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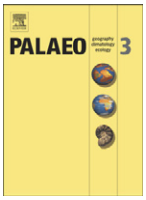

Using ecological niche modeling to assess biogeographic and niche response of brachiopod species to the Richmondian Invasion (Late Ordovician) in the Cincinnati Arch

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ABSTRACT

Within the Cincinnati, Ohio region, the beginning stage of a large-scale biotic invasion is recorded in the C4 depositional sequence (Late Ordovician, Richmondian Stage), which includes the Arnheim Formation and its correlates. The fauna and strata of this region are well studied and the ecological changes present provide a unique opportunity to study biogeographic changes associated with the onset of a biotic invasion. In this study, GIS-based ecological niche modeling (ENM) is used to examine the biogeographic and paleoecological impacts of the biotic invasion during the C4 sequence. In particular, this study assesses whether species respond to invasion pressure through niche conservatism (exhibiting stasis and maintaining the parameters of their ecological niche through time) or niche evolution (altering the ecological parameters of their niche through adaptation).

Ranges of ten rhynchonelliform brachiopod species were modeled for three temporal intervals within the C4 sequence. Modeled ranges provide the basis for quantitatively assessing the shifting roles of native and invasive species throughout the C4 sequence. GARP (Genetic Algorithm for Rule-set Prediction), a computer-learning based ENM program, was used to model species' ecological niches from environmental data as estimated from sedimentological variables associated with known species occurrence data. Once environmental parameters of the niche were modeled, the resulting rule set was used to project the geographic boundaries of potential habitat and estimate the spatial extent occupied by each species. Three prominent trends are apparent within the fauna. (1) Generalist species tended to track their preferred ecological niches closely from the early into the middle time slice and maintained or expanded the size of their geographic range during this transition. (2) Ecologically specialized species exhibited decreasing geographic range size through the sequence and were more likely to shift geographic areas inhabited within the study area. (3) The amount of niche evolution increased as the invasion progressed; species that adapted to the new biotic regime though niche evolution persisted through the invasion interval while species with high levels of niche conservatism did not.

During early C4 sequence, species respond individualistically to changes in abiotic conditions (shallowing upward), but do so primarily by tracking their previously preferred environmental conditions laterally and maintain high fidelity of niche dimensions through time. This matches the null hypothesis that species will exhibit niche conservatism during intervals of slow or gradual environmental change. Following the geologically sudden introduction of the intrabasinal invaders in the second half of the C4 sequence, native species responded to the combined abiotic (shallowing upward) and biotic (invader introduction) changes in the Cincinnatian environmental by altering the parameters of their ecological niches and through fundamental changes in geographic distribution. Extrapolating these results to modern ecosystems, suggests that most species should exhibit niche conservatism and habitat tracking in response to gradual changes in environmental conditions, while species should exhibit niche evolution and adaptive response following rapid environmental changes. Furthermore, modern species with reduced potential for adaptive response may also be the most susceptible to extinction.

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1. Introduction

Within the Cincinnati, Ohio region, the Late Ordovician strata of the C4 depositional sequence (Arnheim Formation and its correlates) record the beginning stages of a large-scale biotic immigration event, the Richmondian Invasion. Both the fauna and the strata of this interval have been studied extensively since the early 1900s (ex., Brett and Baird, 1997; Foerste, 1912; Holland, 1990; Nickles, 1902; Patzkowsky and Holland, 1996; Wolford, 1930), and the paleoecological changes that occur at the onset of the Richmondian Invasion are so substantial that they were once thought to mark the boundary between the Ordovician and Silurian (e.g., Foerste, 1912; Shideler, 1916; Ulrich, 1914). In this paper, the early stages of the Richmondian Invasion are examined by analyzing biogeographic patterns in ten species of articulated brachiopod before, during, and after the onset of the invasion within a paleoecological context.

The Richmondian Invasion occurred in several pulses over the course of the approximately 750,000 year long C4 depositional sequence (Holland and Patzkowsky, 1996). Migrant taxa that entered the Cincinnati region during the Richmondian Invasion include numerous species of brachiopods, bryozoans, mollusks, arthropods, corals, and echinoderms (e.g. Foerste, 1912; Holland, 1997). Particularly notable are the introductions of species belonging to the orders Rugosa and Rhynchonellida, as no representatives of these clades had been present in the Cincinnati region for at least two million years prior to their reintroduction (Stigall, 2010). The immigrant taxa have been considered to have entered the region from either the warmer paleoequatorial waters of the western United States and Canada (Holland and Patzkowsky, 2007) or marginal basins along southern Laurentia (Jin, 2001, pers. comm.) At the start of the C4 sequence, the taxonomic communities and paleoecological structure were very similar to those of the first three Cincinnatian sequences (C1–C3) and exhibit low levels of faunal turnover (Holland, 1997; Holland and Patzkowsky, 2007). Rates of faunal turnover increased during the C4 sequence following the onset of the Richmondian Invasion (Holland and Patzkowsky, 2007). The first wave of the invasion was marked by ecological epibole beds, horizons containing high concentrations of a single species present only for an abbreviated time (Brett and Baird, 1997; Foerste, 1912), which are dominated by invader species, such as *Retrorsirostra carleyi* and *Leptaena richmondensis*. The community structure during the second half of the C4 sequence resembled that of the overlying C5 and C6 sequences, which exhibit the post-invasion fauna and paleoecological structure (Holland, 1997; Holland and Patzkowsky, 2007). By the early C5 sequence, the invader taxa had become well established in the Cincinnatian ecosystem as evidenced by both the presence and high relative abundance of numerous invasive species (Anstey, 1986; Holland, 1997; Holland and Patzkowsky, 2007).

