Invited review article

Biotic immigration events, speciation, and the accumulation of biodiversity in the fossil record

Alycia L. Stigall [a,*,1], Jennifer E. Bauer [b,1], Adriane R. Lam [c,1], David F. Wright [d,1]

[a] Department of Geological Sciences and OHIO Center for Ecology and Evolutionary Studies, Ohio University, 316 Clippinger Laboratories, Athens, OH 45701, USA
[b] Department of Earth and Planetary Sciences, The University of Tennessee, Knoxville, 1412 Circle Drive, TN 37996, USA
[c] Department of Geosciences, University of Massachusetts Amherst, 233 Morrill Science Center, 611 North Pleasant Street, Amherst, MA 01003, USA
[d] School of Earth Sciences, The Ohio State University, 155 South Oval Mall, Columbus, OH 43210, USA

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ABSTRACT

Biotic Immigration Events (BIMEs) record the large-scale dispersal of taxa from one biogeographic area to another and have significantly impacted biodiversity throughout geologic time. BIMEs associated with biodiversity increases have been linked to ecologic and evolutionary processes including niche partitioning, species packing, and higher speciation rates. Yet substantial biodiversity decline has also been documented following BIMEs due to elevated extinction and/or reduced speciation rates. In this review, we develop a conceptual model for biodiversity accumulation that links BIMEs and geographic isolation with local (α) diversity, regional (β) diversity, and global (γ) diversity metrics. Within the model, BIME intervals are characterized by colonization of existing species within new geographic regions and a lack of successful speciation events. Thus, there is no change in γ-diversity, and α-diversity increases at the cost of β-diversity. An interval of regional isolation follows in which lineage splitting results in successful speciation events and diversity increases across all three metrics. Alternation of these two regimes can result in substantial biodiversity accumulation.

We tested this conceptual model using a series of case studies from the paleontological record. We primarily focus on two intervals during the Middle through Late Ordovician Period (470–458 Ma): the globally pervasive BIMEs during the Great Ordovician Biodiversification Event (GOBE) and a regional BIME, the Richmondian Invasion. We further test the conceptual model by examining the Great Devonian Interchange, Neogene mollusk migrations and diversification, and the Great American Biotic Interchange. Paleontological data accord well with model predictions.

Constraining the mechanisms of biodiversity accumulation provides context for conservation biology. Because α-, β-, and γ-diversity are semi-independent, different techniques should be considered for sustaining various diversity partitions. Maintaining natural migration routes and population sizes among isolated regions are vital to preserving both extant biodiversity and biogeographic pathways requisite for future diversity generation.

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* Corresponding author.
  E-mail address: stigall@ohio.edu (A.L. Stigall).
[1] All secondary authors contributed equally and are listed alphabetically.

1. Introduction

One of the primary tasks of historical geology and evolutionary science is to construct a more complete description of the origin, maintenance, and modification of biodiversity across multiple scales of biological organization. Field-based and experimental studies of natural populations offer high resolution insight into how evolutionary dynamics shift over successive generations (e.g., Rice and Hostert, 1993; Coulson et al., 2001; Grant and Grant, 2002; McKinnon and Rundle, 2002), but the investigation of large-scale spatial and temporal patterns is primarily the domain of paleontology and phylogenetic comparative biology, where patterns are manifested at geologic timescales (Simpson, 1953; Pennell and Harmon, 2013; Slater and Harmon, 2013). Simple inspection of the history of life demonstrates that biotic diversity, discussed herein in terms of taxonomic richness, is ever changing, a continuous trade-off between the origination and extinction of species through time. Despite the waxing and waning of individual clades over the ~3.5 billion years of life's history on Earth, the overall diversity pattern has been net accumulation—from a single common ancestor in the Archean Eon to more than 8.7 million species today (Mora et al., 2011; Hug et al., 2016). Anthropogenically-induced climate change, habitat destruction, and the introduction of invasive species have placed significant stress on modern species (Millien et al., 2006; Kolbert, 2014; Pimm et al., 2014; De Vos et al., 2015; Plotnick et al., 2016), with some analyses indicating these impacts approximate those of the most severe extinction event in the history of life: the Permian-Triassic mass extinction (e.g., Barnosky et al., 2011; Payne and Clapham, 2012; Ceballos et al., 2015; McCallum, 2015). Thus, examining the mechanisms of biodiversity accumulation is critical for understanding both the history of life and accurately projecting future biodiversity.

Fundamentally, the accumulation of biodiversity hinges on the process of speciation. The formation of new species requires a population to become reproductively isolated and differentiated from the ancestral population. Biological barriers to gene flow can develop in several ways, including shifts in reproductive timing, breakdown of mate recognition, or accumulation of character differences within a single geographic area (sympatric speciation) or in geographically isolated populations (allopatric speciation) (Coyne and Orr, 2004). Furthermore, these newly formed isolated populations must exhibit appreciable phenotypic divergence and endure some degree of persistence as an independently evolving lineage to be recognized in the fossil record (Eldredge et al., 2005; Rabosky, 2016). Thus, the process of speciation includes geographic, temporal, phenotypic, and phylogenetic components. By examining speciation events within a combined spatial and temporal context, it is possible to uncover the impact of biotic and abiotic environmental factors on diversity accumulation (Stigall, 2015).

Analyzing biodiversity is further complicated because diversity can be assessed at multiple spatial levels, ranging from local to global in scale. Because these levels are hierarchically structured, increasing diversity at one scale may not necessarily translate to increased diversity at other levels (Whittaker, 1972; Badgley, 2010; Barton et al., 2013). Notably, Biotic Immigration Events (BIMEs), in which species migrate from their ancestral region into another area, may increase regional diversity without the formation of any novel species (Hubbell, 2001; Vermeij,

2005a). Focusing on differences between hierarchical scale and diversity provides a framework to consider how diversity is developed through time (Eldredge, 1985; Sepkoski, 1988; Sepkoski, 1992; Harper, 2010).

In this contribution, we explore the relationships among Biotic Immigration Events, speciation mode, and biodiversity patterns at various scales. BIMEs have impacted biodiversity throughout geologic time (Stehli and Webb, 1985; Vermeij, 1991b; Vermeij, 2005a; Stigall, 2010a; McGhee, 2013). Some BIMEs have been linked to diversification via processes such as niche partitioning, species packing, and elevated speciation rates, yet substantial biodiversity decline has also been documented following BIMEs due to elevated extinction and/or reduced speciation rates. Herein we develop a conceptual model linking biodiversity and BIMEs and apply that model to examine biodiversity change within shallow epicontinental seas during the Middle to Late Ordovician Period (470–443 million years ago). This interval includes both regional and global immigration events, dramatic changes in biodiversity on all scales, and shifting speciation dynamics. Ordovician patterns are also compared with other intervals of geologic time to assess the general applicability of the conceptual model. Lastly, we discuss the impact of BIMEs on the modern biota.

2. Mechanisms of diversity generation

The processes involved with biodiversity accumulation vary across multiple geographic scales, taxonomic levels, and among clades (Alroy, 2010b; Rabosky et al., 2012). Consequently, diversity is often partitioned into alpha (α), beta (β), and gamma (γ) components relating to diversity within discrete areas, differences among areas, and overall diversity, respectively (Fig. 1) (Barton et al., 2013). At the largest scale, global (γ) biodiversity increases when the number of speciation events exceeds the number of extinction events. Thus, the biotic and abiotic environmental factors impacting speciation and extinction rates exert primary controls on the net accumulation of γ-diversity. Numerous studies have analyzed trends in the trajectory of γ-diversity through time and its influence of the history of life during the Phanerozoic (e.g., Alroy et al., 2008; Alroy, 2010c; Hautmann, 2014; Mondal and Harries, 2016). At the other end of the scale is α-diversity, which is defined as species richness within a local area (Whittaker, 1972). Alpha diversity is determined by the number of species within the regional species pool that are able to sustain populations within the local environment (Whittaker, 1972). Hence α-diversity is strongly controlled by local ecology and niche requirements of species.

Alpha and γ-diversity are linked via processes that influence the geographic distribution of species, notably dispersal and migration. For example, a newly differentiated species comprising a single population and occupying a geographically restricted area will affect both γ- and α-diversity. The origination of this new species will add to γ-diversity, but the geographic restriction of the initial populations increases α-diversity within only a single area. The subsequent migration of this new species to one or more additional geographic areas will have no impact on γ-diversity; however, local α-diversity will increase with each successful immigration event.

The third component of diversity, β-diversity, is used to signify differences among areas. Numerous mathematical variations of β-diversity equations exist (e.g., Whittaker, 1972; Wilson and Shmida,
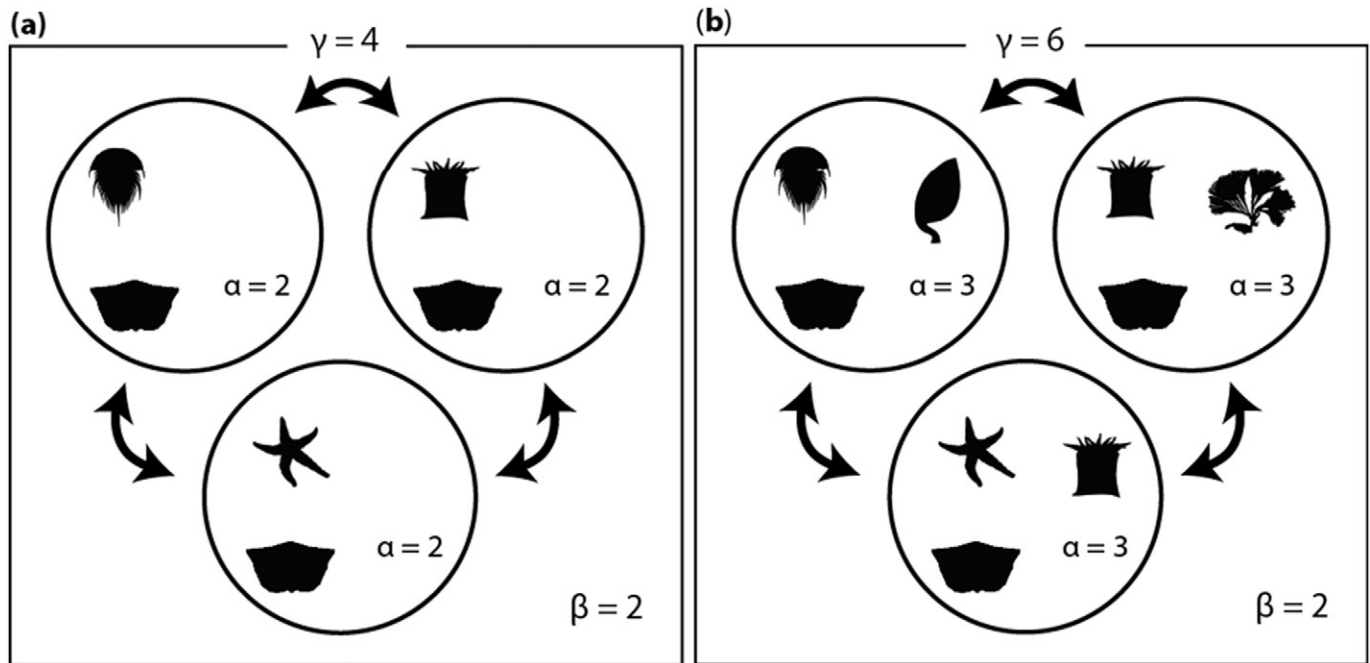
Fig. 1. Hierarchical relationships among of levels of diversity (α, β, γ). Alpha diversity is calculated as species richness within an area, and γ-diversity is total species richness across all regions. Beta diversity is calculated as γ-diversity divided by mean α-diversity. Comparison of (a) and (b) demonstrates that β-diversity can remain stable regardless of changes in α- and γ-diversity, and vice versa.

