Application of niche modelling to analyse biogeographic patterns in Palaeozoic brachiopods: evaluating niche stability in deep time

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The ecological niche of a species can be estimated from a set of species occurrence points associated with data about the environmental conditions at those locations using a method known as ecological niche modelling (ENM). This technique has been widely employed with modern organisms, and great potential exists for ENM studies in the fossil record. By modelling a species' niche during multiple time slices, the relative degree of niche conservatism or niche evolution a species undergoes during intervals of biotic, environmental, or climatic change can be assessed. In this case study, the relative stability of ecological niches of eight Late Ordovician (Katian) brachiopods from the Cincinnati Arch of eastern North America is assessed across an extra-basinal immigration event, the Richmondian Invasion. This framework provides an opportunity to examine whether species altered the parameters of their ecological niches more in response to species invasions and ecosystem turnover or during gradual environmental changes preceding the invasion event. Niches were modelled for nine time slices spanning the interval before, during, and after the invasion using the Maxent program based on environmental parameters estimated from the sedimentary record including: inferred water depth, lithology, bedding thickness, bedding style and physical sedimentary structures. Niche stability was assessed through pairwise comparisons of the percent contribution of each environmental parameter to species' niche models between adjacent time slices. Bray-Curtis similarity among environmental contributions to species niche models through time varied. Species exhibited low similarity (niche evolution) prior to the onset of the Richmondian Invasion, but high similarity (niche stability) during the invasion interval. Similarity levels (niche stability) relax post-invasion, although similarity values still significantly exceed pre-invasion levels. Cincinnatian brachiopod species which successfully persist through the invasion, therefore, appear to have responded to invasion pressure through niche conservatism.

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THE GEOGRAPHIC area inhabited by a species is constrained by its ecological niche, the multidimensional set of environmental variables that determines where members of a species can survive and maintain viable populations (Grinnell 1917). Individual organisms have the physiological capacity to inhabit any geographic location characterised by physical parameters within the constraints of the species' fundamental niche, although most species actually occupy a smaller, realised niche that is further constrained by biotic interactions such as predation and competition (Hutchinson 1957; Soberón 2007). A species' geographic distribution may be further limited due to stochastic processes, dispersal limitations, or source-sink dynamics which are encapsulated in the "mechanistic" or population growth-based niche concepts (Liebold 1995; Liebold *et al*. 2004; Tomašových & Kidwell 2009). Fundamentally, however, the ecological niche exerts a primary control on species distribution because populations of the species cannot exist outside the bounds of the environmental gradients that condition species presence or absence. This study, therefore, focuses on estimating the physical parameters associated with species' ecological niches and how the definitions of the physical parameters of those niches change over geologic time.

A fundamental question about evolution is whether species adjust to environmental and biotic changes in their ecosystem by maintaining

the parameters of their ecological niche and tracking their preferred environmental conditions laterally (= niche conservatism, habitat tracking) or by adapting to the changing conditions and altering the parameters of their niche (= niche evolution) (e.g., Eldredge 1989; Peterson *et al*. 1999; Wiems & Graham 2005; Brett *et al*. 2007). These two end-member responses are often difficult to tease apart in modern taxa because the temporal duration of data is necessarily restricted to years or a few decades whereas the process of niche evolution occurs over many generations (Wiems & Graham 2005). Analysis of species response to shifting environmental conditions within a tightly constrained temporal framework in the fossil record, however, can provide data to test the relative frequency of niche evolution vs. niche conservatism.

Characterising the relative importance of niche conservatism versus niche evolution in species is important in order to accurately predict the long term impacts of current environmental changes, such as global climate change, habitat degradation and species invasions. Most species in the fossil record are morphologically stable (i.e., lacking discernible, directed morphological change) for hundreds of thousands or millions of years (Eldredge & Gould 1972; Eldredge 1989; Lieberman *et al*. 1995; Jackson & Cheetham 1999; Benton & Pearson 2001; Brett *et al*. 2007; Lieberman *et al*. 2007). Absence of directed morphological change has been linked to variations in the selective regime experienced by local populations individually; because each local population responds to different selective regimes, no net directed evolution occurs across the species as a whole (Lieberman & Dudgeon 1996; Eldredge *et al*. 2005). Hence, niche stability is expected to be common in geologic time. However, the process of speciation and development of new morphological features through adaptation indicates that niche evolution is a fundamentally important component of life's history. Combining punctuated equilibrium (Eldredge & Gould 1972), the turnover pulse hypothesis (Vrba 1992, 1996), and allopatric speciation theory (Mayr 1942) with these observations establishes the null hypothesis that species niches are stable during most types of environmental change, and that niche evolution is largely restricted to intervals of directed evolutionary change associated with either more profound or more rapid intervals of environmental change.

Studies of modern taxa have documented both niche conservatism and niche shifts within the past 100 years (reviewed by Pearman *et al*. 2007). However, no clear pattern has emerged about whether niche stability or niche evolution is more prevalent during intervals of climatic (or other abiotic change) or following species invasions (or other changes in biotic conditions) (Pearman *et al*. 2007). This is partly due to the limited timescales available to modern biologists; it is often difficult to determine whether observed shifts will manifest permanently or if they represent short term deviations within an otherwise steady-state system. Nonetheless, niche stability is often assumed in studies that apply species distribution models to examine biogeographic patterns of species over both ecological and longer time scales, such as between Pleistocene and modern populations (e.g., Fløjgaard *et al*. 2009; Kitchener & Rees 2009; Nogués-Bravo *et al*. 2008).

Ecological Niche Modelling (ENM) methods provide quantitative tools to estimate species' niches and to potentially test the question of niche stability. ENM methods include a series of multivariate techniques to estimate the parameters of the fundamental niche (Grinellian niche *sensu* Soberón 2007; functional niche *sensu* Leibold 1995) of a species by comparing a set of known occurrence points with the environmental conditions at each of those sites. ENM analysis is widely employed by biologists studying modern and Quaternary species (e.g., see reviews by Stockwell 2007; Pearman *et al*. 2007; Fløjaard *et al*. 2009) and has been applied in a limited way with fossils in deep time (e.g., Stigall Rode & Lieberman 2005; Maguire & Stigall 2009; Dudei & Stigall 2010; Walls & Stigall 2011). In recent years, two common uses of ENM are to forecast the geographic distribution of species following global climate change (e.g., Peterson *et al*. 2002; Nunes *et al*. 2007) or predict the potential geographic distribution of invasive species in new geographic regions (e.g., Medley 2010). Both of these applications assume that the parameters that define a species' ecological niche are stable in space and time. However, this assumption is rarely assessed.

Identification of niche shifts requires the comparison of two or more independently constructed niche models for a species. These models can reflect the distribution of a species in two geographic regions (e.g., Ebeling *et al*. 2008; Medley 2010) or during multiple time intervals (e.g., Nogués-Bravo *et al*. 2008; Maguire & Stigall 2009). In this study, ecological niche modelling (ENM) methods are applied to Late Ordovician brachiopods in the Cincinnati Arch of North America during nine time slices to test hypotheses of niche stability in geologic time. By comparing the reconstructed ecological niche for individual species across multiple time slices, it is possible to determine how stable species' niches are

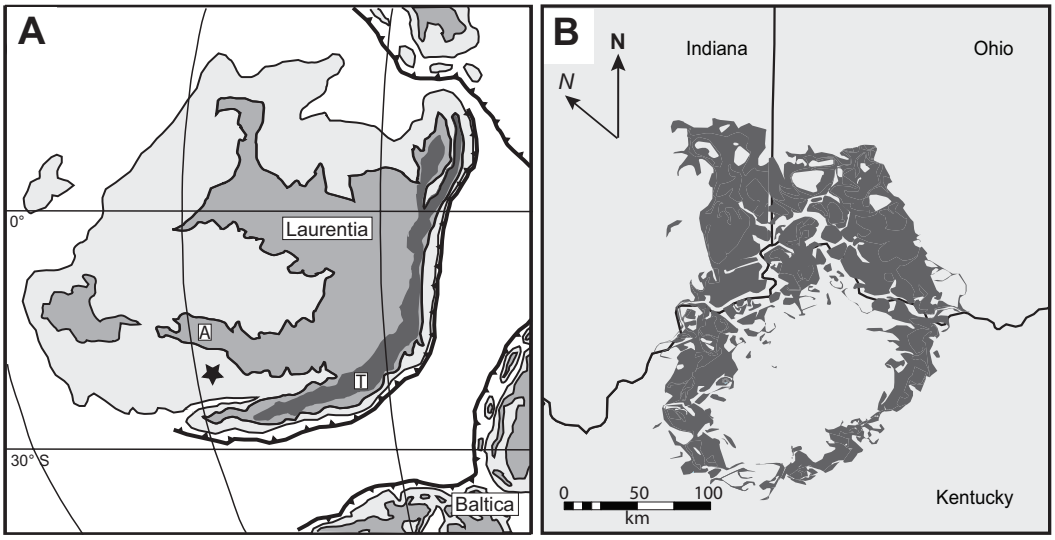

Figure 1. Palaeogeographic position of study area and outcrop belt. **A**, Palaeogeographic position of Laurentia. Cincinnati region indicated with star, Taconic Highlands with T, and Transcontinental arch with A. **B**, Shaded region denotes outcrop belt of the C3, C4, and C5 sequences. Older units outcrop in the core of the arch and younger units outcrop toward the margins. N indicates present north, *N* indicates palaeo-north.

through geologic time. Changes in both physical environmental and biotic conditions occur during this interval due to relative sea level fall and inter-basinal species invasions, respectively, and provide a framework to test hypotheses related to the type of environmental change. Based on the theoretical framework outlined above, the expected results are that species will respond to gradual change through niche conservatism and habitat tracking, whereas rapid changes in the environment will trigger niche evolution. This sets up two testable hypotheses: (1) that species will respond to gradual sea level decline by tracking their habitat laterally (= niche conservatism), and (2) species will respond to the sudden influx of invasive species through niche evolution.

BACKGROUND

For ENM analyses of fossil organisms to be successful, studies should focus on common taxa deposited in sedimentary sequences characterised by a detailed stratigraphic framework that crop out widely within the study region (Stigall 2008). The case study presented herein focuses on the highly fossiliferous Late Ordovician strata of the Cincinnati Arch in eastern North America. These strata crop out extensively and have been densely sampled; both in terms of biotic content and sedimentology over the past 150 years (see review by Meyer & Davis 2009).

Geologic Setting

Strata of the Cincinnati Arch crop out in the present tri-state region of Ohio, Indiana and Kentucky, USA (Fig. 1). During the Late Ordovician, the Cincinnati region was located nearly 20 degrees south of the equator and rotated approximately 45 degrees clockwise from its present orientation. The region was covered by a shallow epicontinental sea which was the distal extension of the foreland basin formed as a result of the Taconic Orogeny on the southern seaboard of Laurentia. The basin assumed a ramp topography which deepened toward the northwest (Holland 1993). Both the Taconic highland and Transcontinental arch were emergent and formed barriers to faunal migration through much of Cincinnatian time. Cincinnatian strata underwent structural deformation associated with later orogenic events to form a structural dome, although this feature is referred to as the Cincinnati Arch (Pope *et al*. 2009). The present outcrop, therefore, forms a concentric pattern where the oldest strata lie medially and youngest strata occur more distally. Deposits in the southern extent of the Arch represent nearshore and peritidal conditions and are generally non-fossiliferous (Holland 1993), so they are not included in this study.

Active basin subsidence and high sedimentation from the nearby Taconic highlands resulted in thick, relatively conformable accumulations. Using sequence stratigraphic methods, Cincinnatian strata have been divided into six depositional sequences (C1 through C6; Holland 1993; Holland & Patzkowsky 1996) (Fig. 2). Each sequence includes thin transgressive systems tract deposits followed by thick highstand systems

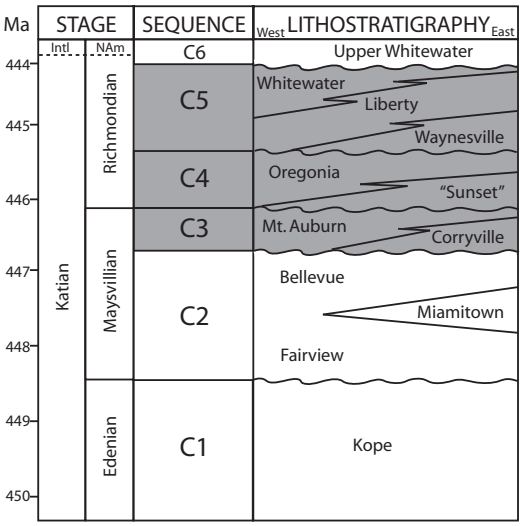

Figure 2. Cincinnatian stratigraphy. Study interval shaded.

tract deposits. Each sequence shallows upward, and the sequences shoal upward overall due to basin infilling. This study focuses on brachiopods from the C3, C4 and C5 depositional sequences. The C3 sequence represents the late Maysvillian Age and includes the Corryville and Mount Auburn Formations which record deep and shallow subtidal environments, respectively. The C4 sequence is the first Richmondian Age sequence and comprises the Oregonia and Sunset Formations which record deep and shallow subtidal environments, respectively. The C5 sequence includes four facies bounded formations, the Waynesville, Liberty, Whitewater and Saluda Formations which represent offshore, deep subtidal, shallow subtidal, and peritidal conditions, respectively. Each of these three sequences has recently been further subdivided into early, middle and late time slices based on parasequence boundaries which represent correlative flooding surfaces (Dudei 2009; Dudei & Stigall 2010, Swisher 2009; Walls 2009; Walls & Stigall 2011). Within each sequence, the early time slice includes the transgressive systems tract and the early highstand deposits, and the middle and late time slices are composed exclusively of highstand deposits.

