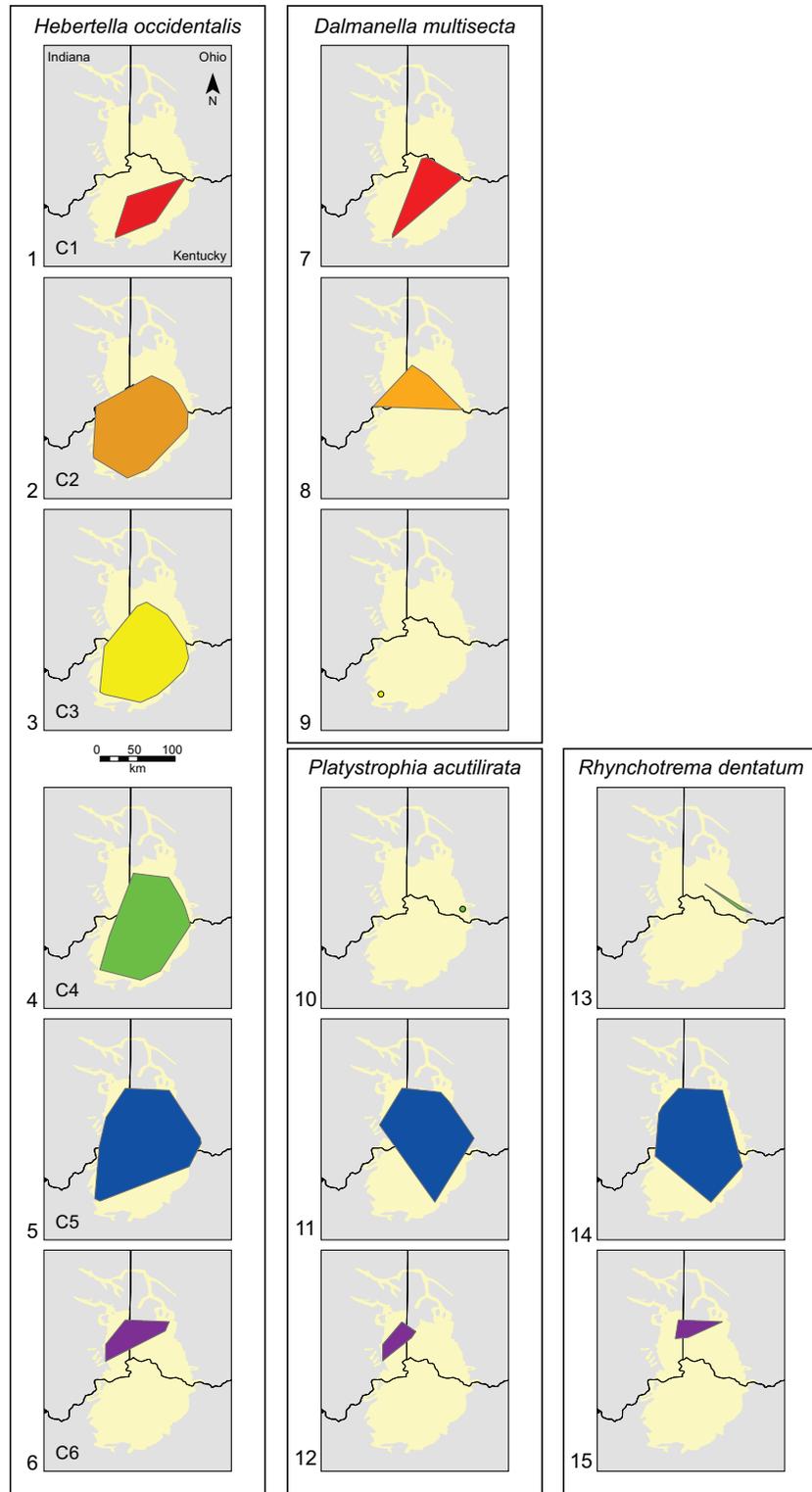


FIGURE 4. Representative species-level paleogeographic reconstructions. (1-6) Range reconstructions for a carry-over species, *Hebertella occidentalis* in the C1 through C6 sequences, (7-9) Range reconstructions for a Edenian to Maysvillian restricted species, *Dalmanella multisecta* in the C1 through C3 sequences, (10-12) Range reconstructions for a native descendant species, *Platystrophia acutilirata* in the C4 through C6 sequences, (13-15) Range reconstructions for an invasive species, *Rhynchotrema dentatum* in the C4 through C6 sequences.

using the area standardized range values will be discussed in the text.