The Richmondian Invasion provides a unique opportunity to analyze species-level paleobiogeographic patterns during a large-scale biotic invasion within a sequence stratigraphic framework. In this study, changes in the geographic ranges of individual brachiopod species are quantified during three intervals in the C4 sequence using an ecological niche modeling (ENM) approach. Using ENM, a species' niche is modeled as the set of environmental conditions under which that species can survive and maintain a population. Defined in this way, a species ecological niche is equivalent the fundamental niche *sensu* Grinnell (1917), the prospective niche *sensu* Valentine (1968, 1969), and the Grinellian niche *sensu* Soberón (2007) ENM methods model a species' niche by estimating the physical parameters that constrain the niche from a set of known species occurrence points within the context of the environmental conditions present at those locations (Stockwell and Peters, 1999). The ecologic limits of the modeled niche can then be projected into geographic space and the potential geographic distribution of the species within the region can be analyzed. Patterns of range shift, expansion, and contraction can be quantitatively assessed and compared temporally (Stigall and Lieberman, 2006; Stigall, 2008). The ability to quantify change in range size and location allows elucidation of species-level paleobiogeographic patterns within an ecological context during the C4 sequence.

To date, ENM analyses of fossil taxa have been successful with both shallow marine organisms (Devonian invertebrates: Stigall Rode and Lieberman, 2005; Maysvillian brachiopods: Walls and Stigall, in review) and terrestrial organisms (Miocene horses: Maguire and Stigall, 2009). By estimating species ranges by combining sedimentological data with species occurrences, many of the sampling errors associated with using raw species range data can be mitigated (Stigall, 2008). While outcrop availability does control the quality and quantity of environmental data available in the fossil record, the density of species occurrence data and type of environmental parameters available are similar to the modern record. The modeling system in this study, GARP, is designed for data that is neither uniform nor evenly distributed (Stockwell and Peters, 1999); consequently, this technique is very appropriate for densely sampled paleontological data sets.

In this study, we reconstruct the geographic ranges for ten species of rhynchonelliform brachiopods across three sequence stratigraphically-defined time slices within the C4 sequence. Using ENM, the geographic ranges of native and invader species are reconstructed in order to determine whether species exhibit range expansion, contraction, or stable range size during the invasion interval. Spatial shifts in geographic range between time slices are quantified to examine whether brachiopod species exhibit shifting habitat preferences following the onset of the Richmondian Invasion. Lastly, the relative amount of habitat tracking and niche evolution is investigated for those native species that persist following the onset of the invasion. In particular, this study assesses whether native species responded to invasion pressure through niche conservatism, which involves maintaining the parameters of their ecological niche through time (= ecological stasis) and habitat tracking, or via niche evolution (altering the ecological parameters of their niche through adaptation).

1.1. Geologic setting

During the Late Ordovician, a shallow marine siliciclastic ramp, which sloped from southwest to northeast, was present in the Cincinnati region (Brett and Algeo, 1999; Holland, 1993). Paleogeographically, the study area was located between 20 and 25° south of the equator in the subtropical zone and rotated approximately 45° clockwise relative to its current orientation (Brett and Algeo, 1999). The ramp was bordered on the east by the Taconic foreland basin and on the west by a peripheral bulge (Brett and Algeo, 1999). The weathering of the Taconic highlands, which formed when the Taconic allochthon collided with the southern margin of Laurentia (Ettensohn, 1992), provided the fine grained siliciclastic sediments that accumulated in the Cincinnati region (Brett and Algeo, 1999).

Cincinnatian strata are composed of alternating shale (mudstone) and limestone layers (Hay et al., 1992). Shale layers represent the background deposition of sediments weathered from the Taconic highlands under quiet water conditions (Frey, 1987). Limestone layers include skeletal packstones and grainstones, which represent storm-winnowed lag deposits resulting from subtropical hurricane activity (Brett and Algeo, 1999; Jennette and Pryor, 1993). The relative abundance of storm layers serves as a basic proxy for water depth. In offshore facies, shale beds are dominant and little to no limestone is present due to deposition below normal storm wave base (Jennette and Pryor, 1993). The percentage and thickness of limestone beds increases as water depth decreases. Areas of quiet water deposition accumulate only the background sediments, which are mostly clay-sized particles (Brett and Algeo, 1999); whereas shallow water depositional environments are dominated by limestone layers due to constant perturbation winnowing away fine sediments (Frey, 1987).