Cincinnatian strata include alternating layers of clay-rich mudstone (locally referred to as shale) and bioclastic packstone to grainstones. Siliciclastic input is sourced from the weathering Taconic highlands, whereas the bioclastic fragments are locally derived. The relative percentages of these two lithotypes vary with water depth: deeper water deposits are characterised by high percentages of mudstone whereas shallow water deposits are dominated by limestone layers (Tobin 1986), Bioclasts are primarily of benthic organisms and are dominated by brachiopods and bryozoa with associated echinoderms, trilobites, gastropods, bivalves, cephalopods and corals (Feldmann 1996; Davis 1998). Classically, the fossiliferous limestone deposits are considered to be storm beds or tempestites, resulting from hurricane activity (Jennette & Pryor 1993; Drummond & Sheets 2001). In this scenario, increased wave activity during storm events would impact seafloor sediments, winnowing away the mud in these layers, while leaving an amalgamated layer of skeletal debris behind. Quiet sedimentation would resume once periods of increased hurricane activity ceased and result in mudstone deposition (Holland 1997; Holland & Patzkowsky 2007). An alternate interpretation of Cincinnatian deposition was recently proposed by Dattilo *et al*. (2008). They interpret the shell beds as the product of normal, episodic sediment starvation between intervals of relatively high sediment input and energy which resulted in thick siliciclastic mud deposits. In either case, the limestone layers clearly represent amalgamations of skeletal debris that record time-averaged accumulations of taxa present between subsequent storm events. Even though storm processes affect primary lithologic textures, lateral transport of skeletal debris was limited to a few metres or tens of metres as shown by the ability to resolve detailed palaeoecological changes within limestone units at the outcrop scale (Frey 1987; Barbour 2001).

Richmondian Invasion

The early Richmondian C4 sequence records an influx of extra-basinal taxa into the Cincinnati region, known as the Richmondian Invasion, which resulted in a fundamental shift of community structure (Foerste 1912; Patzkowsky & Holland 1996). Detailed gradient ecology and biofacies analyses by Holland & Patzkowsky (2007) indicated that the C1 to C3 communities exhibited high levels of similarity in community structure with segregation of communities based on water depth and substrate conditions. The C4 sequence preserves a fundamental restructuring of biofacies in which the onshore-offshore gradient breaks down and faunal differentiation diminishes. Well defined biofacies are re-established only during the C5 sequence, although C5 biofacies differ significantly from those of the Maysvillian due to the ecological dominance of many invader taxa. The shift in biofacies pattern was controlled primarily by the loss of ecological specialists coincident with the early waves of invasion and the subsequent geographic expansion of eurytopic species through the outcrop belt (Stigall 2010).

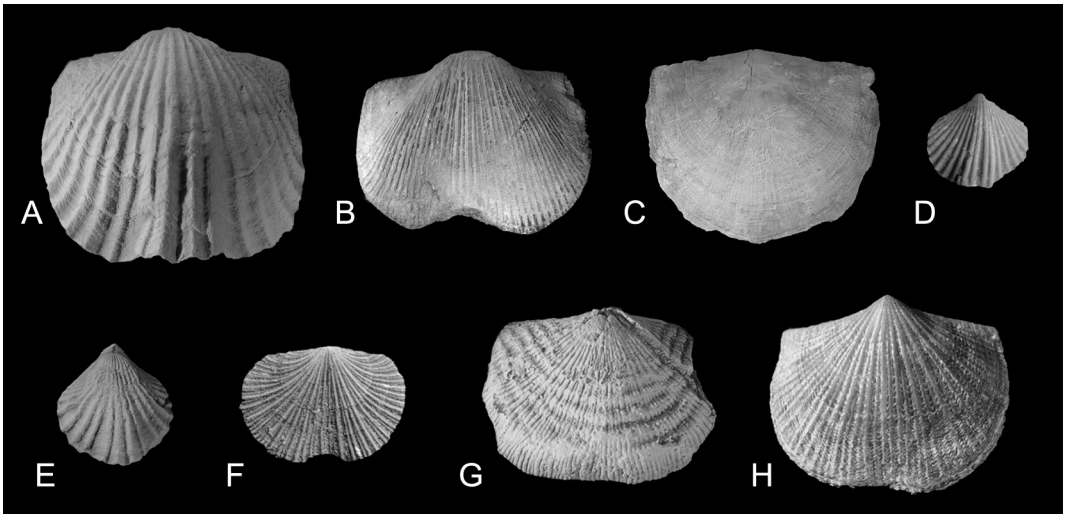

Figure 3. Taxa included in analysis. **A**, *Vinlandostrophia ponderosa*, 0.75x. **B**, *Hebertella occidentalis*, 1.0x. **C**, *Rafinesquina alternata*, 1.0x. **D**, *Zygospira modesta*, 3.0x. **E**, *Rhynchotrema dentatum*, 1.25x. **F**, "*Dalmanella*" *meeki*, 2.0x. **G**, *Leptaena richmondensis*, 1.75x. **H**, *Glyptorthis insculpta*, 1.25x.

The set of ecological changes present during the Richmondian Invasion mirrors those experienced during modern invasive regimes (Lockwood *et al*. 2007). The Richmondian Invasion, therefore, serves as a useful palaeontological analogue for the potential long term impacts of modern invasive species (Stigall 2010).

The Richmondian Invasion was a cross faunal 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 ultimate source of the immigrant taxa is presently unclear. Holland & Patzkowsky (1996, 2007, 2009) argued for a unidirectional migration from the palaeoequatorial region of western United States and Canada. Holland & Patzkowsky (2009) cite the presence of invader genera *Grewingkia*, *Streptelesma* and *Rhynchotrema* in the Steamboat Point Member of the Bighorn Dolomite of Wyoming, which is correlative with the C2 sequence, as support for this interpretation. A palaeoequatorial source for the invaders has been questioned, however, by Jin (2001, pers. comm. 2009) and Copper (pers. comm. 2009) who note that invader taxa more closely resemble the morphotypes present in marginal basins along Laurentia than the large and heavily calcified equatorial fauna. Resolving the ultimate source of the invaders will likely require phylogenetic and evolutionary analyses of brachiopod lineages, which are currently lacking. Regardless of the geographic source of the invader taxa, their introduction to the Cincinnatian ecosystem resulted in significant shifts in community structure and biogeographic patterns (Stigall 2010). This study investigates whether these shifts occur with or without concomitant changes in species niche parameters.

METHODS

Experimental Design

To assess niche stability across the invasion interval, the C3, C4 and C5 sequences were each divided into three time slices, for a total of nine study intervals, each approximately 250,000 to 350,000 years in duration. The effects of time averaging within each time slice, result in data that permit estimation of species ecological niches that incorporate fluctuating conditions during the interval, rather than a snapshot of the niche at an instant in ecological time. The effects of time averaging, however, are actually beneficial within the project design. Firstly, storm winnowed deposits concentrate rare species, thereby providing a better census for species occurrence data (Finnegan & Droser 2008). Furthermore, time averaged deposits have reduced noise introduced by low frequency variations, such as seasonality, and effectively capture processes operating at the metacommunity scale (Tomašových & Kidwell 2010) while preserving environmental gradients within the data (Frey 1987; Tomašových & Kidwell 2010).

To test the hypothesis that native species alter their niche parameters during an inter-basinal species invasion, five native species present in the C3 sequence that persisted into the C4 sequence were selected as the core taxa for analysis (Fig. 3). Of these, *Dalmanella meeki* (Miller, 1875), *Hebertella occidentalis* (Hall,

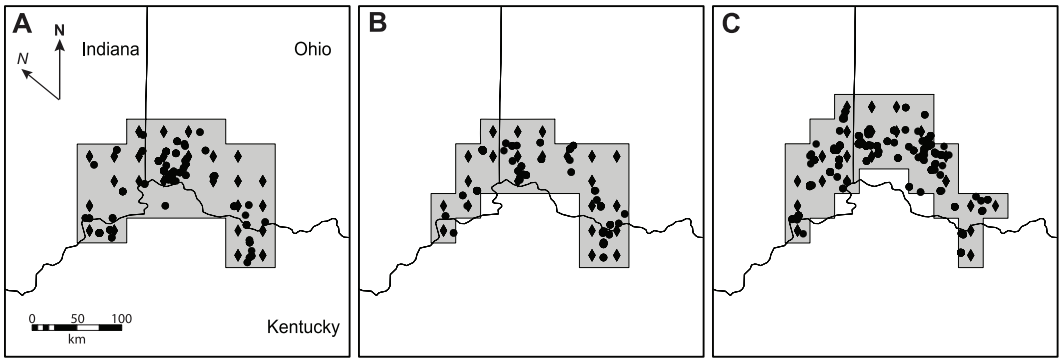

Figure 4. Data distribution for the (**A**) C3, (**B**) C4, and (**C**) C5 sequences. Region modelled is shaded. Circles denote locations of species occurrence data, diamonds denote locations of environmental data. N indicates present north, *N* indicates palaeo-north.

		Pre-invasion			Invasion Interval			Post-invasion		
		C3-1	C3-2	C3-3	C4-1	C4-2	C4-3	C5-1	C5-2	C5-3
Native	*Dalmanella meeki*	x	x	x	x	x	x	x	x	
	Hebertella occidentalis	x		x	x	x	x	x	x	x
	Rafinesquina alternata	x	x	x	x	x	x	x	x	x
	Vinlandostrophia ponderosa	x	x	x	x	x	x			
	Zygospira modesta	x		x			x	x	x	x
Invader	*Rhynchotrema dentatum*				x	x			x	x
	Glyptorthis insculpta							x	x	x
	Leptaena richmondensis							x	x	x

Table 1. Species modelled per time slice.

Percent mudstone
Average value of mudstone percentage per time slice
Inferred water depth
1. Deep subtidal: below fair weather wave base
2. Shallow subtidal: above fair weather wave base
Limestone thickness
Average thickness of limestone layers per time slice; in cm
Limestone bedding style
Characteristic limestone bedding averaged through time slice
1. Planar
2. Wavy
3. Rubbly/Nodular
Biofacies
1. Dominated by offshore or muddy substrate taxa
2. Mixed community characteristics
3. Dominated by nearshore/shoreface or sandy substrate taxa

Table 2. Environmental parameter coding strategy for construction of environmental base maps.

1847), *Rafinesquina alternata* (Conrad, 1838) and *Zygospira modesta* (Say in Hall, 1847) survive to the end of the C6 sequence, whereas *Vinlandostrophia ponderosa* (Foerste, 1909) becomes extinct at the end of the C4 sequence. Three invasive species, *Rhynchotrema dentatum* (Hall, 1847), *Glyptorthis insculpta* (Hall, 1847) and *Leptaena richmondensis* Foerste, 1909 were also included for comparison (Fig. 3). Each of these species is characterised by robustly calcified shells which are preserved as recrystallised calcite; basic uniformity of preservation can be assumed for these taxa in this suite of depositional environments. Species niches were modelled for each interval in which the species was extant and for which five or more spatially discrete occurrence points were available (Tables 1, 3). Relative niche stability was determined by statistically comparing the parameters of the species' niche between adjacent time slices.

Data Collection

Two independent data sets are required for ENM analysis: species occurrences recorded as discrete geographic coordinates and environmental parameters recorded as continuous surface layers (Stockwell 2007). The data set for this analysis was constructed by combining and synthesising three ENM data sets originally developed for the C3, C4 and C5 sequences separately by Dudei (2009) [later published in part as Dudei & Stigall (2010)], Swisher (2009) and Walls (2009) [later published in part as Walls & Stigall (2011)] (Fig. 4). For each sequence, the study area was divided into 15 minute grid boxes and the modelling region was cropped to an irregular polygon that included the region of data coverage while minimising area without data in order to generate the most statistically robust niche models (Fig. 4). The modelled extent varies by sequence due to shifts in outcrop location by sequence related to the arch structure.

Species occurrence data. In palaeontological ENM applications, species occurrence data

Timeslice	# sp occ points	biofacies	bedding style	limestone thickness	mud percent	water depth
Dalmanella meeki						
C3-1	9	0	68.9739	17.2157	13.8103	0
C3-2	9	2.4711	0	0	97.5289	0
C3-3	6	90.1578	0	9.8422	0	0
C4-1	6	0	3.8086	0	0	96.1914
C4-2	7	0	0	0	0	100
C4-3	5	48.7574	0	0.1126	51.1301	0
C5-1	38	22.9047	7.8137	43.6828	25.5988	0
C5-2	38	8.8446	21.9837	0	64.3587	4.8129
Hebertella occidentalis						
C3-1	12	38.4606	0	0.0075	61.5319	0
C3-2	10	0	0	0	0	0
C3-3	14	0	21.357	0.5351	0	78.108
C4-1	6	98.8502	0	0	1.1498	0
C4-2	10	0	0	10.1255	0	89.8745
C4-3	7	0	0	0	0	100
C5-1	20	4.8959	0.6256	56.9848	35.5713	1.9223
C5-2	38	7.1114	14.2371	5.7055	61.1509	11.795
C5-3	37	7.2439	15.7146	49.1423	3.4953	24.4039
Rafinesquina alternata						
C3-1	29	28.3133	43.5024	14.6571	0	13.5272
C3-2	33	19.8917	0.6845	9.8458	2.364	67.214
C3-3	31	53.663	13.4092	6.6726	24.1058	2.1495
C4-1	10	0	0	0	100	0
C4-2	20	5.8735	0.6711	2.8903	79.9525	10.6126
C4-3	18	18.158	0	62.554	19.288	0
C5-1	23	29.8866	3.471	59.2114	3.8316	3.5994
C5-2	34	6.3334	47.7885	8.3317	34.3645	3.1819
C5-3	22	8.728	6.7099	46.7121	2.0598	35.7903
Vinlandostrophia ponderosa						
C3-1	13	6.1186	0	0	93.2916	0.5899
C3-2	40	52.945	0.4192	0.1854	4.8713	41.5792
C3-3	39	13.0773	16.4621	31.2717	35.3014	3.8875
C4-1	13	1.8418	0	2.0442	96.1141	0
C4-2	10	0	61.2966	31.9805	0	6.7228
C4-3	9	0	0	18.6085	0	81.3915
Zygospira modesta						
C3-1	10	100	0	0	0	0
C3-2	11	0	0	0	0	0
C3-3	14	27.1528	72.4184	0.4288	0	0
C4-1	8	0	0	0	0	0
C4-2	11	0	0	0	0	0
C4-3	11	87.8981	0	0	12.1019	0
C5-1	22	17.6241	0.5893	58.2978	23.4886	0.0001
C5-2	22	9.493	43.332	2.8197	43.8843	0.4709
C5-3	14	0	0	53.5027	0	46.4973
Rhynchotrema dentatum						
C4-1	5	35.0237	0	34.1674	22.6424	8.1665
C4-2	6	0	95.5743	0	4.4257	0
C4-3	0					
C5-1	7	0	0	0	0	0
C5-2	9	100	0	0	0	0
C5-3	16	100	0	0	0	0
Glyptorthis insculpta						
C5-1	24	36.1734	35.6249	21.6274	0.0943	6.48
C5-2	33	0.4126	48.6274	5.6507	21.9341	23.3752
C5-3	15	0	4.1025	14.9189	55.2897	25.6889
Leptaena richmondensis						
C5-1	14	100	0	0	0	0
C5-2	18	70.6849	29.3151	0	0	0
C5-3	9	0	0	0	0	100

Table 3. Maxent model results. The percentage contribution of each environmental parameter to the final model is indicated. Model results in grey are not statistically different from random and were excluded from further analysis.

records geographic and stratigraphic positions from where fossils of a particular species were collected (Stigall Rode & Lieberman 2005). These data must be accurate at a spatial resolution of several kilometres and a stratigraphic resolution to time slice in order to be included within the data set. For this study, species occurrence data were collated from Dudei (2009), Swisher (2009) and Walls (2009) for the C4, C5 and C3 sequences, respectively. The data in each of these sources were assembled from museum collections (Cincinnati Museum Center, Miami University Limper Museum and the Ohio State University Orton Geological Museum), targeted field work, and data from Holland & Patzkowsky (2007) downloaded from the Paleobiology Database (paleodb.org). At each museum, specimens were inspected in order to verify (or correct) species identifications. All occurrences of species with detailed locality information were included within the dataset; 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. The final species occurrence database includes 954 unique species occurrence data points (Fig. 4, Appendix 1).