1984; Tuomisto, 2010; Barton et al., 2013), but each formulation attempts to capture the degree of biotic differentiation among two or more two regions. Beta diversity is semi-independent from α- and γ-diversity; two examples could have identical β-diversity but differ in α- and γ-diversity values (Fig. 1). BIMEs between basins link these three diversity levels and are common features of the fossil record (Stigall, 2016). These differences among hierarchical components of biodiversity provide a framework to consider how the various diversity partitions are developed through time.

3. Diversity cycle

Alternating the processes of immigration, partitioning of available niche space, and ultimately speciation can result in a cycle that increases overall diversity. Cyclical processes, such as taxon pulses (Erwin, 1985; Hoberg and Brooks, 2010) and geodispersal (Lieberman, 2000; Lieberman, 2008) are well established for increasing diversity within individual clades, but biotic immigration processes can also impact diversity patterns among faunas (Badgley et al., 2016). Herein, we present a cyclical model for diversity generation. In the model, geographic regions are alternately isolated and subsequently connected to one another via what we term Biotic Immigration Events (BIMEs).

A hypothetical time-series of our model is presented in Figs. 2 and 3 to demonstrate the potential impact of this cyclical isolation and connectivity. Initially, each of the four basins is occupied by a single species yielding low α-diversity (Fig. 2b). However, each basin hosts a unique species, so overall β- and γ-diversities are comparatively higher. The following interval is characterized by dispersal events (BIMEs) between basins (Fig. 2c). The resulting basin scale changes lead to higher α-diversity within each basin, but the immigration event reduces opportunities of isolation, so no new species form and γ-diversity is unchanged. Accordingly, β-diversity declines. Following this interval, the basins become separated again (Fig. 2d). Vicariance of previously widespread species promotes the formation of one new species in each basin, which increases α, β, and γ diversity. Within the model, the BIME and

vicariance phases then repeat (Fig. 2e–f). As before, new species do not form during the BIME intervals, so increases in α-diversity cause reductions in β-diversity. The following vicariance phase once again prompts speciation, which increases α, β, and γ diversity.

Extinction effects (although not incorporated explicitly here) are expected to be variable—increasing competition from immigrant taxa may promote extinction for some species whereas the increased geographic ranges of other species may provide extinction resistance (Jablonski and Sepkoski, 1996). Although extinction can have a pronounced effect on diversity components, particularly during mass extinctions (Darroch and Wagner, 2015), the existing paleobiological literature indicates that regional biotic invasions do not typically lead to extinction events but instead act to increase diversity, at least temporarily (Vermeij, 1991a; Jablonski and Sepkoski, 1996; Patzkowsky and Holland, 2007). Thus, the effect of extinction is expected to be minimal as long as the rate of species origination outpaces extinction for the timespan considered.

To summarize this conceptual model, BIME intervals result in increased local diversity, reduced differentiation between basins, and no change to global diversity levels. Given the lack of geographic barriers, speciation is limited as there are fewer opportunities for sustained reproductive isolation to develop among populations. Invasive regimes have the capacity to greatly impact α- and β-diversity, but cannot contribute to substantial increases in γ-diversity required for substantial increases in global species richness. Conversely, speciation is facilitated by geographic isolation during vicariance intervals, leading to an increase within all three biodiversity metrics. However, the timing of speciation events is closely related to the timing of population vicariance. Speciation rate is highest immediately after isolation. Speciation rate declines once newly isolated species become adapted to the new conditions and subsequently exhibit stasis and habitat tracking (Eldredge et al., 2005). Consequently, alternation of the BIME and vicariance phases of our model is required for sustained increases in global species richness. Greater α-diversity within basins during subsequent
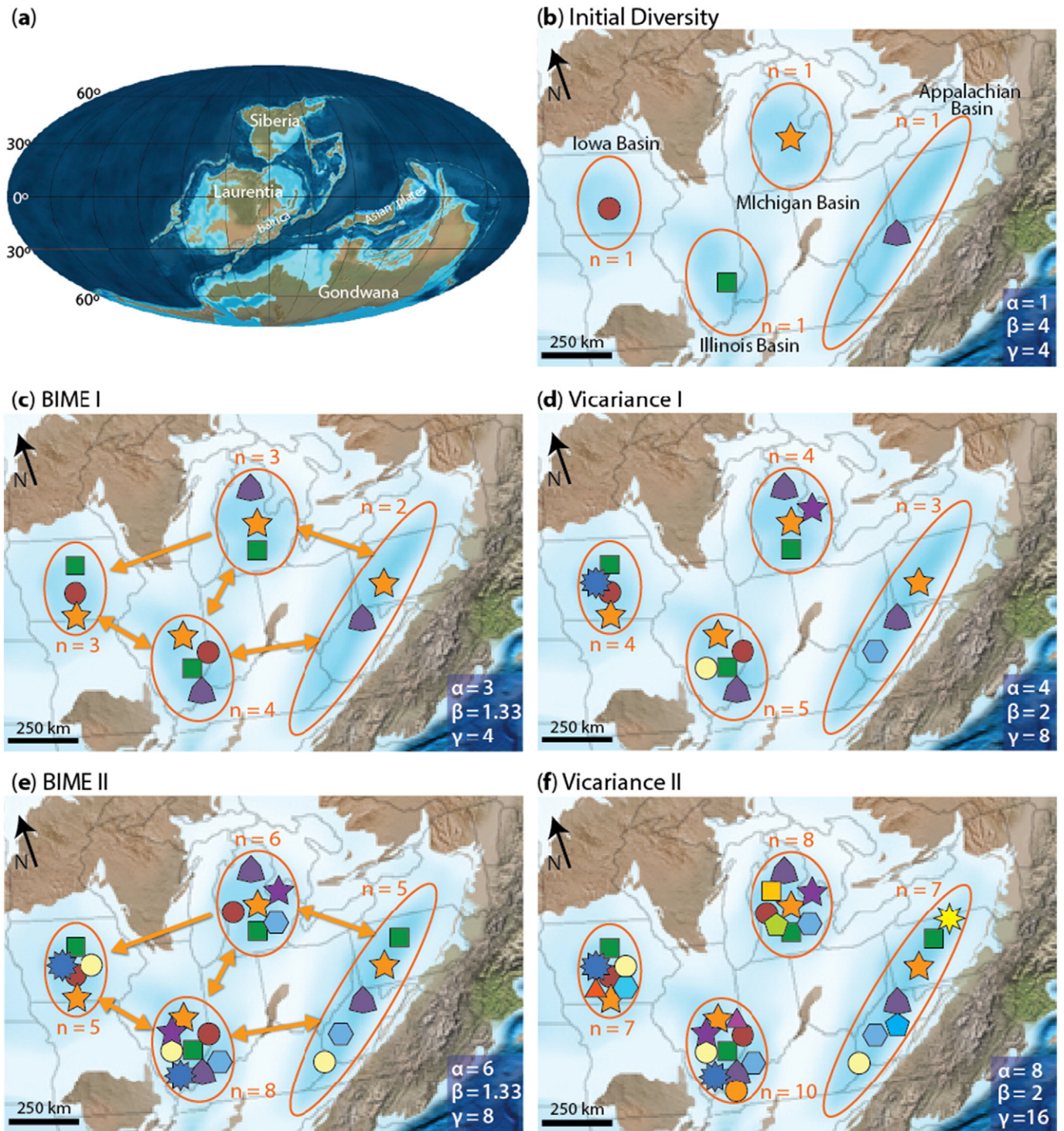
Fig. 2. Conceptual model of biodiversity accumulation represented spatially. (a) Paleogeographic reconstruction for the Late Devonian Period (370 Ma). During this time, much of the continent of Laurentia was covered with shallow epicontinental seas, which were intermittently connected and disconnected based on changes in tectonic stresses translated from the continental margins. (b) Four Devonian basins in what is today the eastern United States are used to illustrate the theoretical model. Initially, each basin contains a single unique species, resulting in the diversity metrics in the lower right. (c) During the next temporal bin, an increase in sea level facilitates dispersal among basins via a biotic immigration event (BIME). This increases α-diversity, but γ-diversity is unchanged as no lineage splitting events occur, and β-diversity declines due to increased similarity among the various faunas. (d) Subsequent iso-lation of the basins during a fall in sea level promotes one event of allopatric speciation via vicariance in each basin, producing an increase in all diversity metrics. (e) A second BIME occurs during sea level rise, again increasing α-diversity and reducing β-diversity with no impact on γ-diversity. (f) In the final stage of the model, the basins are once again isolated facilitating speciation within each basin. As standing diversity is greater than in (d), two new species develop per basin, which elevates α, β, and γ-diversity levels greatly. Paleogeographic base maps from Blakey (2012, 2013) used with permission.

BIMEs facilitates a greater number of speciation events, and thereby produces even more substantial increases in γ-diversity. Hence, gen-eration of substantial net diversity is facilitated by mechanisms that alternately promote and restrict immigration between basins.