Statistical Analyses

To assess whether certain types of species responded differently to the invasive regime, species were categorized into four groups: (1) species native to the Cincinnati region which did not persist beyond the Maysvillian Stage, (2) species native to the Cincinnati region which were extant in the Maysvillian and carryover into the Richmondian, (3) species that evolved in the Richmondian from Cincinnati natives, and (4) extrabasinal invaders (Tables 1-4, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html). For generic analyses, only categories 1, 2, and 4 were used. Because phylogenetic relationships are almost entirely unknown for Cincinnati brachiopods, species group membership was coded in two ways. In the first coding strategy (indicated in Tables 1-4, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html), category 3 includes all Richmondian species assigned to a genus that existed Cincinnati during the Maysvillian, and category 4 includes all Richmondian species assigned to a genus absent from Maysvillian strata of the Cincinnati region. This coding scheme assumes that all of the Richmondian members of a Maysvillian genus occur in Richmondian strata due to speciation within the basin and that none of these species migrated to Cincinnati as part of the Richmondian Invasion. While this interpretation is the most parsimonious, it may not be accurate for all species in the category; some species of native genera may be. This may have arrived in the Cincinnati region as part of the invasion, particularly true for species of *Strophomena*. This genus is absent from C3 strata of the Cincinnati region (Table 1, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html), which may represent extirpation from the basin. Furthermore, some Richmondian species, notably *Strophomena planumbona*, occur in the Maquoketa Formation on the west side of the basin during the C3 sequence (Leighton, personal commun., 2009). Therefore, a second coding strategy was employed in which all Richmondian species of *Strophomena* were treated as invasive rather than as native descendants. For generic analyses, *Strophomena* was treated as a carryover taxon in the first coding strategy. In the second coding strategy, C1 and C2 *Strophomena* were treated as Maysvillian

restricted genus while the C4-C6 *Strophomena* were treated as an invasive genus.

Two sets of statistical analyses were conducted based on the estimated geographic ranges. The first assessed differences in geographic range versus taxon group; whereas the second set analyzed changes in geographic range by sequence. Differences in geographic response by taxon group were analyzed using one-tailed *t*-tests, and temporal patterns were assessed using analysis of variance (ANOVA). All analyses were conducted with Minitab 15 (Minitab Inc. 2007). Analyses were conducted separately for the two taxon group coding strategies.

RESULTS

Comparison by Group Membership

Geographic range reconstructions for species representative of each taxon group are illustrated in Figure 4. Visual comparison of the 95% confidence intervals of the mean geographic range of the four taxon groups delineated above suggests significant differentiation of geographic range size within these groups. Congruent results were obtained regardless of coding strategy or standardization procedure (Figure 5.7, Appendix 5). A series of hypotheses related to how taxonomic groups responded to the invasive regime were assessed using one-tailed *t*-tests (Table 5, Appendices 3, 6, 8, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html).

Results indicate that among native Cincinnati taxa, species or genera that cross over into the Richmondian had statistically larger geographic ranges than those that do not (Table 5.1, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html). Species area, species linear, and generic area analyses are highly significant under both coding strategies. The genus linear analysis is significant at the level of $p = 0.096$ when *Strophomena* is treated as native and $p = 0.021$ when *Strophomena* is treated as a Richmondian invader. For those native taxa that carry over into the Richmondian, geographic ranges are statistically identical in all analyses (Table 5.2, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html), indicating that the introduction of the invader taxa did not produce a significant range size shift in these taxa. The mean Richmondian range size of carryover taxa is larger than that of the invasive taxa. When Richmondian