Environmental data. For ENM analyses of fossil taxa, environmental parameters must be estimated from the sedimentological characteristics of the strata in which fossils occur (Stigall 2008). The set of potential environmental variables to include, therefore, is limited to characteristics of the depositional environment which are preserved in the rock record. Potentially useful parameters such as annual variations in water temperature and salinity, consequently, cannot be applied in palaeontological ENM models. Because brachiopods are benthic organisms, many aspects of the substrate that do control species distribution can be evaluated from proxy information preserved in the rock record, such as substrate type, frequency of wave energy and relative water depth (Rudwick 1970).

For this analysis, species ranges are modelled based on five environmental parameters: percent mudstone (a proxy for substrate type), inferred water depth, limestone thickness (a proxy for storm frequency; higher storm frequency results in thicker, amalgamated beds rather than thin individual storm beds), limestone bedding style (a proxy for amount of wave energy impacting the seafloor), and biofacies (a proxy for biotic interactions). Environmental parameters were evaluated for each outcrop included by Dudei (2009), Swisher (2009) and Walls (2009) according to the coding scheme in Table 2. For outcrops that contain multiple time slices, environmental parameters were coded separately for each time slice. When multiple stratigraphic sections occurred within a single 15 minute grid

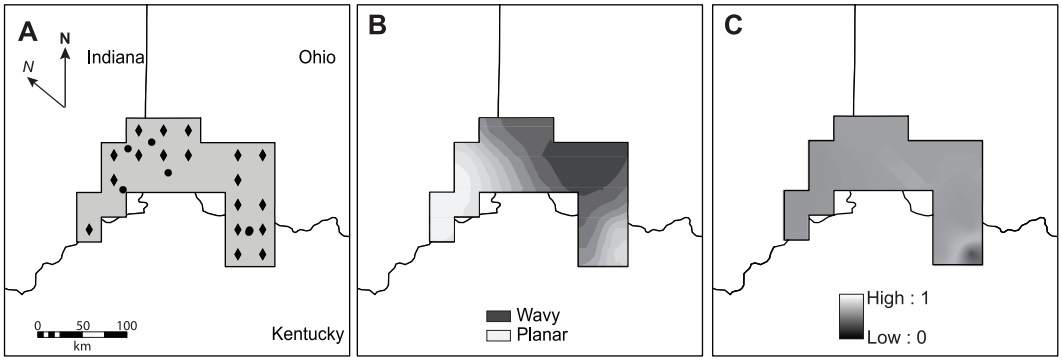

Figure 5. Steps in environmental niche model creation for "*Dalmanella*" *meeki* in the first time slice of the C4 sequence. **A**, Distribution of occurrence (circle) and environmental (diamond) data. N indicates present north, *N* indicates palaeo-north. **B**, Interpolated surface of limestone bedding style parameter. **C**, Predicted geographic distribution shaded based on inferred habitat suitability across the study region.

box, the parameter value for the grid box was determined by averaging the coding for each section following the protocol of Stigall Rode & Lieberman (2005). Coded environmental parameter values are presented in Appendix 2.

For analysis, environmental data must be presented as a continuous surface layer (Phillips *et al*. 2006) (e.g., Fig. 5). Interpolated environmental layer maps were created in ArcGIS 9.2 (ESRI 2006) using the Geostatistical Wizard tool. Ordinary kriging method was employed for layer creation because it generated the most significant interpolation surfaces. Output maps were exported as ASCII files to be compatible with the Maxent interface.

Environmental Niche Model Development

Species niches were modelled using the Maxent modelling program (Phillips *et al*. 2004, 2006; http://www.cs.princeton.edu/~schapire/maxent/). The Maxent program estimates a species niche by determining the probability distribution of maximum entropy (i.e., that is most spread out, or closest to uniform) based on the incomplete information about the species distribution obtained from the set of known occurrence points (Phillips *et al*. 2006). This approach has several strengths over competing ENM programs. First, it operates with presence data only, which is critical in palaeontological investigations as absences may reflect under-sampling or lack of outcrop availability rather than true absence. Also, the niche limits are determined through a generative process, in which an original model is generated then modified in multiple analytical generations to improve model fit to the data (Pearson *et al*. 2007). This results in high model accuracy at low species occurrence sample sizes (Pearson *et al*. 2007). Furthermore, the model outputs are amenable to statistical analyses. Finally, side-by-side comparisons of model accuracy between multiple ENM programs have repeatedly demonstrated that the accuracy of Maxent models exceeds almost all other ENM programs currently in use (e.g., Elith *et al*. 2006; Giovanelli *et al*. 2010). Of particular interest are comparisons that indicate Maxent models exhibit higher predictive accuracy than those of Desktop GARP (Genetic Algorithm for Rule-set Prediction) (Stockwell & Peters 1999; http://www.nhm.ku.edu/desktopgarp/) (e.g., Elith *et al*. 2006; Phillips *et al*. 2006; Peterson *et al*. 2007; Phillips 2008). All previous ENM studies in the fossil record have used Desktop GARP (i.e., Stigall Rode & Lieberman 2005; Maguire & Stigall 2009; Dudei 2009; Swisher 2009; Walls 2009; Dudei & Stigall 2010; Stigall 2011; Walls & Stigall 2011), and secondary field validation has shown high accuracy of GARP models in Cincinnatian brachiopods (Walls 2009). The application of the Maxent modelling program to this data is, therefore, expected to produce even more accurate results for fossil brachiopods than the previous related analyses of Dudei (2009), Swisher (2009), Walls (2009), Dudei & Stigall (2010) and Walls & Stigall (in press).

In this analysis, species' niches were modelled using Maxent version 3.1.1. Each model was created using the default parameters with a L-1 regularisation of 1, test data set to 25% and pixel size increased by 1. Model output is produced as a cumulative prediction map as illustrated in Figures 5 and 6. One of the most powerful attributes of the Maxent modelling system is the amount of output data provided to the user. The geographic range projection map indicates the location of the point data used for training and testing the model, so it is possible to visually inspect the model fit (Fig. 6). The area under the curve (AUC) value for the receiver operator

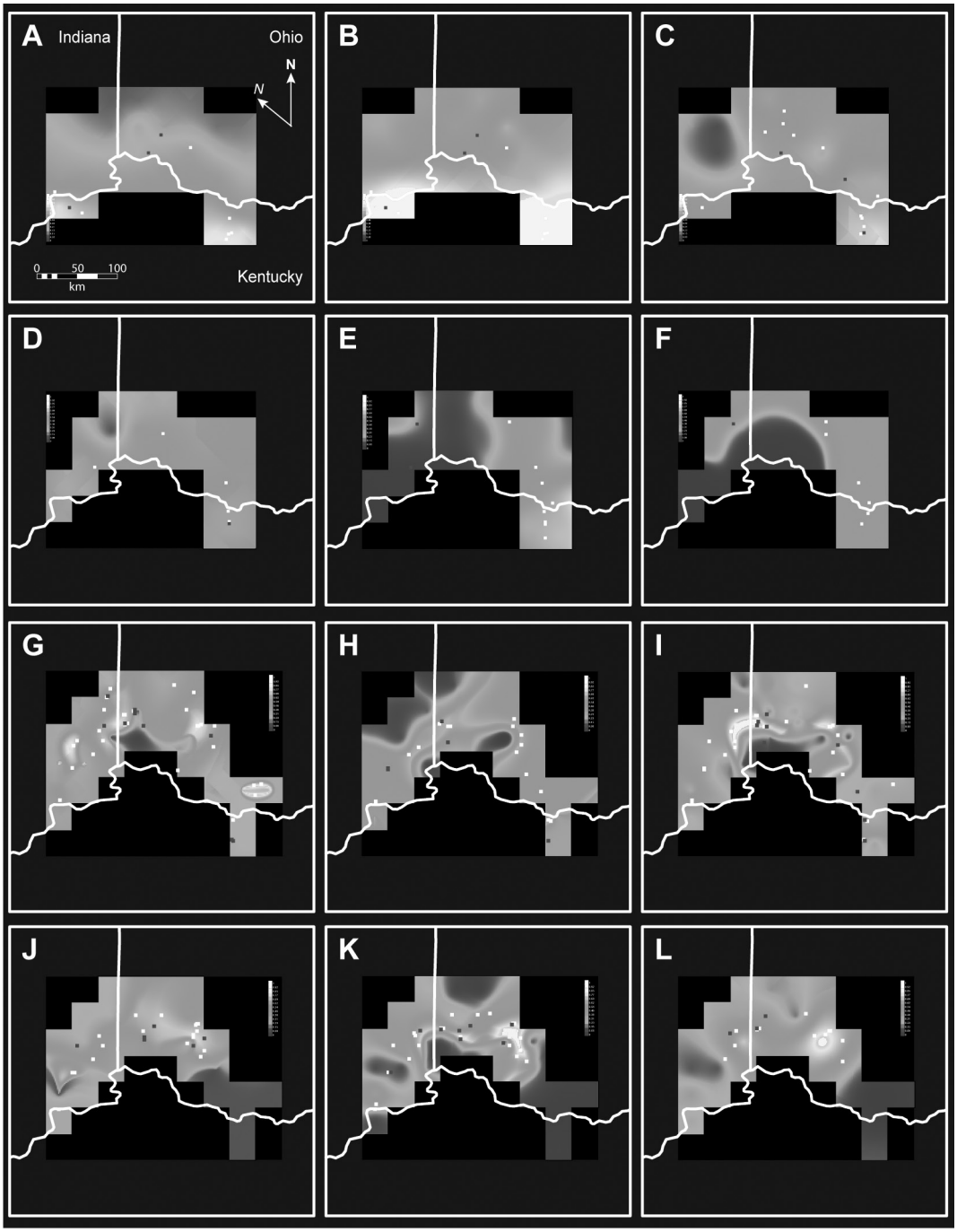

Figure 6. Example projected geographic distribution maps. Greyscale indicates cumulative probability of habitat suitability from dark = 0 (unsuitable) to white = 1 (completely suitable). N indicates present north, *N* indicates palaeo-north. White squares indicate sites used for training data and dark squares indicate the test data locations. **A-I**. Illustrate the predicted geographic range of *Hebertella occidentalis* in the C3-1, C3-2, C3-3, C4-1, C4-2, C4-3, C5-1, C5-2, and C5-3 time slices, respectively. **J-L**. Illustrate the predicted geographic range of *Glyptorthis insculpta* in the C5-1, C5-2, and C5-3 time slices, respectively.

		Pre-invasion			Invasion Interval			Post-invasion	
		C3-1 & C3-2	C3-2 & C3-3	C3-3 & C4-1	C4-1 & C4-2	C4-2 & C4-3	C4-3 & C5-1	C5-1 & C5-2	C5-2 & C5-3
Native	*Dalmanella meeki*	0.138	0.025	0	0.962	0	0.486	0.423	
	Hebertella occidentalis			0	0	0.899	0.019	0.487	0.423
	Rafinesquina alternata	0.439	0.318	0.241	0.8	0.281	0.812	0.252	0.266
	Vinlandostrophia ponderosa	0.116	0.224	0.392	0.02	0.253			
	Zygospira modesta						0.297	0.364	0.033
Invader	*Glyptorthis insculpta*							0.483	0.551
	Leptaena richmondensis							0.707	0
	Rhynchotrema dentatum				0.044				1.000

Table 4. Calculated Bray-Curtis similarity values for niche models of adjacent time slices based on the percent contribution of each environmental parameter to the final model.

characteristic (ROC) curve, a graphical plot of the sensitivity, or true positive rate versus false positive rate, is also provided. The AUC is a goodness of fit measure, ranging from 0.5 (random accuracy) to 1.0 (perfect discrimination); values greater than 0.7 indicate strong signal in the data (Hanley & McNeil 1982; Elith *et al*. 2006). The contribution of each environmental variable to the final niche model is provided in three forms: a table indicating the percent contribution of each variable in the final model, a graph indicating the directionality of variable contribution, and graphic results following a jackknife procedure to identify how each variable performs in isolation which allows the impact of correlated variables to be clearly ascertained (Phillips *et al*. 2006).