4. Diversity within Ordovician seas

The spectacular fossil record preserved in Middle to Late Ordovician strata of North America and Europe documents a series of immigration
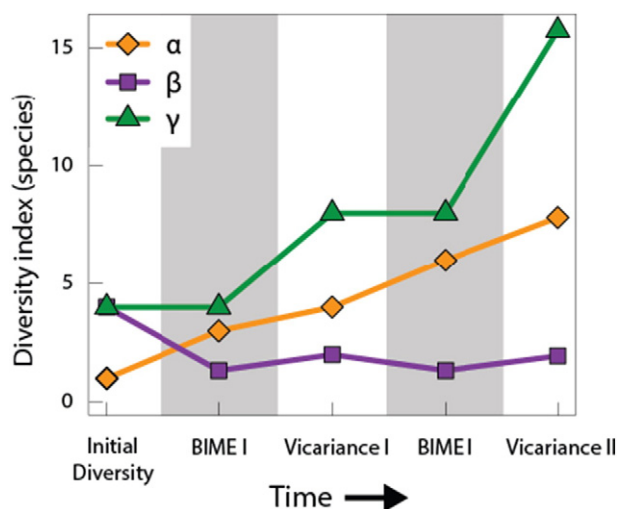
Fig. 3. Conceptual model of biodiversity accumulation represented graphically. Plot of α, β, and γ-diversity values produced in Fig. 2. BIME intervals produce increased α-diversity, but the lack of novel species production results in stable γ-diversity and a decline in β-diversity. Speciation events during vicariance intervals increase all three types of diversity. Alternation of vicariance and BIME regimes promote the greatest speciation rates.

events and biodiversity increases that provide a framework to test the tenants of the conceptual model (Fig. 4). Herein, we analyze two case studies in detail to examine the link between BIMEs and biodiversity: 1) a set of globally pervasive BIMEs during the Great Ordovician Biodiversification Event (GOBE) and 2) a regionally developed BIME during the Richmondian Invasion.

4.1. Building global diversity: the Great Ordovician Biodiversification Event

One of the most dramatic global diversity increases of the Phanerozoic Era occurred during the Great Ordovician Biodiversification Event (GOBE) (Miller and Foote, 1996; Droser and Finnegan, 2003; Harper, 2006). The GOBE was characterized by biotic immigration events (BIMEs) among paleocontinents (Servais et al., 2009; Servais et al., 2010; Harper et al., 2013; Harper and Servais, 2013) which culminated in a dramatic increase in γ-diversity including a three to four fold increase of family-level diversity (Sepkoski, 1988). Diversification varied among clades, which triggered ecological turnover in the marine realm. Members of the Cambrian Evolutionary Fauna, such as trilobites and archaic mollusks, declined in diversity, whereas members of the Paleozoic Evolutionary Fauna, such as articulated brachiopods, rapidly radiated at the generic and familial levels (Fig. 5). Clades characteristic of the Modern Evolutionary Fauna, such as gastropods and bivalves, also radiated, albeit at a slower rate. These changes substantially modified marine food webs and established the first complex marine ecosystems with tiering, intricate trophic cascades, and ecospace partitioning (Ausich and Bottjer, 1982; Servais et al., 2009; Servais et al., 2010).
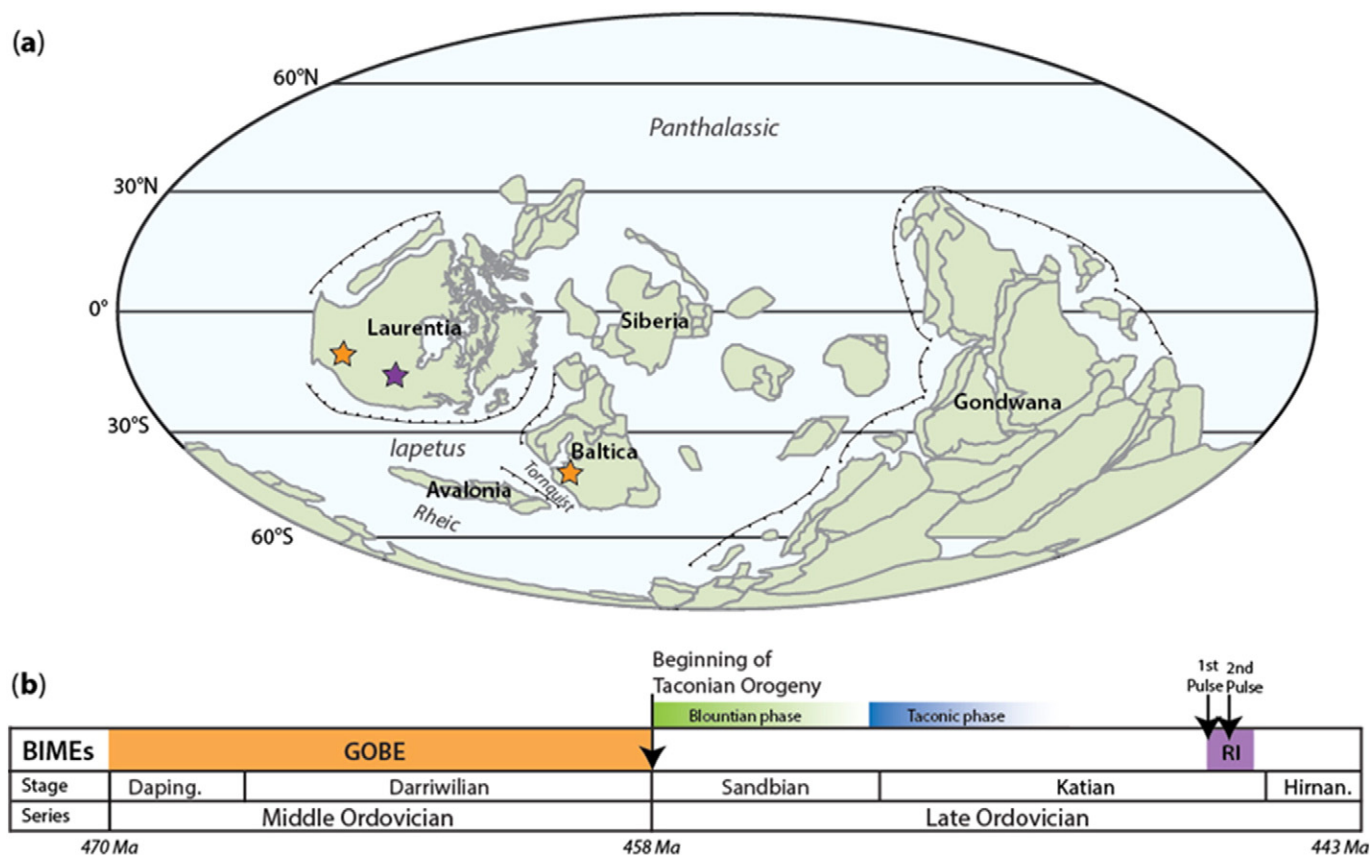

Fig. 4. Paleogeographic reconstruction and timeline for the Middle to Late Ordovician Period (470 Ma). (a) Late Ordovician (Sandbian) paleogeographic reconstruction illustrating major continents and terranes, major oceans, and subduction zones (sawtooth lines). Orange stars represent the locations discussed in the GOBE case study. Purple star represents the location of the Cincinnati Basin, where the Late Ordovician Richmondian Invasion occurred. (b) Middle to Late Ordovician timescale with global stratigraphic stages and key events labeled. Biotic immigration events (BIMEs): Great Ordovician Biodiversification Event (GOBE; orange interval), the Richmondian Invasion (RI; purple interval). '1st pulse' and '2nd pulse' refer to the two phases of the Richmondian Invasion. Tectophases, of the Taconian Orogeny are indicated at the top of the time scale. The Richmondian Invasion occurred after the Taconic tectophase as sediment regimes within the Cincinnati Basin switched to a tropical-style carbonate environment. Paleogeographic map after Torsvik and Cocks (2013); timescale from Cohen et al. (2013, updated); Taconian tectophases after Ettensohn (2010).
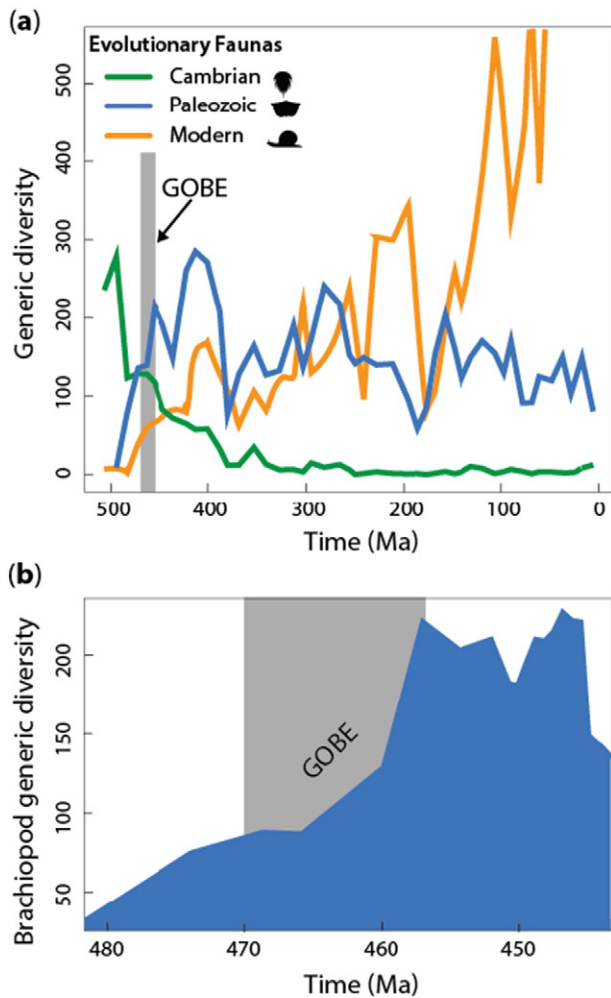
Fig. 5. Global diversity trends among marine animal genera. (a) Individualized diversity curves depicting the trajectory of all marine animal genera partitioned by Sepkoski's (1981) three Evolutionary Faunas. Diversity was estimated from taxonomic occurrences using shareholder quorum subsampling (Alroy, 2010a). Data were downloaded from the Paleobiology Database (paleobiodb.org) on 4/25/2016. Timing of the Great Ordovician Biodiversification Event (GOBE) indicated by the gray bar. Diversity of Paleozoic and Modern faunas increase during his interval. (b) Global genus richness (γ-diversity) of rhynchonelliform brachiopods, a dominant component of the Paleozoic Evolutionary Fauna, during the Ordovician Period. Generic richness increased sharply during the GOBE interval (shaded in gray). Taxonomic range data for brachiopods from Harper et al. (2013).