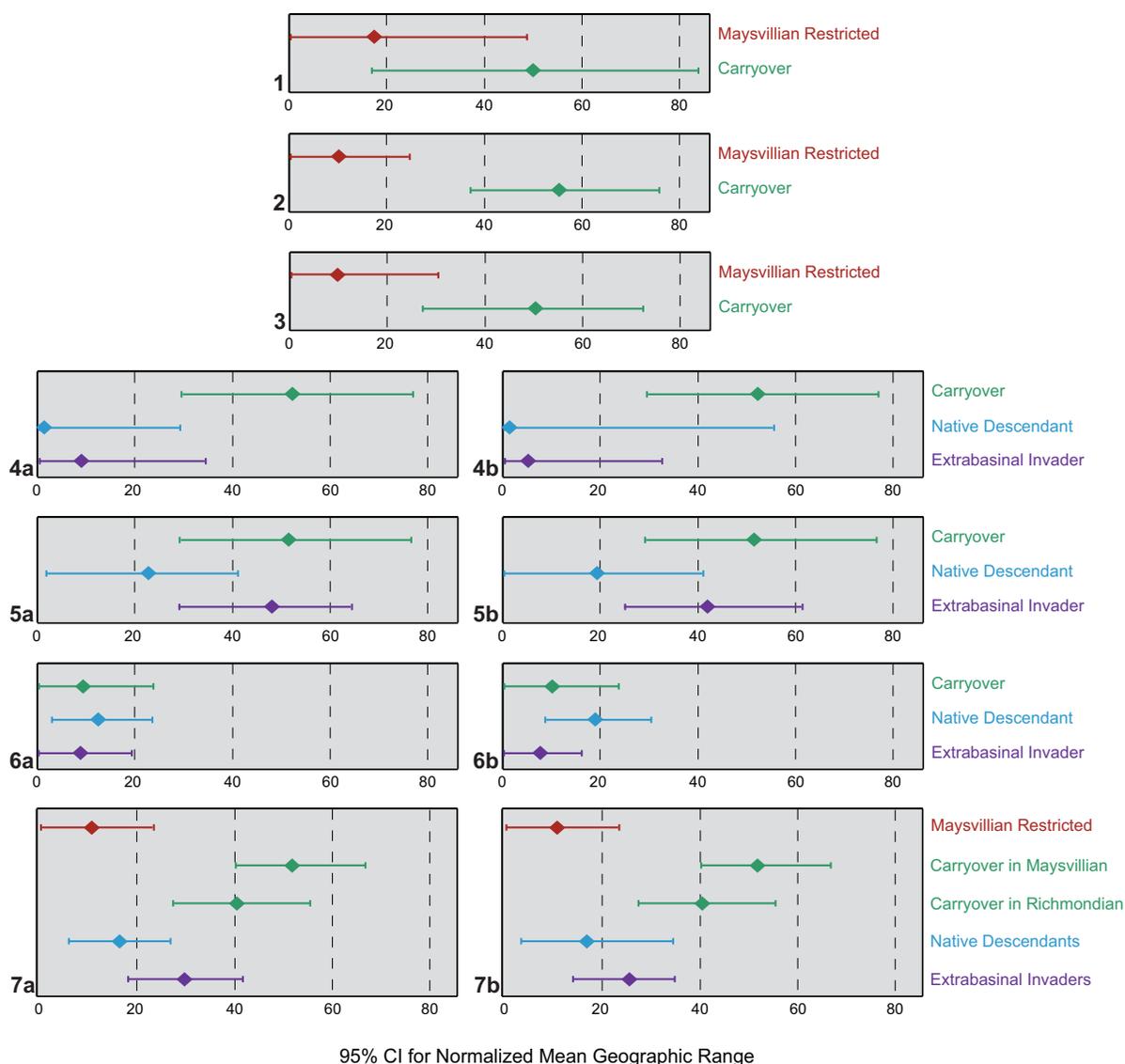


FIGURE 5. Comparison of the normalized mean species range from the area method for each species group by sequence (1-6 relate to corresponding sequence number) and for the entire study interval (7). 4-7 (a) treat Richmondian *Strophomena* species as native descendants, while (b) treat Richmondian *Strophomena* species as invasive. Individual 95% confidence intervals for mean geographic range are based on pooled standard deviation.