Analysis

To determine the relative stability of a species' niche from one time slice to the next, the percent contribution of each environmental variable to the niche model of that species was compared between adjacent time slices using the Bray-Curtis similarity index (Bray & Curtis 1957). This index is frequently used for ecological analyses of abundance data, which is analogous to the percent of the whole model contributed by a single variable, and its output has been shown to reflect true similarity (Bloom 1981). Possible calculated similarity values range from 0 indicating complete dissimilarity to 1.0 indicating complete overlap of parameters. The statistical significance of apparent similarity patterns was assessed using analysis of variance (ANOVA) and Student's T-tests. All analyses were conducted with Minitab 15 (Minitab Inc. 2007). Data were tested for statistical normality prior to conducting parametric statistics.

The comparison metric used in this analysis directly compares the relative amount of the ecological niche model explained by each environmental variable. The Bray-Curtis similarity values, therefore, provide a general assessment of one aspect of niche stability—the degree of stability within each of the modelled parameters. Certainly this only examines one aspect of the niche. Stability or shifts in other niche parameters that are not amenable to palaeontological modelling, such as nutrient load and temperature, are not detectable with this metric. Similarly, changes in species preference in directionality of an environmental parameter or other niche processes, such as changes in source-sink dynamics are not tractable with this method. Nonetheless, comparison of the percent contribution of each variable to the modelled niche provides a baseline for comparison. Although this metric may underestimate the total amount of niche evolution due to inability to resolve all parameters of the niche completely, any significant changes in the modelled environmental parameters clearly indicate the occurrence of niche evolution.

RESULTS

A total of 52 species niche models were constructed (Table 3). Based on AUC values, five of these were statistically equivalent to a random result (AUC=0.5), so they were removed from the analysis. The average AUC value for the remaining 47 niche models is 0.74, indicating strong signal in the data. The percent contribution of the environmental variables to each model is presented in Table 3, and example geographic range predictions are presented in Figures 5 and 6.

Similarity calculations

Thirty-five pairwise comparisons could be conducted between niche models developed from adjacent time slices (Table 4). Simple inspection of the Bray-Curtis results indicates that niche stability was low during the pre-invasion interval (average value of 0.20) and relatively high during the invasion and post-invasion intervals (average values of 0.40 and 0.42, respectively). In addition, each of the three native species that persist into the post invasion exhibit at least one episode of very high niche stability (similarity > 0.8) during the invasion interval. An episode of very high niche stability (0.55 to 1.0) also occurs in the successful invader taxa. Interestingly, *Vinlandostrophia ponderosa*, a common native species during the

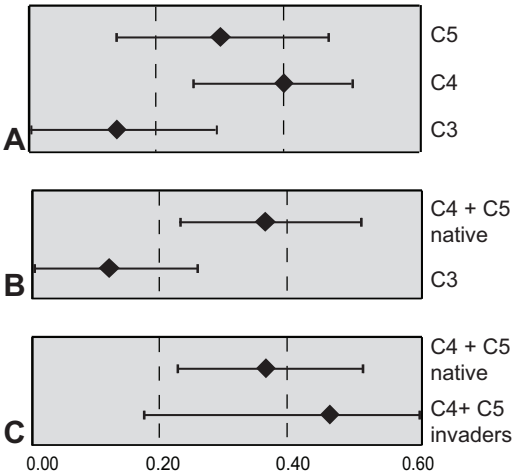

Figure 7. Comparison of the mean similarity values with 95% confidence intervals (based on pooled standard deviation) by species group. **A**, Comparison of similarity levels by sequence for native species. **B**, Comparison between similarity levels of native species in the pre-invasion Maysvillian interval (C3 sequence) versus the post-invasion Richmondian interval (C4 and C5 sequences). **C**, Comparison of native versus invader species during the post-invasion Richmondian interval (C4 and C5 sequences).

C2 and C3 sequences does not undergo an interval of high niche stability during the invasion interval and also does not survive into the post-invasion interval.

Statistical analyses

To determine whether statistical differences occurred in the similarity of species niches between time slices before, during, or after the Richmondian Invasion or between native and invasive species, a series of statistical tests were conducted. Specific comparisons analysed were (1) whether niche stability of native species is constant between the pre-invasion (C3 sequence), invasion (C4 sequence) and post-invasion intervals (C5 sequence), (2) whether niche stability of native species is constant before (C3 sequence) and after (C4 and C5 sequences combined) the Richmondian Invasion, (3) whether native and invasive species exhibited the same level of niche stability during the Richmondian Stage (C4 and C5 sequences combined).

Analysis of variance (ANOVA) confirms that the mean similarity values vary among sequences for the native species, although statistical support is only significant at the $p = 0.07$ level due to the high degree of overlap in the values between the C4 and C5 sequences (Fig. 7A). For native species, similarity values for the C4 and C5 sequences are statistically indistinguishable (T-test, $p = 0.92$). A T-test confirms that the degree of niche conservatism in native species during the pre-invasion interval (C3 sequence) is less than the degree of niche conservatism after the onset of the invasion (combined C4 and C5 sequences) at high levels of significance (one-tailed T-test, $p = 0.03$) (Fig. 7B). The pre-invasion level of niche similarity is lower than post-invasion (C4+C5 sequences) even when both native and invasive Richmondian taxa are compared with the C3 species (one-tailed T-test, $p = 0.05$) (Fig. 7B). It is also noteworthy that the degree of niche similarity during the post-invasion interval is not statistically different between native and invader taxa (T-test, $p=0.61$) (Fig. 7C).

DISCUSSION

Cincinnatian brachiopods do not exhibit the predicted niche conservatism across the nine temporal intervals. Instead the relative level of niche stability varies greatly during the study interval. Cincinnatian species exhibit a high degree of niche evolution between time slices prior to the onset of the Richmondian Invasion. However, once the invasion begins, species niches become more stable and the similarity in niche parameters between time slices increases significantly. Specifically, the highest level of niche stability occurs during the invasion itself, followed by a relaxation of niche stability, although species in the post-invasion interval still exhibit stability levels that significantly exceed those of the pre-invasion interval.

The pattern of niche stability observed in this set of Cincinnatian brachiopods contradicts the initial hypothesis that species should conserve the parameters of their niches during intervals of slow, gradual change but modify them during intervals of rapid environmental change. Instead, these taxa exhibit relatively low levels of niche stability during the C3 sequence, during which the primary environmental changes resulted from a gradual shallowing of the basin over approximately 500,000 years. Conversely, species exhibit significantly higher mean niche stability levels—including at least one time slice marked by an extremely high degree of niche conservatism—during the invasion interval (C4 sequence), which is marked by sudden biotic change. Species continue to exhibit high degrees of niche conservatism during the post-invasion interval (early C5 sequence) when the community structure is still in flux. This combination indicates that, at least for the taxa studied here, niche evolution occurred during intervals of relatively low selection pressure and gradual environmental change whereas niche conservatism occurred during intervals marked

by significant selection pressure during the rapid influx of extra-basinal invaders.

As noted earlier, the analytical technique employed here only examines stability within one aspect of a species niche: the relative importance of the five modelled environmental parameters through time. Analysis of other aspects of niche space may provide partly divergent results. Furthermore, it is possible that the ecological niche or mechanistic niches of the included species were not shifting through time, but simply that the expression that can be observed in this analysis records a biased aspect of the true niche. The statistical robustness of the recovered patterns, however, supports the significance of the Bray-Curtis results as a general test of niche stability in these taxa, even if the details of the analysis may be more sensitive to niche evolution than stability.

Each of the temporal intervals preserves the same basic suite of facies and environmental conditions, although the distribution and relative abundance of these vary by interval. Because each sequence records highstand deposition, the lowermost interval of each sequence includes a larger geographic extent of deeper palaeoenvironments, and the uppermost interval records mainly shallow water conditions. Comparison of predicted distribution maps with the interpolated environmental layers indicates that niche shifts do not simply represent species utilising environments that were previously not available within the study region. Instead, species appear to partly track their original environmental conditions while partly exploiting other conditions that were an extension of their previous niche. No substantial shifts in facies preferences were observed in species, even during the C3 sequence interval of high niche evolution.

Cincinnatian brachiopod species apparently responded to the invasive regime by becoming restricted to tightly constrained niches during the initial waves of invasion in the C4 sequence. Notably, the interval of highest niche similarity is not coincident among the species examined in this study (Table 4). Each of the three native species characterised by at least one interval of extreme niche conservatism, *Dalmanella meeki*, *Hebertella occidentalis* and *Rafinesquina alternata*, exhibit this property between different time slices, C4-1 vs. C4-2, C4-2 vs. C4-3 and C4-3 vs. C5-1, respectively. This offset further supports the interpretation that niche conservatism in these species is a response to the shifting biotic conditions. An abiotic trigger, such as a change in oceanographic conditions within the basin, should have affected the three taxa simultaneously. On the other hand, a biotic trigger, such as sudden competition with a specific invader species, would be expected to affect each species individually as potential competitors migrated into the Cincinnati region in waves (Holland 1997).

In addition, relative niche stability during the post-invasion interval is not statistically different between native and invader taxa (Fig. 7). Both groups, therefore, were likely responding to the same set of pressures. That pressure is unlikely to be related to abiotic factors, such as relative sea level fall, because the same relative sea level fall is observed in all three depositional sequences but niche conservatism does not occur during the C3 sequence. Hence, it is reasonable to suppose that the increased species richness on the Cincinnatian seafloor following the Richmondian Invasion (Patzkowsky & Holland 2007), which resulted in resource limitations (Stigall 2010), compelled species to become more ecologically specialised and channelised into narrowly defined ecological niches. Thus, niche partitioning due to increased local competition may have promoted niche stability during the Richmondian Invasion.

CONCLUSIONS

Based on these results, it appears that assumptions of niche stability required in some types of commonly employed ENM analyses may not be valid for intervals of environmental change. For Cincinnatian brachiopods, the minor environmental change of relative sea level fall during the C3 sequence was associated with dramatic niche evolution. If relatively minor environmental changes result in niche evolution, it is probable that larger scale environmental alterations would as well. Nevertheless, the relationship between niche evolution and abiotic environmental change may be scale dependent. It is possible that species niches could be stable during rapid/dramatic change but unstable over gradual/slower changes. Scale dependency of this type has previously been established for other macroecological patterns such as community organisation (Miller 2002, 2004; Tomašových & Kidwell 2010). Additional analyses, particularly niche stability analyses of species from other geologic intervals or regions could test this hypothesis.

On the other hand, it appears that the assumption of niche stability is less problematic for ENM analyses that attempt to predict the potential limits to geographic expansion of invasive species. At least for these Cincinnatian brachiopods, species responded to the invasive regime by becoming entrenched in tightly constrained niches during the initial invasion waves in the C4 sequence. In fact, *Vinlandostrophia ponderosa*, the only native species in this study that did not follow

that pattern did not persist into the post-invasion interval. Some studies of modern invasive species have recovered similar absence of niche evolution between the native and introduced ranges of invasive species (e.g., Ebeling *et al*. 2008), although others have observed demonstrable niche shifts (e.g., Medley 2010) (see review by Pearman *et al*. 2007). Comparative analysis of niche stability in a larger sampling of species within Cincinnatian and additional strata would help to better resolve the generality of the observed pattern in geologic time.

Examining patterns of niche evolution in articulate brachiopod species across nine time intervals in the Late Ordovician provides a long-term framework in which to assess temporal changes in the biogeographic distribution of species and generates data from which the relative stability of species' ecological niches can be assessed. For Cincinnatian brachiopods, species' niches were only weakly conserved during intervals of gradual abiotic change but were highly conserved during the initial wave of extra-basinal invasion and the subsequent ecosystem reorganisation. For these species, niche evolution resulted from gradual environmental pressure whereas rapid biotic reorganisation caused species niches to become restricted and stabilised. These results add to the growing body of comparative analyses of niche conservatism in modern taxa (reviewed by Pearman *et al*. 2007) and provide a long-term perspective on niche evolution through time.

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APPENDIX 1: Species occurrence data. Data compiled from Dudei (2009), Swisher (2009) and Walls (2009).