Various global environmental triggers, including cooling oceanic temperatures, increased oxygenation, and major sea level transgressions, have been invoked as preconditions that set the stage for diversification (Fortey, 1984; Trotter et al., 2008; Servais et al., 2009; Edwards and Saltzman, 2016; Rasmussen et al., 2016). Notably, the timing of radiation varied among clades and paleocontinents (Miller, 1997; Zhan and Harper, 2006) indicating that dispersal among regions significantly impacted the net accumulation of global diversity and its spatial distribution at finer geographic scales (Servais et al., 2009; Harper, 2010; Trubovitz and Stigall, 2016).

Rhynchonelliform brachiopods are among the most abundant, diverse, and well-known fossil clades from many paleocontinents during the GOBE, and numerous studies (including this one) have used them as exemplar taxon to analyze diversification dynamics during this interval. Rhynchonelliform diversity curves have been produced for Baltica (Rasmussen et al., 2007), South China (Zhan and Harper, 2006), Laurentia (Trubovitz and Stigall, 2016), Argentina (Waisfeld et al., 2003), Wales (Lockley, 1983), the Iapetus region (Harper et al., 1996), and parts of Gondwana (Havlíček, 1971). Comparison of the regional

α-diversity curves demonstrates commonalities in overall patterns of diversification timing and magnitude. On most paleocontinents, diversification rates reached maximum levels during the Darriwilian Stage (~464 Ma), which increased α-diversity from fewer than ten to thirty or more contemporaneous species (Fig. 6a,b). However, differences in the taxonomic composition of brachiopod faunas among paleocontinents are striking, indicating high β-diversity (Fig. 6c,d; Harper et al., 2013).

The dual importance of immigration and isolation in developing the dramatic increase in global species richness during this interval has long been appreciated (McKerrow and Cocks, 1976; Miller, 1997; Harper, 2006). Limited faunal similarity among paleocontinents indicates that substantial barriers to migration were present at stages during diversification, and many authors have commented on the importance of regional isolation or within-region heterogeneity in promoting regional diversification (Harper and Mac Niocaill, 2002; Waisfeld et al., 2003; Rasmussen et al., 2007; Benedetto et al., 2009). Other analyses (e.g. Harper et al., 2013) have noted the significance of immigration and dispersal processes. Certainly, dispersal was required to produce the initial set of brachiopod species for diversification during the onset of the GOBE, and subsequent waves of migration were necessary to produce the broadly distributed taxa of the Sandbian and Katian Stages (Harper et al., 2013; Trubovitz and Stigall, 2016). For example, members of the order Strophomenida are absent from Middle Ordovician strata of Baltica, but comprise a substantial component of both the Laurentian and global brachiopod fauna (Fig. 6; Harper et al., 2013). Dispersal of strophomenid species to Baltica occurred near the end of the Darriwilian stage; strophomenids subsequently diversified in the region and comprised a substantial component of Late Ordovician species diversity in Baltica (Rõõmusoks, 1981). Thus, both processes operated, but at alternate times.

Thus, the dramatic increase in global species richness that characterizes the GOBE resulted from a set of alternating vicariance and dispersal events comparable to the conceptual model outlined above. Early Ordovician dispersal established preconditions of low γ-diversity accompanied by low regional α-diversity and moderate β-diversity. During the initial GOBE interval, speciation within clades restricted to isolated basins produced greater α-diversity and enhanced β-diversity, which multiplied during subsequent alternations to generate rapidly escalating γ-diversity. Post-GOBE migration events lowered β-diversity, and thereby slowed the rapid rise of γ-diversity escalation in the Late Ordovician.

4.2. Building regional diversity: the Richmondian Invasion

During the Late Katian stage, oceanographic changes facilitated inter-basinal migration into what is now the tri-state area of Ohio, Kentucky, and Indiana (the Cincinnati Basin). This event, termed the Richmondian Invasion (Holland, 1997; Stigall, 2010b), was a regional scale BIME that caused substantial ecosystem turnover.

During the Late Ordovician, the Cincinnati Basin was located in the paleotropics and was subjected to frequent tropical storms that buried the shelly inhabitants of the shallow sea, producing an extensive fossil record (Meyer and Davis, 2009). The shallow marine communities preserved in the lower strata exhibit a coherent and stable community structure that was primarily controlled by onshore-offshore gradient and substrate composition (Holland and Patzkowsky, 2007; Patzkowsky and Holland, 2007). This community structure was stable for approximately five million years, but rapidly broke down with the introduction of extra-basinal immigrants from all trophic levels and modes of life during the Richmondian Invasion (Stigall, 2010b). Following an interval of community restructuring, new communities with a strong onshore-offshore gradient were established (Holland and Patzkowsky, 2007), although new communities exhibited greater species richness and increased niche partitioning relative to pre-invasion communities (Patzkowsky and Holland, 2007; Holland, 2010; Brame and Stigall, 2014; Stigall, 2014; Novack-Gottshall, 2016).
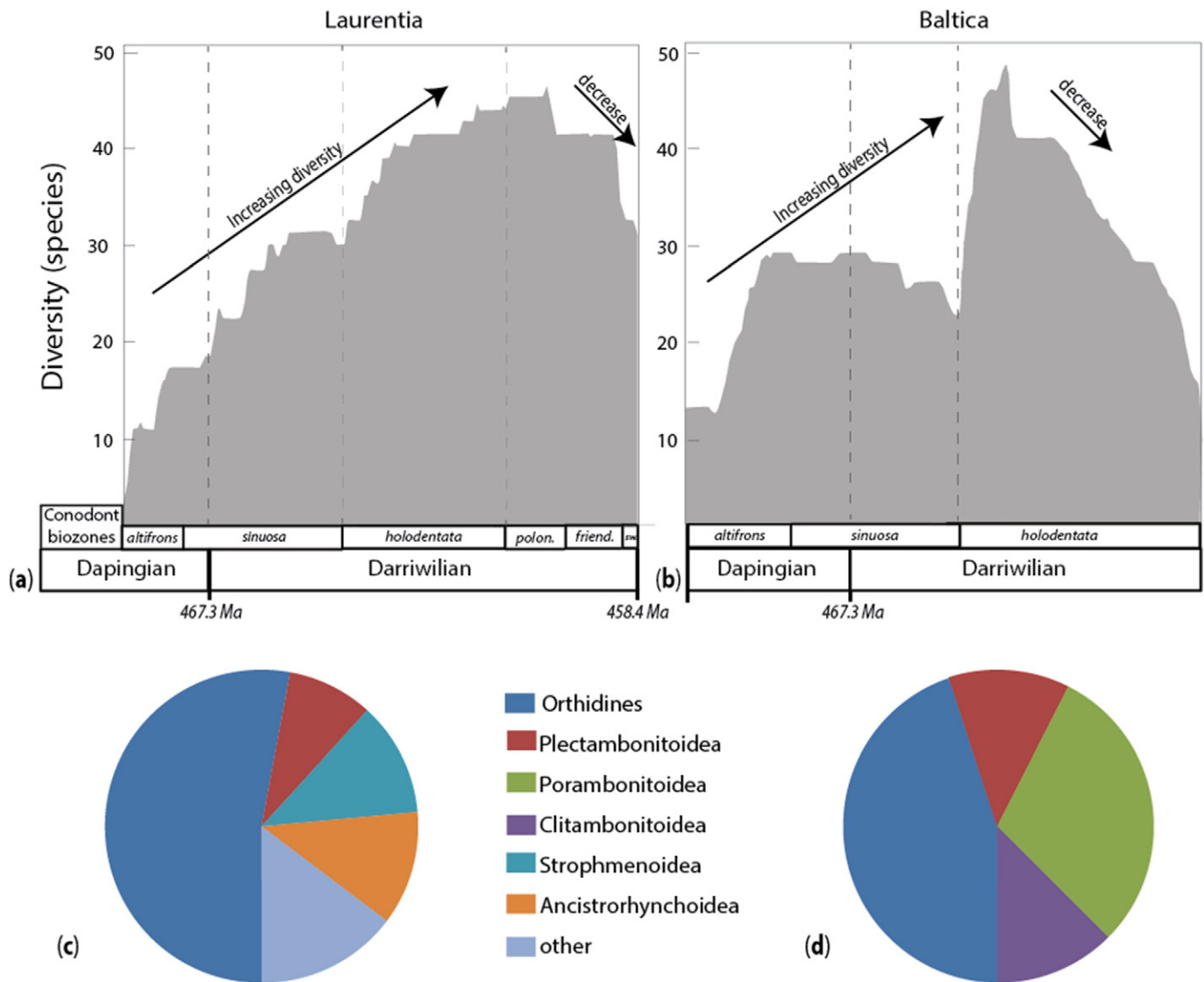
Fig. 6. Comparison of diversity patterns among rhynchonelliform brachiopods of Laurentia and Baltica during the GOBE interval. (a) Cumulative α-diversity curve for Laurentian brachiopod species based on the fauna of the Simpson Group of Oklahoma. A substantial increase in α-diversity occurs during through the early Darriwilian Stage followed by a diversity decline. (b) Cumulative α-diversity curve for Baltic brachiopod species based on the fauna in the region around St. Petersburg, Russia. Overall trends, timing, and α-diversity levels compare closely with those of Laurentia. (c) Relative distribution of species in (a) and (b) among brachiopod superfamilies. Substantial differences between the distributions reflects high β-diversity between regions. Laurentian data based on Trubovitz and Stigall (2016); Baltic data based on Rasmussen et al. (2007).

The two pulses of the Richmondian Invasion occurred over an interval of less than 500,000 years (Fig. 4) and included migrations from at least three source regions (Wright and Stigall, 2013a; Bauer and Stigall, 2014; Lam and Stigall, 2015; Stigall, 2016). The impact of the Richmondian Invasion on diversity within the Cincinnati Basin has long been of interest to paleontologists (Foerste, 1905; Patzkowsky and Holland, 2007; Stigall, 2010b; Novack-Gottshall, 2016). Immigration increased α-diversity at the genus-level because the limited extinction of native genera was more than offset by the number of immigrant genera (Fig. 7) (Patzkowsky and Holland, 2007). The post-invasion interval was characterized by significant increase in niche evolution among both native and invasive taxa (Malizia and Stigall, 2011; Brame and Stigall, 2014). Post-invasion taxa were primarily ecological generalists that adjusted to the increased biotic competition in post-invasion communities by contracting the breadth of their ecological niches (Malizia and Stigall, 2011; Brame and Stigall, 2014; Stigall, 2014). Niche contraction provides a mechanism for the niche partitioning previously reported by Patzkowsky and Holland (2007) and Holland (2010). By partitioning the available ecospace, a greater number of species were able to persist within the basin.