Strophomena species are coded as native descendants, this pattern is statistically significant only for the generic area analysis (Table 5.3, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html); however, when *Strophomena* species are treated as invasive, ranges of invader taxa are significantly smaller in all analyses except the species linear analysis. Finally, the geographic ranges of new species that evolve in the Richmondian from Cincinnati ancestors are significantly smaller than the ranges of carryover taxa in the Richmondian in

all analyses (Table 5.4, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html).

Comparison by Sequence

A second way to assess the biogeographic impact of the Richmondian Invasion is to examine species ranges illustrated in Figure 4 are representative of patterns for each time slice. Geographic range size for species groups within each depositional sequence were assessed through Analysis of Variance (ANOVA)

tests. Results are similar regardless of normalization procedure or whether Richmondian occurrences of *Strophomena* were coded as native or invasive in origin (Figure 5, Table 6, Appendices 4, 5, 7, 9, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html). Differences in statistical significance between tests using the different coding strategies are relatively minor and are restricted to the C4 and C5 sequences (Table 6, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html).

In the C1 sequence, there is no statistical difference between geographic ranges of taxa which will ultimately survive into the Richmondian and those that become extinct by the end of the Maysvillian (Figure 5.1, Table 6.1, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html). In the C2 sequence, Maysvillian restricted taxa occupy smaller geographic ranges than carryover taxa, although this is statistically significant in only half of the analyses of the species area method (Figure 5.2, Table 6.2, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html). In the C3 sequence, Maysvillian restricted taxa occupy geographic ranges that are statistically smaller than carryover taxa in all analyses (Figure 5.3, Table 6.3, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html).

The C4 sequence includes the earliest evidence of extrabasinal invaders and represents the initial phases of the invasion and establishment of invasion ecology. In this sequence, invader taxa occupy restricted geographic ranges with respect to the carryover taxa (Figure 5.4). When *Strophomena* species are coded as native descendants, new speciation is limited to three species (Tables 1, 3, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html), but these species are narrowly distributed (Figure 5.4). If *Strophomena* species are coded as invasive, then only one native descendant species, *Platystrophia clarksvillensis*, occurs in the sequence, which renders analysis of that taxon group spurious. Even so, differences between carryover, native descendant, and invasive species are statistically significant or nearly so in all analyses (Table 6.4), note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html).

In the C5 sequence, the most broadly distributed taxa are still the carryover taxa, but invaders

exhibit larger ranges than they did in the C4 sequence (Figure 5.5). Newly evolved species, however, continue to occupy restricted ranges (Figure 5.5). Whereas statistical differences between the three classes remain at the genus level, the overlap between carryover and invader taxa at the species level renders these groups biogeographically indistinguishable (Table 6.5, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html). By the late Richmondian C6 sequence, all class size differentiation has broken down and differences are no longer statistically significant in any analysis (Figure 5.6, Table 6.6, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html).

DISCUSSION

Variations in Geographic Range between Taxon Groups

The patterns of differentiation in the geographic ranges observed in taxonomic groups of Cincinnati brachiopods can be explained, at least partly, by the relationship between geographic range size and niche breadth. The geographic range inhabited by a species is a manifestation of a species ecological niche at two levels, the fundamental and realized niche (Lomolino et al. 2006). The largest geographic range that a species may potentially occupy is the area of occurrence of a species' fundamental niche, the sum of the ecological parameters under which a species is able to maintain a population (Hutchinson 1957). All species, however, actually occupy a smaller geographic region, which is referred to as the realized niche. The difference between a species' fundamental and realized niches is determined by biotic interactions such as competition and predation (Hutchinson 1957). Species geographic ranges, therefore, are directly tied to the breadth of their ecological niche. A positive correlation between niche breadth and geographic range has been recovered in numerous studies (e.g., Jackson 1974; Jackson et al. 1985; Brown 1984; Thompson et al. 1999; Gaston and Spicer 2001; Fernández and Vrba 2005; but see Williams et al. 2006 for a counterexample). Species with broad environmental tolerances, known as generalist or eurytopic species, exhibit larger geographic ranges than specialist or stenotopic species, which are characterized by highly constrained niches (MacArthur 1972; Mayr 1963; Stanley 1979). Because specialists can utilize only a limited array

of ecological parameters, the geographic region, which encompasses their niche, will necessarily be smaller than those of eurytopic species.