Species	Longitude	Latitude
C3 sequence: Time Slice 1		
Dalmanella meeki	-85.152	38.553
Dalmanella meeki	-85.040	39.020
Dalmanella meeki	-84.818	39.096
Dalmanella meeki	-84.601	39.425
Dalmanella meeki	-84.407	39.330
Dalmanella meeki	-84.204	39.435
Dalmanella meeki	-85.100	39.440
Dalmanella meeki	-84.840	39.430
Dalmanella meeki	-84.833	39.892
Dalmanella meeki	-85.376	38.749
Hebertella occidentalis	-84.526	39.128
Hebertella occidentalis	-85.152	38.553
Hebertella occidentalis	-84.818	39.096
Hebertella occidentalis	-83.759	38.505
Hebertella occidentalis	-83.790	38.683
Hebertella occidentalis	-84.122	39.172
Hebertella occidentalis	-84.404	39.297
Hebertella occidentalis	-85.274	38.602
Hebertella occidentalis	-85.417	38.751
Hebertella occidentalis	-83.781	38.304
Hebertella occidentalis	-83.738	38.369
Hebertella occidentalis	-83.760	38.352
Hebertella occidentalis	-85.274	38.601
Rafinesquina alternata	-84.610	38.876
Rafinesquina alternata	-84.527	39.128
Rafinesquina alternata	-84.526	39.128
Rafinesquina alternata	-84.577	39.140
Rafinesquina alternata	-84.402	39.184
Rafinesquina alternata	-84.537	39.194
Rafinesquina alternata	-84.548	39.203
Rafinesquina alternata	-84.463	39.212
Rafinesquina alternata	-84.518	39.216
Rafinesquina alternata	-84.425	39.258
Rafinesquina alternata	-85.274	38.601
Rafinesquina alternata	-85.040	39.020
Rafinesquina alternata	-84.818	39.096
Rafinesquina alternata	-84.581	39.168
Rafinesquina alternata	-84.112	39.178
Rafinesquina alternata	-85.280	38.600
Rafinesquina alternata	-85.417	38.751

Rafinesquina alternata	-83.800	38.780
Rafinesquina alternata	-83.767	38.883
Rafinesquina alternata	-84.410	39.480
Rafinesquina alternata	-84.260	39.620
Rafinesquina alternata	-83.759	38.505
Rafinesquina alternata	-83.790	38.683
Rafinesquina alternata	-84.122	39.172
Rafinesquina alternata	-84.404	39.297
Rafinesquina alternata	-84.678	39.328
Rafinesquina alternata	-84.601	39.425
Rafinesquina alternata	-85.274	38.602
Rafinesquina alternata	-85.376	38.749
Rafinesquina alternata	-83.917	38.872
Rafinesquina alternata	-85.417	38.751
Rafinesquina alternata	-85.100	39.440
Zygospira modesta	-85.152	38.553
Zygospira modesta	-85.040	39.020
Zygospira modesta	-84.581	39.168
Zygospira modesta	-83.790	38.683
Zygospira modesta	-84.122	39.172
Zygospira modesta	-84.404	39.297
Zygospira modesta	-84.678	39.328
Zygospira modesta	-84.601	39.425
Zygospira modesta	-83.781	38.304
Zygospira modesta	-85.100	39.440
C3 sequence: Time Slice 2		
Dalmanella meeki	-85.376	38.749
Dalmanella meeki	-85.040	39.020
Dalmanella meeki	-84.625	39.229
Dalmanella meeki	-84.625	39.229
Dalmanella meeki	-84.407	39.330
Dalmanella meeki	-84.601	39.425
Dalmanella meeki	-84.840	39.430
Dalmanella meeki	-84.204	39.435
Dalmanella meeki	-84.417	39.500
Dalmanella meeki	-84.490	39.528
Hebertella occidentalis	-83.759	38.505
Hebertella occidentalis	-85.274	38.601
Hebertella occidentalis	-85.274	38.602
Hebertella occidentalis	-85.170	38.632
Hebertella occidentalis	-83.790	38.683
Hebertella occidentalis	-83.913	38.870
Hebertella occidentalis	-84.526	39.128
Hebertella occidentalis	-84.122	39.172
Hebertella occidentalis	-84.404	39.297
Hebertella occidentalis	-84.678	39.328
Hebertella occidentalis	-84.502	39.406
Rafinesquina alternata	-83.759	38.505
Rafinesquina alternata	-85.280	38.600
Rafinesquina alternata	-85.274	38.601
Rafinesquina alternata	-85.274	38.602
Rafinesquina alternata	-85.170	38.632
Rafinesquina alternata	-83.790	38.683
Rafinesquina alternata	-85.376	38.749
Rafinesquina alternata	-85.142	38.751
Rafinesquina alternata	-85.142	38.751
Rafinesquina alternata	-83.913	38.870
Rafinesquina alternata	-84.610	38.876
Rafinesquina alternata	-83.767	38.883
Rafinesquina alternata	-85.040	39.020
Rafinesquina alternata	-84.526	39.128
Rafinesquina alternata	-84.527	39.128
Rafinesquina alternata	-84.577	39.140
Rafinesquina alternata	-84.588	39.150
Rafinesquina alternata	-84.122	39.172
Rafinesquina alternata	-84.112	39.178
Rafinesquina alternata	-84.112	39.178
Rafinesquina alternata	-84.402	39.184
Rafinesquina alternata	-84.537	39.194
Rafinesquina alternata	-84.547	39.202
Rafinesquina alternata	-84.548	39.203
Rafinesquina alternata	-84.463	39.212
Rafinesquina alternata	-84.518	39.216
Rafinesquina alternata	-84.625	39.229
Rafinesquina alternata	-84.625	39.229
Rafinesquina alternata	-84.425	39.258
Rafinesquina alternata	-85.330	39.290
Rafinesquina alternata	-84.404	39.297
Rafinesquina alternata	-84.678	39.328
Rafinesquina alternata	-84.390	39.355
Rafinesquina alternata	-84.502	39.406
Rafinesquina alternata	-84.601	39.425
Rafinesquina alternata	-84.410	39.480
Rafinesquina alternata	-84.417	39.500
Rafinesquina alternata	-84.490	39.528
Rafinesquina alternata	-84.490	39.528
Rafinesquina alternata	-84.260	39.620
Zygospira modesta	-85.170	38.632
Zygospira modesta	-83.790	38.683
Zygospira modesta	-83.913	38.870
Zygospira modesta	-84.122	39.172
Zygospira modesta	-84.625	39.229
Zygospira modesta	-84.625	39.229
Zygospira modesta	-84.404	39.297
Zygospira modesta	-84.678	39.328
Zygospira modesta	-84.502	39.406
Zygospira modesta	-84.601	39.425
Zygospira modesta	-84.417	39.500
Zygospira modesta	-84.490	39.528
C3 sequence: Time Slice 3		
Dalmanella meeki	-84.601	39.425
Dalmanella meeki	-84.625	39.229
Dalmanella meeki	-84.407	39.330
Dalmanella meeki	-84.204	39.435
Dalmanella meeki	-85.040	39.020
Dalmanella meeki	-84.833	39.892
Dalmanella meeki	-84.840	39.430
Dalmanella meeki	-84.625	39.229

Hebertella occidentalis	-84.526	39.128	*Zygospira modesta*	-84.502	39.406
Hebertella occidentalis	-83.913	38.870	*Zygospira modesta*	-84.404	39.297
Hebertella occidentalis	-84.122	39.172	*Zygospira modesta*	-84.678	39.328
Hebertella occidentalis	-84.502	39.406	*Zygospira modesta*	-85.376	38.749
Hebertella occidentalis	-84.404	39.297	*Zygospira modesta*	-84.625	39.229
Hebertella occidentalis	-84.678	39.328	*Zygospira modesta*	-84.600	39.283
Hebertella occidentalis	-83.759	38.505	*Zygospira modesta*	-84.625	39.229
Hebertella occidentalis	-83.738	38.422	*Zygospira modesta*	-84.525	39.225
Hebertella occidentalis	-85.274	38.602	*Zygospira modesta*	-84.502	39.127
Hebertella occidentalis	-83.738	38.369	*Zygospira modesta*	-83.738	38.369
Hebertella occidentalis	-84.490	39.528	*Zygospira modesta*	-84.490	39.528
Hebertella occidentalis	-83.760	38.352	*Zygospira modesta*	-85.170	38.632
Hebertella occidentalis	-83.760	38.529	**C4 sequence: Time Slice 1**		
Hebertella occidentalis	-83.601	38.712	*Dalmanella meeki*	-83.766	38.599
Hebertella occidentalis	-85.274	38.601	*Dalmanella meeki*	-83.756	38.611
Rafinesquina alternata	-84.577	39.140	*Dalmanella meeki*	-83.759	38.620
Rafinesquina alternata	-84.402	39.184	*Dalmanella meeki*	-85.034	39.027
Rafinesquina alternata	-84.518	39.216	*Dalmanella meeki*	-84.578	39.198
Rafinesquina alternata	-84.463	39.212	*Dalmanella meeki*	-84.983	39.441
Rafinesquina alternata	-84.537	39.194	*Dalmanella meeki*	-84.746	39.507
Rafinesquina alternata	-84.548	39.203	*Hebertella occidentalis*	-83.759	38.485
Rafinesquina alternata	-84.526	39.128	*Hebertella occidentalis*	-83.759	38.505
Rafinesquina alternata	-84.527	39.128	*Hebertella occidentalis*	-83.768	38.607
Rafinesquina alternata	-84.425	39.258	*Hebertella occidentalis*	-83.787	38.874
Rafinesquina alternata	-84.547	39.202	*Hebertella occidentalis*	-85.034	39.027
Rafinesquina alternata	-84.390	39.355	*Hebertella occidentalis*	-84.387	39.346
Rafinesquina alternata	-84.588	39.150	*Leptaena richmondensis*	-83.768	38.607
Rafinesquina alternata	-85.274	38.601	*Leptaena richmondensis*	-84.387	39.346
Rafinesquina alternata	-84.112	39.178	*Rafinesquina alternata*	-83.759	38.485
Rafinesquina alternata	-85.330	39.290	*Rafinesquina alternata*	-83.759	38.505
Rafinesquina alternata	-85.040	39.020	*Rafinesquina alternata*	-83.768	38.607
Rafinesquina alternata	-85.142	38.751	*Rafinesquina alternata*	-83.787	38.866
Rafinesquina alternata	-85.280	38.600	*Rafinesquina alternata*	-85.034	39.027
Rafinesquina alternata	-84.601	39.425	*Rafinesquina alternata*	-84.623	39.228
Rafinesquina alternata	-83.913	38.870	*Rafinesquina alternata*	-84.589	39.277
Rafinesquina alternata	-84.122	39.172	*Rafinesquina alternata*	-84.387	39.346
Rafinesquina alternata	-84.404	39.297	*Rafinesquina alternata*	-84.983	39.441
Rafinesquina alternata	-84.678	39.328	*Rafinesquina alternata*	-84.398	39.515
Rafinesquina alternata	-83.759	38.505	*Rhynchotrema dentatum*	-83.545	38.793
Rafinesquina alternata	-84.502	39.406	*Rhynchotrema dentatum*	-83.787	38.874
Rafinesquina alternata	-84.625	39.229	*Rhynchotrema dentatum*	-83.787	38.874
Rafinesquina alternata	-85.274	38.602	*Rhynchotrema dentatum*	-83.826	38.935
Rafinesquina alternata	-84.525	39.225	*Rhynchotrema dentatum*	-85.040	39.029
Rafinesquina alternata	-84.625	39.229	*Zygospira modesta*	-83.759	38.485
Rafinesquina alternata	-84.600	39.283	*Zygospira modesta*	-83.759	38.505
Rafinesquina alternata	-85.142	38.751	*Zygospira modesta*	-85.040	39.029
Rafinesquina alternata	-83.738	38.369	*Zygospira modesta*	-84.623	39.228
Rafinesquina alternata	-84.490	39.528	*Zygospira modesta*	-84.589	39.277
Rafinesquina alternata	-83.760	38.529	*Zygospira modesta*	-84.387	39.346
Rafinesquina alternata	-83.601	38.712	*Zygospira modesta*	-84.983	39.441
Rafinesquina alternata	-85.170	38.632	*Zygospira modesta*	-84.398	39.515
Zygospira modesta	-84.601	39.425	**C4 sequence: Time Slice 2**		
Zygospira modesta	-83.913	38.870	*Dalmanella meeki*	-84.983	39.441
Zygospira modesta	-84.122	39.172	*Dalmanella meeki*	-85.034	39.027

Dalmanella meeki	-84.978	39.437	*Zygospira modesta*	-84.540	39.186
Dalmanella meeki	-84.605	39.138	*Zygospira modesta*	-84.096	39.451
Dalmanella meeki	-84.096	39.451	*Zygospira modesta*	-84.096	39.451
Dalmanella meeki	-83.766	38.599	*Zygospira modesta*	-84.085	39.216
Dalmanella meeki	-83.759	38.620	*Zygospira modesta*	-83.848	39.028
Dalmanella meeki	-83.756	38.611	*Zygospira modesta*	-83.759	38.485
Hebertella occidentalis	-85.180	38.388	*Zygospira modesta*	-83.759	38.505
Hebertella occidentalis	-85.040	39.029	**C4 sequence: Time Slice 3**		
Hebertella occidentalis	-85.034	39.027	*Dalmanella meeki*	-84.978	39.437
Hebertella occidentalis	-84.977	39.432	*Dalmanella meeki*	-84.977	39.432
Hebertella occidentalis	-84.096	39.451	*Dalmanella meeki*	-84.765	39.432
Hebertella occidentalis	-83.848	39.028	*Dalmanella meeki*	-84.746	39.507
Hebertella occidentalis	-83.787	38.874	*Dalmanella meeki*	-84.605	39.138
Hebertella occidentalis	-83.768	38.607	*Dalmanella meeki*	-84.096	39.451
Hebertella occidentalis	-83.760	38.353	*Hebertella occidentalis*	-85.180	38.388
Hebertella occidentalis	-83.759	38.485	*Hebertella occidentalis*	-85.180	38.388
Hebertella occidentalis	-83.759	38.505	*Hebertella occidentalis*	-84.977	39.432
Hebertella occidentalis	-83.691	38.685	*Hebertella occidentalis*	-84.098	39.336
Leptaena richmondensis	-83.768	38.607	*Hebertella occidentalis*	-84.096	39.451
Leptaena richmondensis	-83.759	38.505	*Hebertella occidentalis*	-83.787	38.874
Rafinesquina alternata	-84.983	39.441	*Hebertella occidentalis*	-83.759	38.485
Rafinesquina alternata	-85.355	38.772	*Hebertella occidentalis*	-83.701	38.585
Rafinesquina alternata	-85.274	38.601	*Hebertella occidentalis*	-83.691	38.685
Rafinesquina alternata	-85.040	39.029	*Leptaena richmondensis*	-84.540	39.186
Rafinesquina alternata	-85.034	39.027	*Leptaena richmondensis*	-83.760	38.353
Rafinesquina alternata	-84.978	39.437	*Leptaena richmondensis*	-83.759	38.505
Rafinesquina alternata	-84.977	39.432	*Leptaena richmondensis*	-83.691	38.685
Rafinesquina alternata	-84.682	39.481	*Rafinesquina alternata*	-84.983	39.441
Rafinesquina alternata	-84.602	39.163	*Rafinesquina alternata*	-85.355	38.772
Rafinesquina alternata	-84.589	39.277	*Rafinesquina alternata*	-85.136	38.874
Rafinesquina alternata	-84.540	39.186	*Rafinesquina alternata*	-84.978	39.437
Rafinesquina alternata	-84.085	39.216	*Rafinesquina alternata*	-84.977	39.432
Rafinesquina alternata	-84.063	39.485	*Rafinesquina alternata*	-84.682	39.481
Rafinesquina alternata	-83.848	39.028	*Rafinesquina alternata*	-84.678	39.328
Rafinesquina alternata	-83.839	39.027	*Rafinesquina alternata*	-84.635	39.485
Rafinesquina alternata	-83.787	38.866	*Rafinesquina alternata*	-84.623	39.228
Rafinesquina alternata	-83.768	38.607	*Rafinesquina alternata*	-84.602	39.163
Rafinesquina alternata	-83.760	38.353	*Rafinesquina alternata*	-84.540	39.186
Rafinesquina alternata	-83.759	38.485	*Rafinesquina alternata*	-84.398	39.515
Rafinesquina alternata	-83.759	38.505	*Rafinesquina alternata*	-84.063	39.485
Rafinesquina alternata	-83.691	38.685	*Rafinesquina alternata*	-84.063	39.485
Rafinesquina alternata	-83.606	38.698	*Rafinesquina alternata*	-83.787	38.866
Rhynchotrema dentatum	-85.274	38.601	*Rafinesquina alternata*	-83.760	38.353
Rhynchotrema dentatum	-85.040	39.029	*Rafinesquina alternata*	-83.759	38.485
Rhynchotrema dentatum	-83.826	38.935	*Rafinesquina alternata*	-83.701	38.585
Rhynchotrema dentatum	-83.787	38.874	*Rafinesquina alternata*	-83.691	38.685
Rhynchotrema dentatum	-83.760	38.353	*Rafinesquina alternata*	-83.606	38.698
Rhynchotrema dentatum	-83.545	38.793	*Rhynchotrema dentatum*	-83.787	38.874
Zygospira modesta	-84.983	39.441	*Rhynchotrema dentatum*	-83.760	38.353
Zygospira modesta	-85.355	38.772	*Rhynchotrema dentatum*	-83.691	38.685
Zygospira modesta	-84.978	39.437	*Zygospira modesta*	-84.983	39.441
Zygospira modesta	-84.977	39.432	*Zygospira modesta*	-85.040	39.029
Zygospira modesta	-84.682	39.481	*Zygospira modesta*	-84.978	39.437
Zygospira modesta	-84.589	39.277	*Zygospira modesta*	-84.977	39.432