Species-level niche dynamics have been best characterized for rhynchonelliform brachiopods. Native species with large geographic ranges persisted through the invasion. However, some species with narrow ranges became extinct, and there was a notable lack of speciation during the invasion interval (Stigall, 2010b; Wright and Stigall, 2013a). Post-invasion communities were comprised exclusively of species with relatively large geographic ranges, which was interpreted by Stigall (2010b) as a correlate of ecological niche breadth. Stigall (2014) attributed the speciation gap to an inability for incipient species to either maintain sufficient genetic isolation or population sizes to persist as discrete lineages due to competition from the native and invasive ecological generalists. The extinction of several species coupled with a speciation gap resulted in a net loss of γ-diversity during the Richmondian Invasion.

The basic diversity patterns of the Richmondian Invasion accord well with the theoretical model of alternating BIMEs. Alpha diversity increased within the Cincinnati Basin as relatively few native species perished and many invader taxa became successfully established. Overall endemism, expressed as β-diversity, declined among depositional basins, and γ-diversity dropped slightly related to low origination
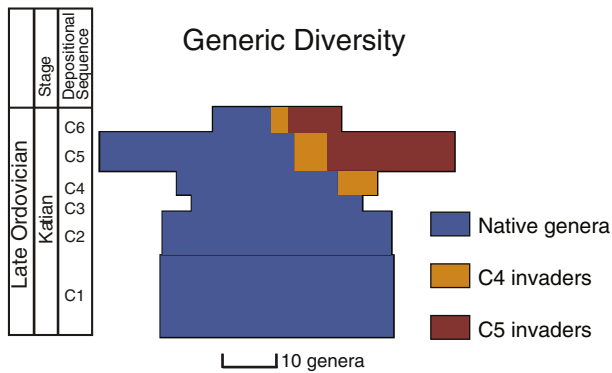
Fig. 7. Cumulative diversity of marine invertebrate genera within the Cincinnati basin through the Richmondian Invasion interval. Only relatively common and ecologically significant genera are plotted in the spindle diagram. The invasion occurred in two primary pulses: within the C4 sequence (1st pulse) and at the beginning of the C5 sequence (2nd pulse) (Fig. 4). Diversity of native taxa was not substantially impacted by the invasion event. Successful invaders from both waves of invasion were able to successfully establish in the basin, producing increased α-diversity following the invasion. Overall decline in α-diversity in the C6 sequence is due to the conversion of the marine basin to a terrestrial environment. Distribution of genera after Holland and Patzkowsky (2007).

rates. These patterns match the predictions for BIME intervals within the diversity cycle model.

4.3. Integrating Ordovician dispersal events with speciation patterns

Phylogenetic biogeography provides another powerful way to examine relationships among diversity, speciation, and dispersal. Because speciation events are subject to phylogenetic, temporal, and geographic constraints, as described above, analyzing dispersal and vicariance events within a phylogenetic context can elucidate processes not discernable from basin or global diversity compilations alone. Notably, mapping ancestral biogeographic distributions onto a phylogenetic tree topology allows differentiation between the two primary modes of allopatric speciation, vicariance and dispersal (Fig. 8) (Lieberman, 2000; Stigall, 2010a). During speciation by vicariance, the geographic range of an ancestral population is divided due to external factors with descendant populations occupying a subset of the ancestral range. A successful vicariance event is recognized when an isolated descendant population accrues sufficient phenotypic differences to be recognized as a distinct species in the fossil record. Vicariance events are identified as range constrictions between ancestor and descendant nodes on the cladogram. Speciation by dispersal occurs when a population actively migrates into an area geographically distinct from the ancestral range and undergoes speciation. This pattern is recognized by a range expansion or shift between nodes on the cladogram.

A series of speciation mode analyses have been conducted for brachiopod and trilobite clades that span the GOBE through the Richmondian Invasion interval (Dapingian through Katian Stages) (Wright and Stigall, 2013a; Bauer and Stigall, 2014; Lam, 2015). The relative amount of speciation attributable to vicariance versus dispersal varied both among clades and through time (Fig. 9). During the GOBE interval, dispersal was more common than vicariance, comprising 80% of identifiable speciation events during the Darriwilian Stage. Although only a minor fraction of total speciation events, the frequency and number of vicariant speciation events during this time is comparable to later intervals. Thus, the total number of speciation events during the GOBE was comparatively high and included both speciation modes. Some clades, such as the brachiopod genus *Glyptorthis*, exhibit alternating dispersal and vicariance events along branches of the cladogram (Fig. 9). The cyclic distribution of speciation types supports our earlier
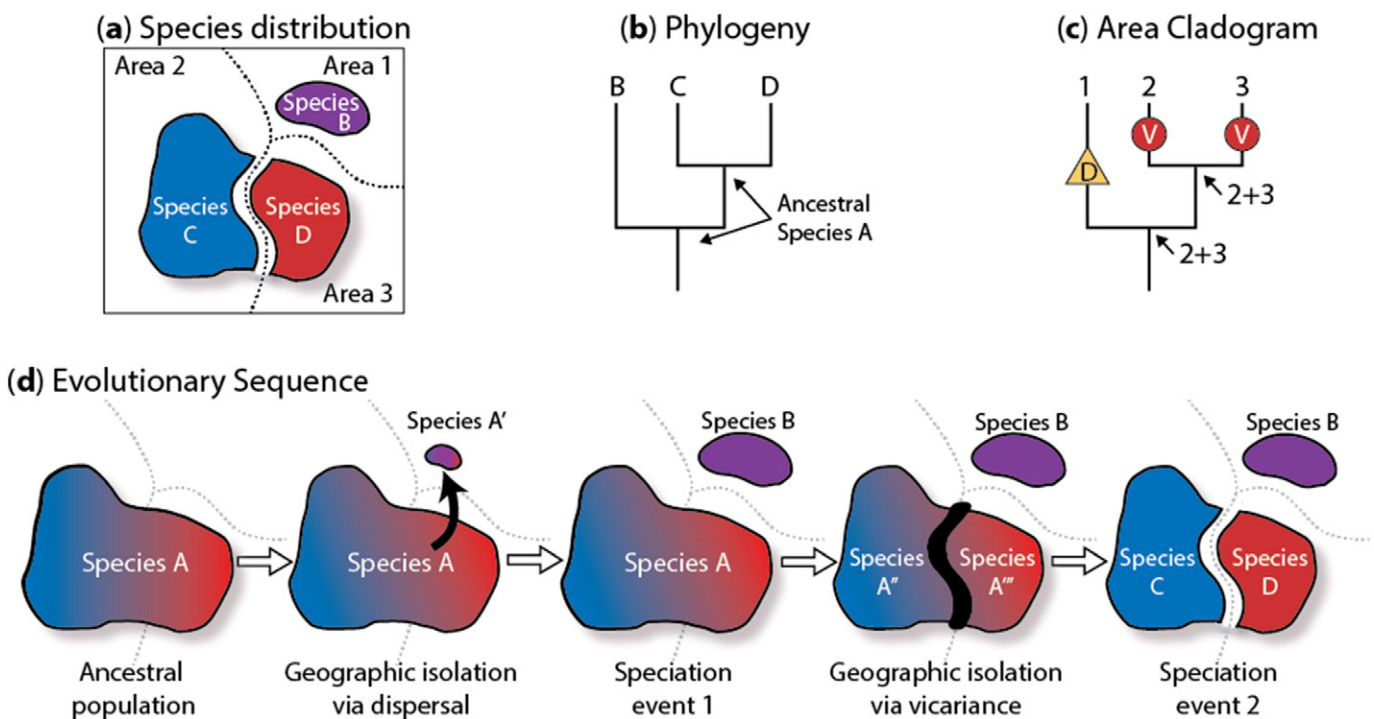