Based on the relationship between geographic range and niche breadth, the ecological characteristics of the four brachiopod groups can be considered. Both Maysvillian restricted taxa and new species that evolve in the Richmondian from native taxa exhibit small range sizes characteristic of ecological specialists (Figures 4, 5.7). Extrabasinal invaders are characterized by intermediate geographic ranges, and carryover taxa exhibit large geographic ranges suggestive of ecological generalists (Figures 4, 5.7). Statistical results further support the classification of the Maysvillian restricted and native descendant species into one category of narrower niche breadth versus the carryover and invasive taxa into a second category of broader niche breadth. The geographic ranges of both the Maysvillian restricted taxa and the native descendant species are statistically significantly smaller than the carryover taxa (Table 5.1, 5.4, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html). Conversely, the geographic ranges of the invader taxa, although smaller on average than carryover taxa, are statistically indistinguishable from the carryover taxa in several comparisons, particularly those conducted at the species level (Table 5.3, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html, Figure 5.7). This apparent disparity between the two generalist groups results from temporal shifts in the geographic ranges of these groups, discussed more fully below.

The assignment of these taxon groups to specialist versus generalist ecologies is also consistent with their macroevolutionary histories. In general, specialist and generalist species exhibit characteristic differences in speciation and extinction rates; namely, generalist species tend to be longer lived with lower rates of extinction and speciation (Jackson 1974; Stanley 1979; Foote et al. 2008). This macroevolutionary relationship is a derivative of niche breadth; the larger the geographic region occupied by a species, the more likely that at least some part of that range will remain habitable following events of environmental or biotic perturbation. Consequently, one would predict *a priori* that the longest lived species in the dataset, the carryover species, should exhibit larger geographic ranges indicative of generalist ecologies; a prediction congruent with the results. In addition, the two specialist groups, the Maysvil-

lian restricted taxa and the newly evolved descendant species, would be predicted to exhibit shorter temporal durations, which is also congruent with the results. Presumably, the native descendant taxa radiated into open specialist niches vacated by the extinction of the Maysvillian restricted species. Furthermore, the interpretation of invader taxa as ecological generalists is consistent with data from the modern invasion biology literature; most of the introduced species that have successfully invaded new ecosystems exhibit broad ecological tolerances (Davis 2009).

The stark difference between the geographic range size of the species and genera that become extinct by the end of the Maysvillian versus the range size of the carryover taxa (Table 5.1, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html) suggests that species with limited niche breadth were unable to succeed in the new invasive regime in contrast to species with broader niches. Because the carryover taxa are present both before and after the influx of the invaders, it is possible that these taxa would have experienced a reduction in their realized niche, and hence geographic range, due to increased biotic interactions with the interbasinal invaders. To test this hypothesis, the geographic ranges of carryover taxa were compared before and after the onset of the invasion. Although mean taxon range decreased slightly after the invasion (more noticeably at the species level than the generic level), these differences were not statistically significant in any analysis (Table 5.2, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html). Prior analyses (e.g., Tyler and Leighton 2007) have noted shifts in morphology of incumbent genera when they co-occur with morphologically similar invaders; however, these differences appear to represent local effects that do not manifest in species or genus-level geographic patterns.

An alternate explanation for the limited range size of invader and native descendant species relates to the relationship between geographic range size and taxon age. All taxa necessarily occupy small geographic ranges immediately following speciation, expand their geographic ranges as population sizes increase through time, and contract their geographic ranges as population size decreases prior to extinction (Vrba and DeGusta 2004; Foote et al. 2008). Consequently, young species may be expected to occupy smaller geographic ranges than older species with large population sizes (Webb and Gaston 2000). Studies of

the timing of range expansion in the fossil record have determined that geographic range size increases rapidly following speciation (Liow and Stenseth 2007), and species typically attain full range size within one million years or less (Vrba and DeGusta 2004; Webb and Gaston 2000). Since the scale of temporal resolution of this study is approximately one million years per time slice, it is unlikely that the estimates of geographic range size analyzed herein capture the early post-speciation phase prior to full range size establishment. This possibility, however, cannot be excluded completely and may contribute to the observed increase in average geographic range of native descendant species from the C4 to C6 sequence or invader species between the C4 and C5 sequences.