Zygospira modesta	-84.682	39.481
Zygospira modesta	-84.678	39.328
Zygospira modesta	-84.635	39.485
Zygospira modesta	-84.540	39.186
Zygospira modesta	-84.096	39.451
Zygospira modesta	-84.096	39.451
Zygospira modesta	-84.096	39.451
Zygospira modesta	-84.063	39.485
Zygospira modesta	-83.759	38.485
Zygospira modesta	-83.701	38.585
C5 sequence: Time Slice 1		
Dalmanella meeki	39.638	-84.401
Dalmanella meeki	39.585	-84.032
Dalmanella meeki	39.509	-84.726
Dalmanella meeki	39.120	-84.875
Dalmanella meeki	39.050	-84.917
Dalmanella meeki	39.026	-83.932
Dalmanella meeki	38.745	-85.424
Dalmanella meeki	39.502	-84.745
Dalmanella meeki	39.014	-84.132
Dalmanella meeki	39.218	-85.046
Dalmanella meeki	39.080	-85.250
Dalmanella meeki	39.438	-84.987
Dalmanella meeki	38.969	-83.572
Dalmanella meeki	39.496	-84.748
Dalmanella meeki	39.503	-84.759
Dalmanella meeki	39.478	-84.063
Dalmanella meeki	39.498	-84.717
Dalmanella meeki	39.218	-85.046
Dalmanella meeki	39.340	-85.204
Dalmanella meeki	38.739	-85.430
Dalmanella meeki	37.661	-85.159
Dalmanella meeki	37.661	-85.159
Dalmanella meeki	39.438	-85.005
Dalmanella meeki	39.480	-84.948
Dalmanella meeki	39.412	-83.989
Dalmanella meeki	39.400	-84.562
Dalmanella meeki	39.238	-84.023
Dalmanella meeki	39.238	-84.023
Dalmanella meeki	39.238	-84.023
Dalmanella meeki	38.866	-83.787
Dalmanella meeki	39.168	-84.974
Dalmanella meeki	39.218	-85.046
Dalmanella meeki	39.238	-83.989
Dalmanella meeki	39.340	-85.204
Dalmanella meeki	39.401	-83.981
Dalmanella meeki	39.435	-84.203
Dalmanella meeki	39.507	-84.745
Dalmanella meeki	39.515	-84.398
Dalmanella meeki	39.480	-84.571
Dalmanella meeki	39.359	-84.361
Dalmanella meeki	39.439	-85.005
Dalmanella meeki	39.485	-84.635
Dalmanella meeki	39.481	-84.682

Dalmanella meeki	39.328	-84.678
Dalmanella meeki	39.437	-84.978
Dalmanella meeki	39.343	-84.954
Dalmanella meeki	39.549	-84.052
Glyptorthis insculpta	39.638	-84.401
Glyptorthis insculpta	38.736	-85.380
Glyptorthis insculpta	37.661	-85.159
Glyptorthis insculpta	39.636	-84.642
Glyptorthis insculpta	39.080	-85.250
Glyptorthis insculpta	39.422	-84.098
Glyptorthis insculpta	39.451	-84.088
Glyptorthis insculpta	39.293	-83.989
Glyptorthis insculpta	39.478	-84.063
Glyptorthis insculpta	39.218	-85.046
Glyptorthis insculpta	39.527	-84.468
Glyptorthis insculpta	39.085	-85.231
Glyptorthis insculpta	39.238	-84.023
Glyptorthis insculpta	39.547	-84.054
Glyptorthis insculpta	39.416	-83.989
Glyptorthis insculpta	39.425	-84.555
Glyptorthis insculpta	39.081	-85.250
Glyptorthis insculpta	39.480	-84.571
Glyptorthis insculpta	39.343	-84.954
Glyptorthis insculpta	39.549	-84.052
Glyptorthis insculpta	39.080	-85.250
Glyptorthis insculpta	39.451	-84.096
Glyptorthis insculpta	39.438	-84.987
Glyptorthis insculpta	39.527	-84.468
Glyptorthis insculpta	39.365	-84.153
Glyptorthis insculpta	39.336	-84.098
Glyptorthis insculpta	39.539	-84.069
Glyptorthis insculpta	39.400	-84.562
Glyptorthis insculpta	39.218	-85.046
Glyptorthis insculpta	39.340	-85.204
Hebertella occidentalis	38.585	-83.701
Hebertella occidentalis	39.026	-83.932
Hebertella occidentalis	39.218	-85.046
Hebertella occidentalis	37.818	-85.448
Hebertella occidentalis	39.503	-84.759
Hebertella occidentalis	39.238	-84.023
Hebertella occidentalis	39.301	-83.981
Hebertella occidentalis	39.283	-84.959
Hebertella occidentalis	39.402	-83.971
Hebertella occidentalis	39.524	-84.734
Hebertella occidentalis	39.238	-84.023
Hebertella occidentalis	39.081	-85.250
Hebertella occidentalis	39.081	-85.250
Hebertella occidentalis	38.866	-83.787
Hebertella occidentalis	39.072	-85.252
Hebertella occidentalis	39.481	-84.682
Hebertella occidentalis	39.328	-84.678
Hebertella occidentalis	38.771	-85.363
Hebertella occidentalis	39.549	-84.052
Hebertella occidentalis	38.596	-83.719

Hebertella occidentalis	38.401	-83.723	*Rhynchotrema dentatum*	39.397	-85.235
Hebertella occidentalis	39.487	-84.656	*Rhynchotrema dentatum*	39.238	-84.023
Hebertella occidentalis	39.478	-84.063	*Rhynchotrema dentatum*	39.481	-84.682
Leptaena richmondensis	39.283	-84.959	*Rhynchotrema dentatum*	38.401	-83.723
Leptaena richmondensis	39.081	-85.230	*Zygospira modesta*	37.767	-85.356
Leptaena richmondensis	39.027	-83.920	*Zygospira modesta*	38.401	-83.723
Leptaena richmondensis	39.498	-84.760	*Zygospira modesta*	39.328	-84.678
Leptaena richmondensis	39.389	-84.094	*Zygospira modesta*	39.343	-84.954
Leptaena richmondensis	39.238	-84.023	*Zygospira modesta*	39.583	-84.758
Leptaena richmondensis	39.081	-85.250	*Zygospira modesta*	39.632	-84.639
Leptaena richmondensis	38.866	-83.787	*Zygospira modesta*	39.218	-85.046
Leptaena richmondensis	39.480	-84.571	*Zygospira modesta*	39.496	-84.747
Leptaena richmondensis	39.481	-84.682	*Zygospira modesta*	39.531	-84.113
Leptaena richmondensis	39.343	-84.954	*Zygospira modesta*	39.191	-84.570
Leptaena richmondensis	39.549	-84.052	*Zygospira modesta*	39.533	-84.083
Leptaena richmondensis	39.487	-84.656	*Zygospira modesta*	39.238	-84.023
Leptaena richmondensis	39.478	-84.063	*Zygospira modesta*	39.507	-84.746
Leptaena richmondensis	39.342	-84.954	*Zygospira modesta*	39.359	-84.361
Rafinesquina alternata	38.585	-83.701	*Zygospira modesta*	39.439	-85.005
Rafinesquina alternata	39.638	-84.401	*Zygospira modesta*	39.485	-84.635
Rafinesquina alternata	39.585	-84.032	*Zygospira modesta*	39.481	-84.682
Rafinesquina alternata	39.509	-84.726	*Zygospira modesta*	39.437	-84.978
Rafinesquina alternata	39.026	-83.932	*Zygospira modesta*	39.549	-84.052
Rafinesquina alternata	39.218	-85.046	*Zygospira modesta*	39.438	-84.987
Rafinesquina alternata	37.767	-85.356	*Zygospira modesta*	39.478	-84.063
Rafinesquina alternata	38.596	-83.719	*Zygospira modesta*	37.748	-84.298
Rafinesquina alternata	38.401	-83.723	*Zygospira modesta*	39.342	-84.954
Rafinesquina alternata	39.474	-84.251	*Zygospira modesta*	39.509	-84.726
Rafinesquina alternata	39.081	-85.250	*Zygospira modesta*	39.120	-84.875
Rafinesquina alternata	38.866	-83.787	*Zygospira modesta*	39.050	-84.917
Rafinesquina alternata	39.072	-85.252	**C5 sequence: Time Slice 2**		
Rafinesquina alternata	39.218	-85.046	*Dalmanella meeki*	-84.401	39.638
Rafinesquina alternata	39.435	-84.203	*Dalmanella meeki*	-84.726	39.509
Rafinesquina alternata	39.507	-84.745	*Dalmanella meeki*	-84.875	39.120
Rafinesquina alternata	39.359	-84.361	*Dalmanella meeki*	-84.917	39.050
Rafinesquina alternata	39.439	-85.005	*Dalmanella meeki*	-83.932	39.026
Rafinesquina alternata	39.480	-84.049	*Dalmanella meeki*	-85.424	38.745
Rafinesquina alternata	39.481	-84.682	*Dalmanella meeki*	-84.745	39.502
Rafinesquina alternata	39.481	-84.682	*Dalmanella meeki*	-84.132	39.014
Rafinesquina alternata	39.481	-84.682	*Dalmanella meeki*	-85.046	39.218
Rafinesquina alternata	39.481	-84.682	*Dalmanella meeki*	-85.250	39.080
Rafinesquina alternata	39.481	-84.682	*Dalmanella meeki*	-84.987	39.438
Rafinesquina alternata	39.481	-84.682	*Dalmanella meeki*	-84.064	39.485
Rafinesquina alternata	39.481	-84.682	*Dalmanella meeki*	-83.572	38.969
Rafinesquina alternata	39.481	-84.682	*Dalmanella meeki*	-84.748	39.496
Rafinesquina alternata	39.481	-84.682	*Dalmanella meeki*	-84.759	39.503
Rafinesquina alternata	39.328	-84.678	*Dalmanella meeki*	-84.063	39.478
Rafinesquina alternata	39.437	-84.978	*Dalmanella meeki*	-84.717	39.498
Rafinesquina alternata	38.771	-85.363	*Dalmanella meeki*	-85.046	39.218
Rafinesquina alternata	39.549	-84.052	*Dalmanella meeki*	-85.204	39.340
Rafinesquina alternata	39.487	-84.656	*Dalmanella meeki*	-85.430	38.739
Rhynchotrema dentatum	38.593	-85.318	*Dalmanella meeki*	-85.159	37.661
Rhynchotrema dentatum	39.438	-84.987	*Dalmanella meeki*	-85.159	37.661
Rhynchotrema dentatum	39.503	-84.759	*Dalmanella meeki*	-85.005	39.438