Fig. 8. Schematic representation of the relationship between geographic distribution, phylogeny, and speciation. (a) The observed distribution of three species (Species B, C, and D) among three areas (Areas 1, 2, and 3) which are separated by barriers indicated by dotted lines. (b) The evolutionary relationships among these three species and the hypothetical ancestor, Species A, a species that is not sampled in the analysis. (c) The area cladogram produced by substituting the names of the terminal species with their areas of occurrence. Ancestral distributions can be determined using the Fitch optimization outlined in Lieberman (2000) or another suitable optimization algorithm given the available data. Speciation mode is identified as dispersal (D) when the daughter species occupies an area different or additional to the ancestral distribution; whereas vicariance speciation (V) is identified when the daughter species occupies a subset of the ancestral range. (d) Evolutionary sequence of the geographic steps through which evolution proceeded in this clade. Modified from Stigall (2015).
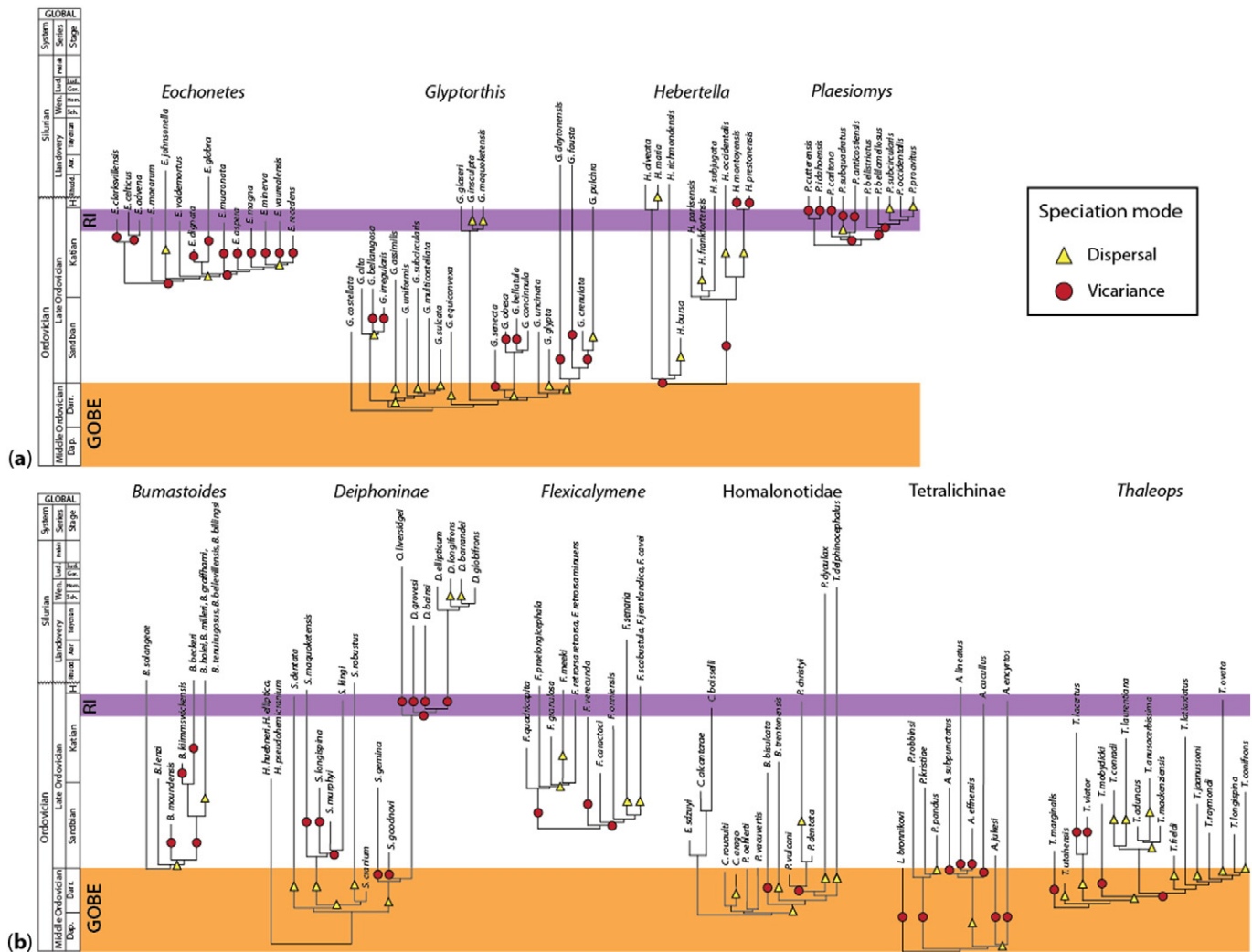
Fig. 9. Phylogenetic biogeography and speciation analyses of Middle to Late Ordovician brachiopod (a) and trilobite clades (b). Phylogenetic hypotheses were scaled to geologic time and ancestral nodes were optimized using Fitch Parsimony following Lieberman (2000). Red circles indicate events of speciation by vicariance, whereas yellow triangles signify speciation via dispersal. The orange shading indicates the time of the Great Ordovician Biodiversification Event (GOBE) and the purple shading indicates timing of the Late Ordovician Richmondian Invasion (RI) BIME (Fig. 4). Within the GOBE interval, speciation via dispersal makes up 80% of all recovered speciation events, consistent with the global nature of this particular BIME. During the Richmondian Invasion, few speciation events occur, but those that do are primarily vicariant. Speciation type alternates along branches within the phylogenies, as observed in *Glyptorthis, Hebertella*, and *Thaleops,* indicating that oscillating modes of speciation led to increases in diversity through geologic time as proposed in the cyclical model (Figs. 2, 3). Figure modified from Lam (2015).

interpretation that alternating BIME and vicariance events were operating during the GOBE interval to produce the dramatic rise in diversity as hypothesized earlier.

Vicariance events outnumbered dispersal events 2:1 during the interval between the GOBE and Richmondian BIMEs. The interval includes the Taconian Orogeny, which comprised two phases of mountain building, the Blountian and Taconic tectophases. These geologic events caused the continental crust to buckle upward forming subaerial arches that divided marine basins and dramatically altered the geographic distribution of habitats (Fig. 4) (Miller and Mao, 1995; Holland, 1997; Ettensohn, 2010). The uplift of these barriers enhanced isolation of shallow marine basins and promoted vicariant speciation (Fig. 9) (Wright and Stigall, 2013a; Lam, 2015).

The Richmondian Invasion interval is characterized by relatively few speciation events among the clades examined (Fig. 9). Unlike the GOBE interval, phylogenetic biogeographic analyses recovered no clear increase in dispersal speciation during the Richmondian Invasion. This is consistent with the observed speciation gap discussed above, which resulted in very few speciation events during this interval. Two species that do exhibit dispersal speciation during this interval, *Glyptorthis insculpta* and *Plaesiomys subquadratus,* both migrated into the

Cincinnati Basin during the Richmondian (Wright and Stigall, 2013b; Wright and Stigall, 2014). Thus, species participating in the Richmondian BIME reflect similar patterns as those in the GOBE.

Results from these phylogenetic biogeographic analyses, thus, are broadly congruent with model expectations: BIME intervals are characterized by limited speciation, whereas speciation rates increase markedly if dispersal is inhibited by basin separation. The alternation of the immigration and vicariance, such as during the GOBE, prompts rapid accumulation of new diversity.

4.4. Ordovician synthesis

Biodiversity, speciation, and immigration patterns recovered from analyses of Middle and Late Ordovician shallow marine faunas of Laurentia and nearby paleocontinents are congruent with our conceptual model for biodiversity accumulation. BIMEs homogenize faunas and decrease the propensity for allopatric speciation. This homogenization reduces β-diversity, but has limited impact on γ-diversity. High α-diversity arising from the spread of immigrant taxa during these intervals, however, is critical for biodiversity aggregation over longer periods. This is because higher α-diversity forms a pre-condition for
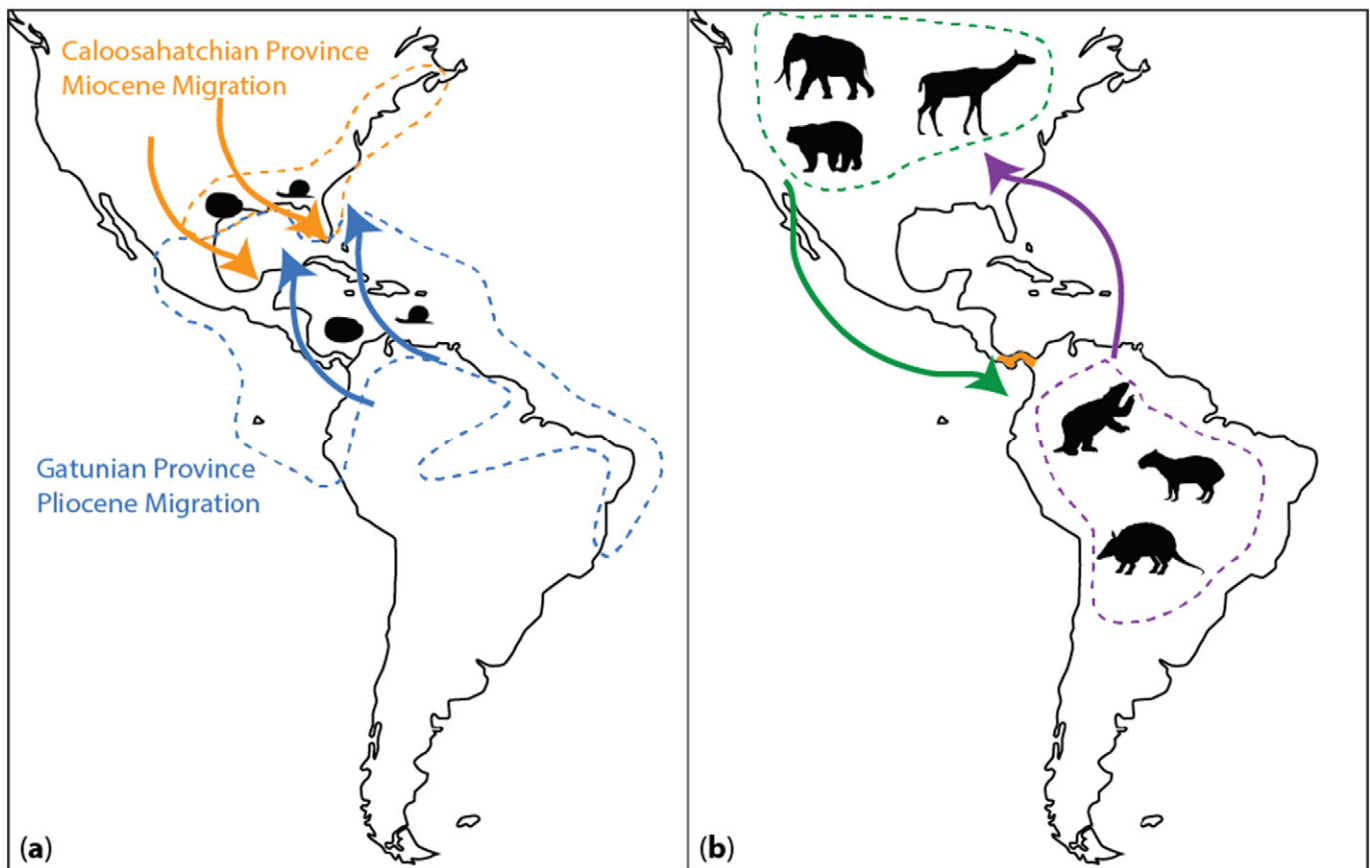
Fig. 10. Dispersal pathways of marine and terrestrial BIMEs between the Americas during the Cenozoic. (a) Molluscan provinces and migration patterns. Taxa from the Caloosahatchian Province migrated south during the Miocene (outlined in orange). Conversely, taxa moved northward from the Gatunian Province during the Pliocene (province outlined in blue). In general, α-diversity increased within each province during both migration episodes. Speciation following disconnection of dispersal pathways led to an increase in γ-diversity, which may partly explain the taxonomic richness in the phylum observed in this region today. Provincial boundaries modified from Vermeij (2005b). (b) The Great American Biotic Interchange (GABI) between North and South American involved the exchange of faunas across the Isthmus of Panama (outlined in orange) after its closure in the Pliocene. The GABI was strongly asymmetrical and more taxa successfully immigrated from North into South America than from South into North America. Subsequently, α-diversity increased more substantially within South America due to post-dispersal speciation, an outcome observed today in the many South American lineages with North American ancestors.

substantial amounts of speciation during the subsequent interval of regional isolation. It is during this vicariance interval that the formation of new species peaks, which produces increases in α-, β-, and γ-diversity. Establishing rapid and sustained increased in γ-diversity requires cyclical alternation of BIME and vicariance regimes, as exemplified by the GOBE interval. The relative impact of a single BIME scales with the geographic scope of the immigration event. Regional events, like the Richmondian Invasion, have a more limited impact than globally pervasive BIMEs, such as the GOBE.