Temporal Variations in Geographic Range

Biogeographic patterns shift dramatically across the six Cincinnati sequences (e.g., Figure 5). From C1 to C3 sequences, carryover taxa exhibit larger mean geographic range size than Maysvillian restricted taxa. However, this difference is statistically significant only during the C3 sequence (Table 6, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html). Apparently, it is during the final Maysvillian sequence only when establishing a larger geographic range is a predictor for taxon success across the invasion interval. At the onset of the Richmondian Invasion in the C4 sequence, carryover taxa are characterized by large mean geographic range sizes, and both new descendant species and invader taxa exhibit smaller ranges than carryover taxa (significant in three of four analyses for either coding scheme). New speciation is limited to only one to three species, but these are narrowly distributed, specialist style species. By the C5 sequence, a very diverse set of taxa is present. The most broadly distributed taxa are still the carryover taxa, but invaders exhibit larger ranges than their C4 sequence counterparts. Newly evolved species continue to occupy restricted ranges characteristic of ecological specialists. Although statistical differences remain at the genus level, the overlap between carryover and invader taxa at the species level renders these groups biogeographically indistinguishable in the C5 sequence. Finally, during the C6 sequence class differentiation breaks down and carryover, new species, and invader taxa have overlapping mean geographic ranges.

Holland and Patzkowsky (2007) interpreted three phases of community organization from their generic-level analysis of paleocommunity structure: stability from C1 to C3, reorganization in C4, and stability in C5 and C6 sequences. Our results are largely congruent with their pattern. Similar biogeographic patterns appear in C1 through C3 sequences, but each of C4, C5, and C6 exhibit different organizational patterns (Table 6, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html, Figure 5).

The observed shifts in Richmondian biogeographic ranges, particularly the increase in invader range between the C4 and C5 sequence and the reduction in range size of both carryover and invader taxa between the C5 and C6 sequences, could potentially be attributed to several causes: response to invasive regime, niche shift of species due to environmental rather than biotic changes, or sampling bias. In this case, sampling bias can be ruled out as a primary driver of the observed pattern. The C4 sequence comprises only two of the four Cincinnati depositional environments (deep and shallow subtidal), whereas the C5 sequence includes deposits of all four environments (also including offshore and peritidal) (Brett and Algeo 2001; Holland 2001). Based on ordination analyses, invader taxa most commonly occur in the deep and shallow subtidal communities, which are preserved in both the C4 and C5 sequences (Holland and Patzkowsky 2007). Because the percent area colonized by invaders increases with additional facies, range increase observed in the C5 sequence cannot be attributed to undersampling of facies. Furthermore, biogeographic patterns recovered when geographic range is normalized by number of localities (a proxy for sampling intensity) are congruent with those recovered from the outcrop area normalization method (compare Table 6 and Appendix 4, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html). This finding indicates that observed biogeographic patterns are not controlled by sampling bias. The C6 sequence exhibits potential for sampling bias as this sequence is both geographically restricted (Figure 1) and limited to only the shallow subtidal and peritidal facies (Hay 2001), and this limitation should be considered when interpreting C6 patterns. Paleoenvironmental changes can be ruled out on similar grounds. All sequences record shallowing upward (Holland 1993); symmetrical biogeographic patterns, therefore, should be expected between sequences if

range sizes are strongly affected by changes in relative sea level. Aside from the oceanographic shift in the early Richmondian—which affected all subsequent sequences equally, no significant paleoenvironmental changes are recorded sedimentologically. The biotic impact of the extra-basinal invaders, therefore, emerges as the most likely cause of the observed biogeographic shift.

Characteristics of Richmondian Invaders

A significant body of research has emerged within the modern invasion biology literature aimed at delimiting the characteristics of species that successfully invade new ecosystems (see review in Davis 2009). For a species to successfully invade a new habitat, four basic stages must occur: transport, establishment, spread, and impact (Lockwood et al. 2007). Modern invasive species must exhibit traits that facilitate both the transport and establishment stages. Certain characteristics, such as access to human transport devices (ship ballast water, fruit cargo containers) are matters of contingency; whereas other characteristics, such as the ability to exploit a variety food sources in the new ecosystem relate directly to the biological parameters of a species.