Dalmanella meeki	-84.948	39.480	*Glyptorthis insculpta*	-84.748	39.496
Dalmanella meeki	-84.298	37.748	*Glyptorthis insculpta*	-84.063	39.478
Dalmanella meeki	-83.989	39.412	*Glyptorthis insculpta*	-84.949	39.480
Dalmanella meeki	-84.954	39.342	*Glyptorthis insculpta*	-85.045	39.216
Dalmanella meeki	-84.954	39.342	*Glyptorthis insculpta*	-85.364	38.776
Dalmanella meeki	-84.719	39.500	*Glyptorthis insculpta*	-85.159	37.661
Dalmanella meeki	-84.562	39.400	*Glyptorthis insculpta*	-84.298	37.748
Dalmanella meeki	-84.023	39.238	*Glyptorthis insculpta*	-84.954	39.342
Dalmanella meeki	-84.023	39.238	*Glyptorthis insculpta*	-84.719	39.500
Dalmanella meeki	-84.023	39.238	*Glyptorthis insculpta*	-85.045	39.216
Dalmanella meeki	-83.787	38.866	*Glyptorthis insculpta*	-84.746	39.507
Dalmanella meeki	-84.974	39.168	*Glyptorthis insculpta*	-84.285	39.642
Dalmanella meeki	-85.046	39.218	*Glyptorthis insculpta*	-84.954	39.343
Dalmanella meeki	-83.989	39.238	*Glyptorthis insculpta*	-84.052	39.549
Dalmanella meeki	-85.204	39.340	*Glyptorthis insculpta*	-85.250	39.080
Dalmanella meeki	-83.981	39.401	*Glyptorthis insculpta*	-84.096	39.451
Dalmanella meeki	-84.203	39.435	*Glyptorthis insculpta*	-84.987	39.438
Dalmanella meeki	-84.745	39.507	*Glyptorthis insculpta*	-84.468	39.527
Dalmanella meeki	-84.398	39.515	*Glyptorthis insculpta*	-84.153	39.365
Dalmanella meeki	-84.571	39.480	*Glyptorthis insculpta*	-84.098	39.336
Dalmanella meeki	-84.361	39.359	*Glyptorthis insculpta*	-84.069	39.539
Dalmanella meeki	-85.005	39.439	*Glyptorthis insculpta*	-84.562	39.400
Dalmanella meeki	-84.635	39.485	*Glyptorthis insculpta*	-85.046	39.218
Dalmanella meeki	-84.682	39.481	*Glyptorthis insculpta*	-85.204	39.340
Dalmanella meeki	-84.678	39.328	*Hebertella occidentalis*	-83.453	38.938
Dalmanella meeki	-84.978	39.437	*Hebertella occidentalis*	-83.701	38.585
Dalmanella meeki	-84.954	39.343	*Hebertella occidentalis*	-83.726	38.404
Dalmanella meeki	-84.052	39.549	*Hebertella occidentalis*	-84.283	39.869
Dalmanella meeki	-83.723	38.401	*Hebertella occidentalis*	-84.659	39.598
Glyptorthis insculpta	-84.401	39.638	*Hebertella occidentalis*	-84.247	39.067
Glyptorthis insculpta	-85.006	39.458	*Hebertella occidentalis*	-84.283	39.078
Glyptorthis insculpta	-84.745	39.507	*Hebertella occidentalis*	-83.932	39.026
Glyptorthis insculpta	-83.932	39.187	*Hebertella occidentalis*	-85.046	39.218
Glyptorthis insculpta	-85.046	39.218	*Hebertella occidentalis*	-84.758	39.583
Glyptorthis insculpta	-85.380	38.736	*Hebertella occidentalis*	-85.251	39.081
Glyptorthis insculpta	-85.159	37.661	*Hebertella occidentalis*	-85.251	39.081
Glyptorthis insculpta	-84.745	39.507	*Hebertella occidentalis*	-85.046	39.218
Glyptorthis insculpta	-84.642	39.636	*Hebertella occidentalis*	-84.745	39.507
Glyptorthis insculpta	-85.250	39.080	*Hebertella occidentalis*	-84.468	39.527
Glyptorthis insculpta	-84.098	39.422	*Hebertella occidentalis*	-85.046	39.218
Glyptorthis insculpta	-84.088	39.451	*Hebertella occidentalis*	-84.748	39.496
Glyptorthis insculpta	-83.989	39.293	*Hebertella occidentalis*	-84.023	39.493
Glyptorthis insculpta	-84.063	39.478	*Hebertella occidentalis*	-85.448	37.818
Glyptorthis insculpta	-85.046	39.218	*Hebertella occidentalis*	-84.751	39.581
Glyptorthis insculpta	-84.468	39.527	*Hebertella occidentalis*	-84.949	39.633
Glyptorthis insculpta	-85.231	39.085	*Hebertella occidentalis*	-84.759	39.503
Glyptorthis insculpta	-84.023	39.238	*Hebertella occidentalis*	-84.023	39.238
Glyptorthis insculpta	-84.054	39.547	*Hebertella occidentalis*	-83.981	39.301
Glyptorthis insculpta	-83.989	39.416	*Hebertella occidentalis*	-84.959	39.283
Glyptorthis insculpta	-84.555	39.425	*Hebertella occidentalis*	-83.971	39.402
Glyptorthis insculpta	-85.250	39.081	*Hebertella occidentalis*	-84.734	39.524
Glyptorthis insculpta	-84.571	39.480	*Hebertella occidentalis*	-84.023	39.238
Glyptorthis insculpta	-84.049	39.480	*Hebertella occidentalis*	-85.250	39.081
Glyptorthis insculpta	-84.064	39.485	*Hebertella occidentalis*	-85.250	39.081

Hebertella occidentalis	-83.787	38.866	*Rafinesquina alternata*	-84.954	39.342
Hebertella occidentalis	-85.252	39.072	*Rafinesquina alternata*	-84.751	39.581
Hebertella occidentalis	-85.204	39.340	*Rafinesquina alternata*	-84.251	39.474
Hebertella occidentalis	-85.204	39.340	*Rafinesquina alternata*	-85.250	39.081
Hebertella occidentalis	-84.049	39.480	*Rafinesquina alternata*	-83.787	38.866
Hebertella occidentalis	-84.949	39.488	*Rafinesquina alternata*	-85.252	39.072
Hebertella occidentalis	-84.682	39.481	*Rafinesquina alternata*	-85.046	39.218
Hebertella occidentalis	-84.678	39.328	*Rafinesquina alternata*	-84.203	39.435
Hebertella occidentalis	-85.363	38.771	*Rafinesquina alternata*	-84.745	39.507
Hebertella occidentalis	-85.365	38.778	*Rafinesquina alternata*	-84.361	39.359
Hebertella occidentalis	-83.719	38.596	*Rafinesquina alternata*	-85.005	39.439
Hebertella occidentalis	-83.723	38.401	*Rafinesquina alternata*	-84.049	39.480
Hebertella occidentalis	-84.987	39.438	*Rafinesquina alternata*	-84.682	39.481
Hebertella occidentalis	-84.656	39.487	*Rafinesquina alternata*	-84.682	39.481
Hebertella occidentalis	-84.063	39.478	*Rafinesquina alternata*	-84.682	39.481
Hebertella occidentalis	-84.949	39.480	*Rafinesquina alternata*	-84.682	39.481
Hebertella occidentalis	-85.364	38.776	*Rafinesquina alternata*	-84.682	39.481
Hebertella occidentalis	-84.954	39.342	*Rafinesquina alternata*	-84.682	39.481
Leptaena richmondensis	-83.453	38.938	*Rafinesquina alternata*	-84.682	39.481
Leptaena richmondensis	-83.512	38.822	*Rafinesquina alternata*	-84.682	39.481
Leptaena richmondensis	-84.401	39.638	*Rafinesquina alternata*	-84.682	39.481
Leptaena richmondensis	-84.032	39.585	*Rafinesquina alternata*	-84.678	39.328
Leptaena richmondensis	-84.726	39.509	*Rafinesquina alternata*	-84.978	39.437
Leptaena richmondensis	-85.204	39.340	*Rafinesquina alternata*	-85.363	38.771
Leptaena richmondensis	-84.745	39.507	*Rafinesquina alternata*	-84.052	39.549
Leptaena richmondensis	-85.365	38.778	*Rafinesquina alternata*	-84.656	39.487
Leptaena richmondensis	-84.987	39.438	*Rafinesquina alternata*	-83.701	38.585
Leptaena richmondensis	-84.949	39.480	*Rafinesquina alternata*	-83.726	38.404
Leptaena richmondensis	-85.364	38.776	*Rafinesquina alternata*	-84.283	39.869
Leptaena richmondensis	-85.250	39.081	*Rafinesquina alternata*	-84.032	39.585
Leptaena richmondensis	-83.787	38.866	*Rafinesquina alternata*	-84.659	39.598
Leptaena richmondensis	-84.571	39.480	*Rafinesquina alternata*	-84.726	39.509
Leptaena richmondensis	-84.682	39.481	*Rafinesquina alternata*	-84.247	39.067
Leptaena richmondensis	-84.954	39.343	*Rafinesquina alternata*	-84.283	39.078
Leptaena richmondensis	-84.052	39.549	*Rafinesquina alternata*	-83.932	39.026
Leptaena richmondensis	-84.656	39.487	*Rhynchotrema dentatum*	-84.987	39.438
Leptaena richmondensis	-84.063	39.478	*Rhynchotrema dentatum*	-84.759	39.503
Leptaena richmondensis	-84.954	39.342	*Rhynchotrema dentatum*	-84.063	39.478
Rafinesquina alternata	-85.046	39.218	*Rhynchotrema dentatum*	-84.949	39.480
Rafinesquina alternata	-84.049	39.480	*Rhynchotrema dentatum*	-84.298	37.748
Rafinesquina alternata	-85.356	37.767	*Rhynchotrema dentatum*	-85.235	39.397
Rafinesquina alternata	-85.365	38.778	*Rhynchotrema dentatum*	-84.023	39.238
Rafinesquina alternata	-84.954	39.343	*Rhynchotrema dentatum*	-84.682	39.481
Rafinesquina alternata	-83.719	38.596	*Rhynchotrema dentatum*	-83.723	38.401
Rafinesquina alternata	-83.723	38.401	*Rhynchotrema dentatum*	-83.512	38.822
Rafinesquina alternata	-84.987	39.438	*Zygospira modesta*	-85.356	37.767
Rafinesquina alternata	-84.064	39.485	*Zygospira modesta*	-83.723	38.401
Rafinesquina alternata	-85.046	39.218	*Zygospira modesta*	-84.949	39.480
Rafinesquina alternata	-84.063	39.478	*Zygospira modesta*	-84.949	39.488
Rafinesquina alternata	-84.949	39.480	*Zygospira modesta*	-85.365	38.778
Rafinesquina alternata	-83.905	39.386	*Zygospira modesta*	-84.949	39.488
Rafinesquina alternata	-85.430	38.739	*Zygospira modesta*	-85.365	38.778
Rafinesquina alternata	-84.745	39.507	*Zygospira modesta*	-84.719	39.500
Rafinesquina alternata	-84.298	37.748	*Zygospira modesta*	-84.745	39.507

Zygospira modesta	-85.046	39.218
Zygospira modesta	-84.745	39.507
Zygospira modesta	-84.758	39.583
Zygospira modesta	-84.639	39.632
Zygospira modesta	-85.046	39.218
Zygospira modesta	-84.747	39.496
Zygospira modesta	-84.113	39.531
Zygospira modesta	-84.570	39.191
Zygospira modesta	-84.083	39.533
Zygospira modesta	-84.023	39.238
Zygospira modesta	-84.746	39.507
Zygospira modesta	-84.361	39.359
Zygospira modesta	-85.005	39.439
Zygospira modesta	-84.635	39.485
Zygospira modesta	-84.682	39.481
Zygospira modesta	-84.978	39.437
Zygospira modesta	-84.052	39.549
Zygospira modesta	-84.987	39.438
Zygospira modesta	-84.063	39.478
Zygospira modesta	-84.298	37.748
Zygospira modesta	-84.954	39.342
C5 sequence: Time Slice 3		
Glyptorthis insculpta	-85.006	39.458
Glyptorthis insculpta	-84.745	39.507
Glyptorthis insculpta	-84.665	39.627
Glyptorthis insculpta	-83.932	39.187
Glyptorthis insculpta	-85.046	39.218
Glyptorthis insculpta	-84.203	39.435
Glyptorthis insculpta	-84.096	39.451
Glyptorthis insculpta	-83.925	39.392
Glyptorthis insculpta	-84.745	39.507
Glyptorthis insculpta	-84.049	39.480
Glyptorthis insculpta	-84.064	39.485
Glyptorthis insculpta	-84.748	39.496
Glyptorthis insculpta	-83.925	39.388
Glyptorthis insculpta	-84.063	39.478
Glyptorthis insculpta	-84.949	39.480
Glyptorthis insculpta	-85.045	39.216
Glyptorthis insculpta	-84.298	37.748
Glyptorthis insculpta	-84.954	39.342
Glyptorthis insculpta	-84.719	39.500
Glyptorthis insculpta	-85.045	39.216
Glyptorthis insculpta	-84.746	39.507
Glyptorthis insculpta	-84.285	39.642
Hebertella occidentalis	-84.758	39.583
Hebertella occidentalis	-85.251	39.081
Hebertella occidentalis	-84.064	39.485
Hebertella occidentalis	-84.665	39.627
Hebertella occidentalis	-83.894	39.477
Hebertella occidentalis	-84.905	39.757
Hebertella occidentalis	-84.047	39.481
Hebertella occidentalis	-85.046	39.218
Hebertella occidentalis	-84.748	39.496
Hebertella occidentalis	-84.023	39.493

Hebertella occidentalis	-84.890	39.829
Hebertella occidentalis	-84.890	39.829
Hebertella occidentalis	-84.890	39.829
Hebertella occidentalis	-84.719	39.500
Hebertella occidentalis	-84.751	39.581
Hebertella occidentalis	-84.949	39.633
Hebertella occidentalis	-85.242	39.300
Hebertella occidentalis	-85.204	39.340
Hebertella occidentalis	-85.204	39.340
Hebertella occidentalis	-85.045	39.216
Hebertella occidentalis	-83.911	39.281
Hebertella occidentalis	-84.746	39.507
Hebertella occidentalis	-84.664	39.627
Hebertella occidentalis	-84.159	39.628
Hebertella occidentalis	-84.649	39.629
Hebertella occidentalis	-84.919	39.753
Hebertella occidentalis	-84.892	39.829
Hebertella occidentalis	-83.927	39.389
Hebertella occidentalis	-84.571	39.480
Hebertella occidentalis	-84.049	39.480
Hebertella occidentalis	-84.089	39.796
Hebertella occidentalis	-85.365	38.778
Hebertella occidentalis	-83.719	38.596
Hebertella occidentalis	-83.723	38.401
Hebertella occidentalis	-84.987	39.438
Hebertella occidentalis	-84.954	39.343
Hebertella occidentalis	-83.521	38.927
Hebertella occidentalis	-83.505	38.828
Hebertella occidentalis	-84.949	39.480
Hebertella occidentalis	-85.364	38.776
Hebertella occidentalis	-84.954	39.342
Hebertella occidentalis	-83.453	38.938
Hebertella occidentalis	-83.726	38.404
Hebertella occidentalis	-84.283	39.869
Hebertella occidentalis	-84.659	39.598
Hebertella occidentalis	-84.247	39.067
Hebertella occidentalis	-84.283	39.078
Leptaena richmondensis	-83.453	38.938
Leptaena richmondensis	-83.512	38.822
Leptaena richmondensis	-84.649	39.629
Leptaena richmondensis	-84.203	39.435
Leptaena richmondensis	-85.204	39.340
Leptaena richmondensis	-84.745	39.507
Leptaena richmondensis	-85.365	38.778
Leptaena richmondensis	-84.987	39.438
Leptaena richmondensis	-84.949	39.480
Leptaena richmondensis	-85.364	38.776
Rafinesquina alternata	-84.044	39.480
Rafinesquina alternata	-83.927	39.389
Rafinesquina alternata	-84.571	39.480
Rafinesquina alternata	-84.049	39.480
Rafinesquina alternata	-84.089	39.796
Rafinesquina alternata	-84.949	39.488
Rafinesquina alternata	-85.356	37.767