5. Testing the model: BIMEs throughout geologic time

The following brief synopses of other BIME intervals provide additional data to assess the generality of the conceptual model's core prediction that alternating BIME and vicariance regimes are critical components of biodiversity accumulation.

5.1. The Great Devonian Interchange

The Great Devonian Interchange (GDI) (McGhee, 1997) is characterized by global immigration of shallow marine invertebrates among epicontinental basins that occurred during the Givetian and Frasnian Stages of the Devonian Period (388–372 Ma). This BIME was prompted by progressive sea-level rise through the Givetian Stage, which flooded continental barriers that had previously prevented species migrations (Fig. 2). Using detailed reconstructions of species' geographic ranges

for Laurentian brachiopod and bivalve species, Rode and Lieberman (2004) documented a clear link between inter-basinal invasion events, dramatic expansion in average species range size, and a loss of ecologically specialized taxa. Thus, the proximate impact of GDI was the reduction in endemicity, indicated by a decline in β-diversity and the subsequent establishment of a homogenous set of invasive species among basins—a pattern that has been reported in many clades (Johnson, 1970; McGhee, 1981; McGhee, 1996; McGhee, 1997; Stigall, 2010a; Stigall, 2012b). The faunal homogenization and dominance of ecological generalists reduced mechanisms for isolation (Stigall, 2012b) and facilitated a significant decline in speciation rates (Bambach et al., 2004; Alroy et al., 2008). Similar to the Ordovician case study, the Devonian speciation decline has been attributed primarily to a shutdown in vicariant speciation (Stigall, 2010a; Stigall, 2012b). Because this speciation decline was combined with slightly elevated extinction rates (McGhee et al., 2004), the GDI led to a decrease in β- and α-diversity in many locations around the world and a subsequent, severe decrease in γ-diversity on a global scale.

5.2. Neogene marine migrations and diversification

The Neogene Period (23.0–2.6 Ma) was a time of widespread BIMEs within marine ecosystems caused by to the reorganization of wind-driven currents due to Antarctic glaciations and the closing of marine gateways (Zachos et al., 2001; Zachos et al., 2008; O'Dea et al., 2016). One set of biotic exchanges among gastropod and bivalve faunas of

two biogeographic provinces, the Caloosahatchian Province of the southeastern United States and Gatunian Province of Central and South America, has been examined in particular detail (Vermeij, 1991b; Vermeij, 2005b; Vermeij, 2005a). During the Miocene and Pliocene Epochs, the molluscan biotas of these regions were highly distinct indicating limited faunal exchange (Petuch, 1982; Landau et al., 2008). However, two long-lived BIMEs occurred that temporarily linked these faunas. Each invasion was predominantly unidirectional (Vermeij, 2005b; Vermeij, 2005a), and directionality reversed between episodes (Fig. 10a). During the early to mid-Miocene Epoch (23.0–11.5 Ma) mollusks migrated southward, whereas migration occurred in the reverse direction during the Pliocene Epoch (5.33–2.6 Ma) (Vermeij, 2005b). The shift in directionality corresponds to changes in climatic and oceanographic conditions. The early Miocene BIME connected two tropical biotas during an interval when the circum-equatorial current was prevalent and inter-basinal Caribbean circulation was relatively limited (Roth et al., 2000; Vermeij, 2005b). The shift to a northerly dispersal route is coincident with the constriction of the Central American Seaway (O'Dea et al., 2016) and related intensification of the north-flowing western boundary current along the eastern edge of North America transporting warmer waters toward the Gulf Coastal Plain (Cronin and Dowsett, 1996; Crowley and Burke, 1998; Dowsett et al., 2009).

Both BIMEs increased α-diversity in the recipient region, had minimal impact on γ-diversity, and reduced provincial differentiation (β-diversity). Vermeij (2005b) noted that dispersal occurred relatively infrequently, which subsequently enabled successfully established immigrant populations to undergo taxonomic differentiation. This secondary speciation promoted increased β-diversity between the two faunal provinces and contributed to total γ-diversity increase that characterizes the Neogene (Johnson et al., 2007).

The progressive closure of the Central American Seaway also restricted (and later fully blocked) faunal exchange between the western Caribbean and eastern Pacific regions. Multiple lines of evidence (reviewed in O'Dea et al., 2016) indicate that the closing of the Central American Seaway and development of the Isthmus of Panama occurred gradually. Based on geochemical data, significant deep water connections were likely shut down by 9.2 Ma (Newkirk and Martin, 2009); however Pacific and Caribbean shallow waters did not become differentiated until 4.6 to 4.2 Ma (Osborne et al., 2014). Caribbean and eastern Pacific marine biotas remained similar until around 4 Ma (Woodring, 1966; Jackson et al., 1993; Landau et al., 2009), and phylogenetic and molecular data indicate a rise in diversification (α-diversity) and faunal divergence (β-diversity) between ~3 and 4 Ma (O'Dea et al., 2016). This faunal differentiation was produced via a combination of basin-scale speciation and limited extinction coincident with the separation of the Caribbean and Pacific regions due the emergence of the Central American Isthmus (Jackson et al., 1993; Landau et al., 2009; O'Dea et al., 2016). This accumulation of biodiversity (increase in α, β, and γ diversity) during a vicariance phase also matches the conceptual model.

5.3. Great American Biotic Interchange

One of the best-known continental BIMEs, the Great American Biotic Interchange (GABI) (Stehli and Webb, 1985) involved the migration of terrestrial mammals between North and South America in several pulses during the Pliocene and Pleistocene. Although a few species dispersed across the narrowing Central American Seaway starting around 9 Ma, the GABI is traditionally defined as the substantial faunal exchange via a terrestrial route following the emergence of the Isthmus of Panama during the Pliocene Epoch (Fig. 10b) (Simpson, 1950; Simpson, 1980; Flynn et al., 2005; Woodburne, 2010; Rincón et al., 2011; Croft, 2012). Recent analyses have identified four pulses of immigration (Woodburne, 2010). The main immigration pulse (GABI I) occurred between 2.2 and 2.4 Ma, starting with the migration of *Glyptotherium* into North America and *Neochoerus* into South America

(Woodburne et al., 2006); subsequent pulses of migration occurred at ~1.8, 1.3, and 0.8 Ma. Timing of the GABI was controlled primarily by climatic factors, notably the onset of Northern Hemisphere glaciation following the Pliocene Climatic Optimum and subsequent glacial pulses (Lisecki and Raymo, 2005; Mudelsee and Raymo, 2005; Sosdian and Rosenthal, 2009; Woodburne, 2010). During the glacial phase of the glacial-interglacial cycles, the Isthmus increased in areal extent due to sea level fall. Further, the cool, dry climate facilitated the dominance of savannah habitat on the Isthmus of Panama (Piperno, 2006; Woodburne, 2010). Such open habitats facilitate dispersal more effectively than closed tropical forests. As most migrating taxa were either adapted to savannah-like conditions or ecological generalists, the ecology of the migrants and the alignment of the immigration events with glacial pulses strongly supports a climate-driven dispersal mechanism (Woodburne, 2010).

Due to ecological gradients, North American taxa established viable populations in South America at a higher frequency than the converse (Vrba, 1992; Webb, 2006). Immediately following invasion pulses, β-diversity between North and South America declined and γ-diversity was largely unchanged. The expansion of tropical forest habitats during interglacial intervals, however, generated barriers and fostered vicariance and diversification of immigrant taxa, producing increases in all three diversity metrics. In general, speciation rates for North American lineages that became established in South America were higher than for taxa that dispersed northward (Webb, 2006; Woodburne, 2010). Consequently, the GABI increased α-diversity within South America substantially (Marshall et al., 1982; Cody et al., 2010), but α-diversity increased only modestly in North America. The post-GABI South American biota resembled the North American biota at a much higher level than the pre-GABI biota (Simpson, 1950; Vrba, 1992; Webb, 2006). Thus, the ultimate impact of the GABI was to reduce β-diversity between the two continents, increase α-diversity-particularly in North America, and increase γ-diversity overall.

5.4. Synthesis of diversity in geologic time and BIMES

Each of the case studied reviewed supports the general tenants of the theoretical model. However, it is also clear that the relationship between BIMEs and biodiversity accumulation is regulated by biotic constraints and contingent factors, such as the initial conditions and characteristic rate of environmental and tectonic changes (Table 1). In general, an individual BIME increases α-diversity within each recipient region and decreases β-diversity between regions. When BIMEs alternate with vicariance intervals, these outcomes are amplified. Impacts of BIMEs on γ-diversity were more variable, which can be explained as a function of extinction versus speciation among local populations. Speciation is limited after BIMEs due to the reduction in geographic isolation and increased extermination of incipient species from competition with ecologically generalized invasive species. Extirpation of ecologically specialized species often follows waves of species invasion. However, a sustained and statistical increase in extinction rates was not observed following any of the BIMEs surveyed. Thus, BIMEs function to produce local diversity and establish pre-conditions for diversification, but it is the later separation of regions that facilitates the development of novel biotic diversity in terms of new species.

6. Linking BIMEs, speciation, and taxon pulses

A common feature of the BIMEs reviewed in this paper is that the intervals of biotic interchange do not directly impact γ-diversity. This is because the immigration events themselves do not facilitate lineage-splitting events. Speciation occurs predominantly within vicariance intervals between BIMEs. Instead, episodes of geographic range expansion impact biodiversity mainly by establishing additional populations and/ or by facilitating population persistence.

Table 1
Summary table of the attributes of BIMES in geologic time.