The most important feature for determining species' success during the transport stage is propagule pressure, both the number of individuals arriving at a location and the frequency of their introduction (Lockwood et al. 2005). In the fossil record, transport occurs through natural, in this case oceanographic, processes. In the Richmondian, successful invaders would have exhibited high larval or adult dispersal in order to establish new populations at such large distances from their ancestral populations. Richmondian propagule pressure was likely much lower than that observed with invaders in modern ecosystems as tens of thousands of years were available for transport and establishment of the Late Ordovician taxa.

Establishment relates to initial colonization of the new habitat by a small number of individuals, whereas spread refers to the stage in which the invader species is both abundant and becoming widespread. Species with broad ecological tolerances are more likely to succeed in these stages than ecological specialists (Duncan et al. 2003; Lockwood et al. 2007). Due to the short duration and small population sizes during this interval, these stages are unlikely to be preserved in the fossil record. Instead, the first appearance of Richmondian Invaders in the fossil record most likely reflects the impact stage, which refers to the inter-

val when the invader taxon is fully established and naturalized or integrated within the community (Lockwood et al., 2007).

Within the rhynchonelliform brachiopods, the Richmondian invaders appear to conform to the basic set of expectations developed from modern invasion biology: high dispersal ability and broad ecological tolerances. Although adult rhynchonelliform brachiopods lack locomotor ability, their larvae are free swimming. The duration of the free-swimming larval stage may persist several weeks (Rudwick 1970, Peck and Robinson 1994), and recent rhynchonelliform brachiopod species have been observed to expand their ranges as much as 3000 to 4000 km in only 10,000 years (Curry and Endo 1991). If Ordovician brachiopods exhibited similar larval development, then propagule pressure would be sufficiently high in these species to produce the observed interbasinal invasions rapidly once the oceanographic patterns shifted in the early Richmondian Age. Furthermore, the geographic ranges of the invader species statistically overlap those of the generalist carryover species (Table 5.3, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html). The Richmondian invaders, therefore, also exhibit the large geographic ranges characteristic of broadly adapted species.

Although the geographic ranges of invader taxa are statistically similar to the carryover taxa at the species level, differences emerge at the genus level (Table 5.3, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html). This pattern is partly attributable to the fact that most invasive genera are monotypic within the Cincinnati region whereas some native genera include multiple species. Since the monophyly of these genera is also questionable, the species-level comparison may be a more robust comparison of carryover versus invasive taxa across the aggregated sequences. However, the sequence level details also suggest a more complex pattern than the species level aggregate analysis. In the C4 sequence, geographic range for invader taxa is significantly smaller (in all variations of analyses) than in the C5 sequence. This apparent shift in range size may be a sampling artifact. There are only three (or five) C4 invaders versus 12 (or 17) C5 invaders, and two of the three species exhibit C4 range sizes close to their C5 range size. Even so, the observed lag in either range establishment or expansion of range size among the invaders potentially indicates that the full biotic impact of the invasion was spread across the C4

and into the C5 sequences, an interval of at least one million years.

Impact of the Richmondian Invaders

The recovered biogeographic patterns suggest that during the early stages of the biotic invasion, in the transition from the C3 to the C4 sequence, narrowly adapted native species did not adjust to the invasive regime and become extinct, while broadly adapted native species persisted and flourished. The native generalists, in fact, appear to be more successful at establishing broad geographic ranges than the newly invading taxa in the first two million years after the initial invasion. Meanwhile, new species that evolved in the Richmondian from Cincinnati natives occupied smaller geographic ranges than either the carryover or invader taxa in both the C4 and C5 sequences (Figure 5, Table 6, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html). The mean range size of the new species overlaps with the range size vacated by the Maysvillian restricted species; this suggests that species evolving after the initial C4 reorganization radiated into open specialist niches. Speciation is very limited in the C4 sequence, which may be due to the introduction of invaders. A pattern of reduced speciation rate associated with intervals of high interbasinal invasion has also been reported for Late Devonian brachiopods (Stigall 2008, 2010).