Rafinesquina alternata	-85.365	38.778	*Rhynchotrema dentatum*	-84.665	39.627
Rafinesquina alternata	-84.954	39.343	*Rhynchotrema dentatum*	-84.905	39.757
Rafinesquina alternata	-83.521	38.927	*Rhynchotrema dentatum*	-84.890	39.829
Rafinesquina alternata	-83.719	38.596	*Rhynchotrema dentatum*	-84.893	39.828
Rafinesquina alternata	-83.505	38.828	*Rhynchotrema dentatum*	-84.919	39.760
Rafinesquina alternata	-83.723	38.401	*Rhynchotrema dentatum*	-84.904	39.786
Rafinesquina alternata	-84.987	39.438	*Rhynchotrema dentatum*	-85.046	39.218
Rafinesquina alternata	-84.064	39.485	*Rhynchotrema dentatum*	-84.746	39.507
Rafinesquina alternata	-85.046	39.218	*Rhynchotrema dentatum*	-84.892	39.829
Rafinesquina alternata	-84.063	39.478	*Rhynchotrema dentatum*	-84.089	39.796
Rafinesquina alternata	-84.949	39.480	*Rhynchotrema dentatum*	-83.512	38.822
Rafinesquina alternata	-83.905	39.386	*Zygospira modesta*	-83.927	39.389
Rafinesquina alternata	-85.430	38.739	*Zygospira modesta*	-84.571	39.480
Rafinesquina alternata	-84.745	39.507	*Zygospira modesta*	-85.356	37.767
Rafinesquina alternata	-84.298	37.748	*Zygospira modesta*	-83.723	38.401
Rafinesquina alternata	-84.954	39.342	*Zygospira modesta*	-84.949	39.480
Rafinesquina alternata	-84.751	39.581	*Zygospira modesta*	-84.949	39.488
Rafinesquina alternata	-84.283	39.869	*Zygospira modesta*	-85.365	38.778
Rafinesquina alternata	-84.659	39.598	*Zygospira modesta*	-84.949	39.488
Rafinesquina alternata	-84.247	39.067	*Zygospira modesta*	-85.365	38.778
Rafinesquina alternata	-84.283	39.078	*Zygospira modesta*	-84.719	39.500
Rhynchotrema dentatum	-84.063	39.478	*Zygospira modesta*	-84.907	39.760
Rhynchotrema dentatum	-84.949	39.480	*Zygospira modesta*	-83.847	39.389
Rhynchotrema dentatum	-84.298	37.748	*Zygospira modesta*	-84.203	39.435
Rhynchotrema dentatum	-83.723	38.401	*Zygospira modesta*	-84.649	39.629
Rhynchotrema dentatum	-84.648	39.654	*Zygospira modesta*	-84.745	39.507
Rhynchotrema dentatum	-85.186	39.501	*Zygospira modesta*	-85.046	39.218
Rhynchotrema dentatum	-84.649	39.629	*Zygospira modesta*	-84.745	39.507
Rhynchotrema dentatum	-85.251	39.380	*Zygospira modesta*	-84.659	39.598

Appendix 2: Coded environmental parameter data. Coding strategy follows Table 2. Data compiled and recoded from Dudei (2009), Swisher (2009) and Walls (2009). Abbreviations: Lat., Latitude; Long., Longitude; M%, Mud percentage; D, water depth; Bed, bedding style; Thick, limestone thickness; Bio, biofacies.

Lat.	Long.	M %	D	Bed	Thick	Bio
C3 sequence: Time Slice 1						
38.375	-83.625		2	3		3
38.375	-83.875	34	2.5	2.75	6.79	2.81
38.625	-83.625	50	2	2.5	2.5	
38.625	-85.375	30	2.5	3	5.5	2.25
38.625	-85.125	45	3	2.5	3.5	2
38.875	-85.375	80	2	1	2.5	3
38.875	-83.625	51	2	1.5	3.5	
38.875	-83.875	51	2	1.3	4	2
39.125	-85.125	78	2	1.5	3	2
39.125	-84.125	58	2	1.33	2.5	2
39.125	-83.875	56	2	1.5	3.5	
39.125	-83.625	57	2	1.5	3.5	
39.125	-84.625	72	2	1	4	1.5
39.125	-84.875	76	2	1	3.5	2
39.375	-85.375	80	2	3	2.5	2
39.375	-84.875	70	2	1.5	3.5	
39.375	-84.375	64	2	1.5	5	
39.375	-83.875	64	2	1.5	5	
39.375	-84.625	52	2	1	5.86	1.81
39.375	-85.125	79	2	1	2.5	1.5
39.625	-84.375	80	2	2	2.5	2
39.625	-84.625	70	2	2	3.3	
39.625	-84.875	70	2	1.5	5	
C3 sequence: Time Slice 2						
38.375	-83.875	28.5	2.63	3	7.5	2.55
38.375	-83.625	13	2.63	3	10.59	2.29
38.625	-85.375	30	2.5	3	4.67	2.25
38.625	-85.125	15	3	2	4	3
38.625	-83.625	30	2.93	2	4.25	
38.875	-85.375	57	3	1.75	2.5	2.75
38.875	-83.875	50	2.2	2.43	4.82	3
38.875	-83.625	42	2.29	1.93	3.93	3
39.125	-85.125	63	2	1.5	5.1	2
39.125	-84.625	54	2.67	2.67	4.83	2
39.125	-84.125	60	2	1.17	2.5	2
39.125	-83.875	53	2.1	1.7	3.6	3
39.125	-83.625	57	2	1.5	3.5	
39.375	-85.375	80	2	1.67	2.5	2
39.375	-85.125	50	2	1	9	1.44
39.375	-84.875	67	2.2	1.8	3.3	3
39.375	-84.625	65	2	1	5	2

Lat.	Long.	M %	D	Bed	Thick	Bio
39.375	-84.375	64	2.18	1.63	4.68	2.45
39.375	-84.125	33	2.5	1.5		2.08
39.375	-83.875	64	2	1.5	5	
39.625	-84.875	68	2.25	1.88	4.63	
39.625	-84.625	50	2	3	5	
39.625	-84.375	76	2.5	1.55	3.9	1.94
C3 sequence: Time Slice 3						
39.375	-85.375	70	2.86	2.33	2.5	2
38.875	-85.375	51	3	2	3.75	2.75
39.375	-84.875	42	3	2.5	5	1.5
39.125	-85.125	51	2	1.5	5	2
39.625	-84.375	74	2.5	2.5	6.25	2.38
39.125	-84.125	58	2.17	1.33	2.5	2
38.375	-83.625	47	3	2.75	12.5	2.94
39.375	-84.125	35	3	2		2
39.625	-84.625	50	3	3	5	
39.375	-83.875	54	2.71	2.57	5	3
39.125	-83.875	24	3	3	4.25	3
39.125	-83.625	40	2.86	1.93	3.5	3
38.875	-83.875	21	3	3	7.5	3
39.625	-84.875	60	3	3	3.5	
38.875	-83.625	18	3	3	5	3
39.375	-85.125	67	2	1	4.35	1.7
39.375	-84.625	43	2.83	2.25	5.17	2.08
39.125	-84.625	40	2.92	2.5	6	2
39.375	-84.375	51	3	3	4.5	2.42
38.625	-83.875	17	3	2.5	2.5	2.83
38.625	-85.125	27	3	2.3	5.4	2.13
38.375	-83.875	45	3	2.75	5	2.5
38.625	-85.375	42	2.88	3	2.5	2.13
38.625	-83.625	40	3	2	2.96	2.88
C4 sequence: Time Slice 1						
38.375	-83.875	40	2	2	8	2
38.375	-83.625	40	3	1		2
38.625	-85.375	33	2	1	5	2
38.625	-83.875	37		2		2
38.625	-83.625	35	2	1	8	2
38.875	-83.875	65.3	2	1.83	4.33	
38.875	-83.625	29		2	3.5	
39.125	-85.125	27	2	1	5	2
39.125	-83.875	64		2	8	
39.375	-85.125	51	2	1	7	1.5
39.375	-84.875	60	2	1.5	2	1
39.375	-84.625	52.7	2	1.67	6.5	1.8
39.375	-84.375			2	3.5	
39.375	-83.875	77	2	2	4	
39.375	-83.625	71		2	3.5	
39.625	-84.875	64		2	3.5	
39.625	-84.625	80	2	2		
39.625	-84.375	53	2	1.75	4.25	1.5

Lat.	Long.	M %	D	Bed	Thick	Bio
C4 sequence: Time Slice 2						
38.375	-83.875	53	2.5	2	5	2
38.375	-83.625	60	3	1		3
38.625	-85.375	57	2	2	5	2
38.625	-83.875	65		1.5		2
38.625	-83.625	20	3	1.5	4	2
38.875	-85.375	60	2	2.5	3	1.5
38.875	-85.125	30	2	1.5	3	1
38.875	-83.875	65.3	2.5	2.17	11.8	
38.875	-83.625	60		2	3.5	
39.125	-85.125	52	3	2.5	3	2
39.125	-84.625	26	2	2		1.5
39.125	-83.875	58	2.5	2	8	1
39.375	-85.125	47	2.75	2.25	6	1.5
39.375	-84.875	60	2.5	2		1.5
39.375	-84.625	57.5	2.5	2	4.25	1.5
39.375	-84.125	52.5	3	3	8	2
39.375	-83.875	60	2.5	2	4	
39.375	-83.625	71		2	3.5	
39.625	-84.875	64		2	3.5	
39.625	-84.625	69	2.5	2	3.5	
39.625	-84.375			2.5	3.5	
C4 sequence: Time Slice 3						
38.375	-83.875	49	3	1.5	4	1.5
38.375	-83.625	56	3	2		2
38.625	-85.375	47	2.5	2.5	5	2
38.875	-85.125	30	3	2	6	2
38.875	-83.625	60		3	3.5	
39.125	-84.625	57	2.5	2	10	2
39.125	-83.875	64		3	8	1
38.875	-83.875	66		2.25	9	
39.375	-85.125	44.5	3	2.5	7	1.5
39.375	-84.875	60	3	3		2
39.375	-84.625	65	3	2	3.5	1.5
39.375	-84.125	59.5	3	2.5		2
39.375	-83.875	43	3	2		
39.375	-83.625	71		2		
39.625	-84.875	64		2		
39.625	-84.625	57	3	2		
C5 sequence: Time Slice 1						
39.875	-84.625	74	1	1		
39.625	-84.125	64	1	2	4	1
39.625	-84.375	65	1	1.5	3	1
39.625	-84.875	65.5	1	1	2	1
39.375	-83.875	65	1	2		
39.375	-84.125	74	1	1	2	1
39.375	-84.625	70	1	1		
39.375	-84.875	65	1	1	3	1
39.375	-85.125	60	1	1	2	1
39.125	-83.875	65	1	1	3	

Lat.	Long.	M %	D	Bed	Thick	Bio
38.875	-85.375	55	1	1	4	1
38.625	-83.625	50	2	1	5	2
38.625	-85.375	40	2	3	6	2
39.125	-84.875	75	1	1	3	1
39.125	-83.875	55	1	1	5	1
C5 sequence: Time Slice 2						
39.875	-84.375	40	2	2	8	2
39.875	-84.625	53	2	2		
39.875	-84.875	45	2	1	6	3
39.625	-84.125	50	1.5	1	7	2
39.625	-84.375	40	1	1.5	6	2
39.625	-84.625	45	2	1	6	3
39.625	-84.875	50	1.5	1.5	7	2
39.375	-83.875	47	1	2		
39.375	-84.125	60	1	1	7	2
39.375	-84.625	60	1	1		
39.375	-84.875	60	2	1	7	3
39.375	-85.125	45	2	1	7	2
39.125	-83.875	65	1	2	6	
39.125	-85.125	35	3	2		
39.125	-85.375	35	3	2	8	
38.875	-83.625	30	3	2	8	
38.875	-85.375	45	2	1	6	3
38.625	-83.625	40	2	2	8	2

Lat.	Long.	M %	D	Bed	Thick	Bio
38.625	-85.375	45	3	2	9	2
38.375	-83.625	35	3	2	9	3
39.125	-84.875	60	1	1	6	1
39.125	-83.875	50	2	1	9	2
C5 sequence: Time Slice 3						
39.875	-84.375	35	3	2	10	2
39.875	-84.625	32	3			
39.875	-84.875	35	3	2	8	3
39.625	-84.125	49	3	2		
39.625	-84.375	30	3	2		
39.625	-84.625	35	2	2	10	2
39.625	-84.875	33	3	3	10	3
39.375	-84.125	52	2	2	8	3
39.375	-84.625	47	2	1		
39.375	-84.875	45	2	2	8	3
39.375	-85.125	33	3	3	10	3
39.125	-85.125	30	3	3	15	3
39.125	-85.375	30	3	3	15	3
38.875	-83.375	25	3	2	15	
38.875	-83.625	20	3	2	15	
38.875	-85.375	35	3	3	10	3
38.625	-85.375	30	3	3	12	3
38.375	-83.625	30	3	2	12	3