BIME	Taxa involved	Potential cause(s) of migration	Impact on α-diversity	Impact on β-diversity	Impact on γ-diversity	Relationship to conceptual model
Great Ordovician Biodiversification Event 470–458 Ma	Shallow marine invertebrates	Cooling climate, increased oxygenation in atmosphere and oceans, sea level transgression	Increase	Low during invasion intervals, increase when basins isolated	Rapid increase followed by a slowdown	Follows full model. Initial dispersal (basin connectivity) produces low β-diversity, subsequent phases of vicariance (basin disconnection) promote speciation and increased α-diversity. The final result after several cycles is a tremendous increase in γ-diversity.
Richmondian Invasion ~448 Ma	Shallow marine invertebrates	Sea level rise, climate change, return to tropical carbonate deposition in Cincinnati Basin	Increase	Decrease	Stable	Follows phase 1 of the model. Dispersal without vicariance leads to increased α-diversity within Cincinnati Basin, β-diversity, and a stable γ-diversity. The effects of this BIME are manifested only at the regional-scale.
Great Devonian Interchange 388–372 Ma	Shallow marine invertebrates	Sea level rise flooded continental arches and removed thermal barriers	Decrease	Decrease	Decrease	Follows phase 1 of the model on a global scale. Rampant dispersal without vicariance on a global scale depresses α- and β-diversity, and subsequently contributed to a dramatic decline in γ-diversity.
Neogene mollusk migrations and diversification 23–3 Ma	Shallow marine invertebrates	Increased thermal gradient, intensification of ocean currents bringing warmer water north, progressive restriction of Central American Seaway (CAS)	Increase in recipient regions	Decrease initially, then increase following post-isolation speciation	Increase following post-isolation speciation	Follows full model. Initial migrations into biogeographic provinces increased α-diversity and reduced β-diversity with limited γ-diversity impact. Vicariance after closure of the CAS promoted vicariance phase which increased all three diversity metrics.
Great American Biotic Interchange 2.4–0.8 Ma	Terrestrial vertebrates	Shifting climate belts during glacial-interglacial cycles, expansion of savanna habitats	Stable within North America; increased in South America	Decrease initially, then increase following speciation	Increase following post-isolation speciation	Follows full model. Initial migrations increased α-diversity in recipient regions and reduced β-diversity between continents. Subsequent speciation post-establishment, particularly in North America, led to an overall increase in γ-diversity. Cycle repeated during multiple waves of invasion.

The limited number of speciation events during intervals of geographic expansion runs counter to a classic expectation that changes in the local environment will instigate speciation within taxa (Janz et al., 2001; Hoberg and Brooks, 2008). This historical expectation was conditioned on the conceptual framework that species are always tightly adapted to a set of preferred environmental conditions. Such tightly adapted species would have difficulty inhabiting new geographic regions without undergoing adaptive change, thus establishing speciation as an expectation. However, recent syntheses (Hoberg and Brooks, 2010; Hoberg and Brooks, 2013) have challenged this historical expectation and instead have promoted the idea that that most species have substantial amounts of flexibility in ecospace utilization, a concept formalized as "sloppy fitness space" (Brooks and Agosta, 2012). Under this paradigm, species have substantial flexibility to occupy geographic spaces with various combinations of ecological parameters by using "ecological fitting" (Janzen, 1975; Agosta, 2006).

However, both paleontological case studies and modern invasion biology indicate that only species with moderate to broadly generalized ecological niches are likely to become established during BIMEs. In modern ecosystems, only 10% of species introduced to novel environments are able to found populations, and only 10% of those established populations are large enough to be considered invasive (Lockwood et al., 2009). Species more likely to succeed are those with broader ecological niches (Hastings et al., 2004; Briggs, 2007; Lockwood et al., 2009; Simberloff et al., 2013) and thus greater capacity for "ecological fitting." Becoming successfully established during an ancient BIME further required that species were able survive transport, either as larvae or adults, between distant geographic areas. Broad ecological niches and high larval dispersal ability has been reported for invasive taxa of the Richmondian Invasion (Stigall, 2010b; Lam and Stigall, 2015) and the Great Devonian Interchange (Rode and Lieberman, 2004; Stigall Rode and Lieberman, 2005). The Richmondian Invasion also preserves a clear pattern of ecological fitting (Brame and Stigall, 2014; Stigall, 2014). The nature of ecological fitting in relatively generalized

immigrant taxa limits speciation and γ-diversity increase during BIME intervals; however, the dispersion of populations into new geographic regions increases species richness within local communities and establishes pre-conditions for possible speciation events following the vicariance phase.

Within our conceptual model, speciation events are largely restricted to intervals when geographic regions undergo vicariance. The separation of geographic basins necessarily limits genetic flow between populations for most species. If ecological conditions among basins differ, then the separated populations may diverge and form separate species. Successful establishment of new species, in this context, is governed by local conditions within the basin and may incorporate aspects of density dependence (Rabosky, 2013; Rabosky, 2016). Speciation events are typically correlated with environmental changes (e.g., Badgley et al., 2016); thus speciation rate is expected be highest immediately following isolation and then decline with time.

Importantly, it is the alternation between BIME and vicariance intervals that provides the mechanism for substantial diversity accumulation. BIMEs facilitate the dispersal of species among many basins, which establishes many broadly distributed taxa within each region as well as disparity among faunas of the geographic regions. If these geographic regions are subsequently isolated by regional vicariance, species in each region can undergo independent evolution potentially resulting in greater γ-diversity for the entire system. Dispersal and vicariance regimes alternate like an epic seesaw. This alternation provides a mechanistic framework to explain frequently observed taxon pulse dynamics in the evolutionary history of clades (e.g., Erwin, 1985; Folinsbee and Brooks, 2007; Hoberg and Brooks, 2010; Badgley et al., 2016)

7. Implications for the modern biodiversity crisis

The introduction and spread of non-native species are primary contributors to biodiversity loss and ecological restructuring in modern

ecosystems (Barnosky et al., 2011; Simberloff et al., 2013; Sutherland et al., 2013; Galiana et al., 2014; Blois et al., 2013). Although modern species invasions are mediated by human activity, the conceptual model and examples discussed herein can provide insight for developing predictive models and strategies for biodiversity maintenance and protection. Dissecting the details of the complex relationships between species richness and regional differentiation is critical for accurate projections of biodiversity (Stigall, 2012a; Hoberg and Brooks, 2013) and for conservation planning (McGuire and Davis, 2014; Dubois et al., 2016; Socolar et al., 2016). Key implications are:

1. **The centrality of alternating dispersal and isolation phases for generating diversity.** Conservation efforts should recognize the importance of providing pathways for immigration and dispersal of species (e.g., Taylor et al., 1993; Dubois et al., 2016). Preservation of dispersal pathways will permit species with moderate ecological niche breadth to track their preferred habitats and maintain healthy population sizes. Maintaining these corridors is crucial for conservation efforts as climate rapidly changes. Relatedly, identify and conserve potential geographic locations that can serve as refugia for species with more specific habitat requirements. In the geologic past, refugia have functioned as museums to sustain α-diversity during unfavorable climatic conditions. These sites may later become regions of speciation during intervals of isolation and sources of immigration during favorable climatic intervals (Hewitt, 2000; Davis and Shaw, 2001; Gavin et al., 2014).

2. **Magnitude of biotic immigration events correlates with impact of the invaders on biodiversity**. Limited extinction of ecologically specialized species occurred following regional BIMEs, but primary outcome of regional invader establishment was increased α-diversity, reduced β-diversity, and limited impact on γ-diversity. This pattern is congruent with studies of modern biological invasions that find introductions of (non-predatory) species rarely result in species extinctions (e.g., Gurevitch and Padilla, 2004; Briggs, 2007; Sax et al., 2007). Our data suggest the same pattern may also hold at evolutionary timescales. However, the globally pervasive GDI resulted in a loss of endemism (expressed as reduced β-diversity) to the point of hosting a single cosmopolitan fauna, which precipitated a biodiversity crisis (McGhee, 1996). Faunal homogenization, another pattern observed on ecological timescales of modern invasions (McKinney and Lockwood, 1999; McKinney and Lockwood, 2001; Smart et al., 2006), thus may have dramatic impacts over evolutionary timescales.

3. **Speciation is restricted to intervals of isolation and is depressed during invasions.** Similar to modern invasive species (McKinney and Lockwood, 1999; McKinney and Lockwood, 2001), immigrant taxa in the geologic past were typically characterized by relatively broad ecological niches. These non-native species utilized portions of their available niche space ("sloppy fitness space") to persist in the novel environments without undergoing speciation. Data from the fossil record indicate that capacity for geographic range expansion without concomitant adaptive changes is high among many types of organisms.

Indirect impacts of human-mediated climate change will generate dispersal pathways and isolation for taxa in specific areas. The conversion of natural environment into anthropogenically-modified landscapes has the potential to produce isolation required for lineage divergence, but because population sizes are simultaneously reduced, habitat fragmentation is more likely to result in extinction rather than successfully establish new species. In regions densely populated or modified by humans, native species migration will be diminished due to lack of natural migration corridors. However, it is possible that climatic changes in regions with more limited direct human modification, like the Arctic, may result in patterns similar to those observed in the fossil record over the next several thousand years.

8. Conclusions

Biodiversity accumulates separately at the local (α) and global levels (γ) via processes that are mediated by geographic connectivity, isolation, and regional (β) differentiation. The fossil record includes a rich archive of Biotic Immigration Events (BIMEs) and provides insight into how diversity is assembled over evolutionary timescales. We reviewed five BIMEs ranging from Paleozoic marine to Plio-Pleistocene terrestrial immigration events. Although each case study presented certain idiosyncrasies, major patterns recurred across all examples. Intervals of active immigration are characterized by minimal to no successful speciation events, increased species richness within regions, reduced differentiation among areas, and limited impact on global species richness. Once the dispersal pathways disconnect and areas become isolated, speciation within basins increases, which results in greater α-, β-, and γ-diversity. Case studies in which dispersal and vicariance regimes alternate, such as the Great Ordovician Biodiversification Event, exhibit profound global diversity increases.

Although the diversity partitions (α, β, γ) each increase and decrease within different contexts and under distinct ecological pressures, they are linked through biogeographic processes. Migration events alone are insufficient to produce biodiversity accumulation. However, BIMEs are important facilitators of geographic range expansion, which produces widespread species and establishes the foundation on which speciation processes can operate during the next interval of regional isolation. The production of broadly distributed species is a significant by-product of immigration events, as species with broader ranges are most extinction resistant than species with narrow ranges (Rode and Lieberman, 2004; Jablonski, 2008; Darroch and Wagner, 2015; Saupe et al., 2015).

Oscillation of area connectivity and isolation can generate a robust and effective mechanism for both substantial accumulation of new biodiversity and persistence of existing species. Paleontological studies can provide a baseline context for understanding the magnitude of the current biodiversity crisis, assist in mitigation efforts by identifying critical areas for protection, and utilize 'deep time' data to help shape long-term conservation strategies.

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