As noted by Patzkowsky and Holland (2007), the overall effect of the introduction of the invader taxa was to increase local diversity. Studies of modern coastal ecosystems have also documented increases rather than decreases in total diversity following the introduction of invasive species (Reise et al. 2006). Although ecologically specialized Maysvillian species become extinct by the end of the C3 sequence as discussed above, this did not result in an abrupt extinction peak because these extinctions are spread out over two sequences (Table 1, note: all tables and appendices are available on the website palaeo-electronica.org/2010_1/index.html; Holland 1997). In modern marine ecosystems, no compelling evidence exists for species extinction caused by competition with invasive species (Davis 2003). Based on the results of the Cincinnati analysis, it appears that the long-term impacts of species invasions, at least in the case of the Richmondian Invasion, also do not result in extinction from direct competition for resources between native and invasive taxa. In fact, based on biogeographic data, it

appears that the influx of invaders had no impact on reducing the realized niche of native carryover taxa. Instead, invasive species were limited by incumbent taxa to smaller realized niches during the C4 sequence compared with their C5 niches. This suggests that native communities, at least the generalist taxa within these communities, are more resilient to invader domination that suggested by short-term ecological observations.

CONCLUSIONS

By analyzing the geographic ranges of Cincinnati rhynchonelliform brachiopod species in a temporal framework, a clear picture of the biogeographic impact of the Richmondian invaders begins to emerge. Native Cincinnati species with small geographic ranges in the Maysvillian do not cross into the Richmondian, whereas species that occupy large geographic ranges do. In fact, native taxa that carryover into the Richmondian have larger geographic ranges than the invader taxa until the C5 sequence—at least one million years after the invasion. Evidently narrowly adapted, ecological specialists were more significantly impacted by ecosystem change associated with the invasive regime than ecological generalists. Conversely, native generalist taxa continue to occupy large geographic ranges with no discernable contraction of range size following the influx of the invaders. The invader taxa exhibit statistically smaller range sizes than native carryover taxa initially, suggesting that native communities were somewhat resilient to invader domination. Speciation rate is low in the C4 sequence during the establishment of the invasive regime, but increases in the C5 sequence. New species that evolve in the Richmondian from Cincinnati natives occupy smaller geographic ranges than either the carryover or invader taxa in both the C4 and C5 sequences. The range size of these new taxa overlaps with the range size vacated by the ecological specialists of the Maysvillian Stage. In the C6 sequence, the differentiation between invader and native taxa appears to break down.

The long-term effects of invasive species of the Richmondian Invasion can be summarized as follows. Geographically restricted stenotopic species are the most susceptible to extinction during the invasive regime. Inferred competition between invader taxa and native eurytopic taxa does not result in either reduction in geographic range size or realized niches of native taxa. Speciation may be reduced during invader establishment, and new species that evolve following invader establishment are ecological specialists. Results also indi-

cate that overall, the ecological effects of the Richmondian Invasion were long lasting—through both the C4 and C5 sequences. The protracted biogeographic response to invasion agrees with results of biofacies analyses by Holland and Patzkowsky (2007) in general, although this analysis suggests that a stable ecosystem may not have re-established until the C6 sequence.

Invasive species pose a significant problem for modern ecosystems. Invasion biologists have documented clear patterns of increased competition, predation, and ecosystem restructuring in the years and decades following invasion events (Lockwood et al. 2007) but lack the temporal data to determine how these short-term patterns may scale up over long time spans. Analyses, such as this one, can provide insight into the ultimate result of these short term impacts. The biogeographic response of native Cincinnati taxa to the Richmondian invasion indicates that ecological specialists are most vulnerable to extirpation during invasive regimes, but competition between native generalists and invasive species does not result in extinction of either native or invasive species. Rather, total ecosystem diversity is enhanced. Although stenotopic species become extinct at the onset of the ecosystem reorganization, they are later replaced by newly evolved species characterized by similar niche breadth. New speciation, however, appears to be retarded during the initial waves of the invasion. Moreover, the results of this analysis indicate that invasion effects are likely to be long lasting. These results indicate that early intervention of new exotic introductions and protection of native ecological specialists in environments that are already impacted by invasion should be conservation priorities in modern ecosystems.

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