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The effects of the Richmondian invasion on benthic invertebrate functional diversity during the Late Ordovician

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Rising temperatures and globalization are enabling widespread biotic invasions today, particularly in marine environments. While the long-term consequences of invasion are poorly understood, the fossil record can be used to assess the impacts of past invasions on ecosystem structure and functioning on evolutionary timescales. During the Late Ordovician (Katian), ~445.25 million years ago, deglaciation and subsequent rising sea level connected formerly isolated shallow epicontinental seas, facilitating the invasion of over 75 genera through larval dispersal in several pulses known as the Richmondian Invasion. Here we examine 1,139 species from these benthic marine communities of the Cincinnati Arch (USA) to quantify the effects of invasive species on functional diversity, which has been shown to influence ecosystem dynamics, stability, productivity, and functioning. Changes in functional diversity were quantified across six 3^{rd}-order stratigraphic sequences to assess the impacts of invasion using functional traits readily identifiable in fossil taxa: tiering above the substrate, feeding mode, motility/attachment, structural robustness, trophic rank, vision, and body form. We find that despite well documented changes in community composition, the arrival of invaders did not significantly add new functional entities or dramatically alter functional diversity, and invaders largely occupied pre-existing functions. While there were changes across the invasion, community structure ultimately returned to a state similar to the pre-invasion community. This suggests that despite changes in community composition across the Richmondian Invasion, ultimately the invasion did not substantially restructure functional diversity, as we observed little change in the number of functions, functional redundancy and over redundancy, vulnerability, and the distribution of species among functional entities. These findings emphasize the decoupling of changes in community composition and functional diversity, and the importance of functional diversity in assessing the potential ecological impacts of marine invasions today.

KEYWORDS

invasion, invasive species, paleo community, paleoecology, traits

1 Introduction

Biotic invasions are a growing global threat to biodiversity and ecosystem health and are becoming more widespread due to anthropogenic climate change (Lovell et al., 2006). Although marine ecosystems are far less studied relative to those in other environments (Rilov and Crooks, 2009; David et al., 2017; Luypaert et al., 2020), invasive species spread easily in marine ecosystems due to the interconnected nature of ocean basins enhanced by canals and larval dispersion (Cowen and Sponaugle, 2009). The establishment of nonnative taxa frequently alters essential ecosystem properties (e.g., nutrient cycling and productivity) and can impact ecosystem functioning (Vitousek, 1990; Lodge, 1993; Mack et al., 2000; Simberloff, 2014). However, previous studies have typically focused on how a particular invader impacts other species (David et al., 2017; Mollot et al., 2017), relying largely on species richness and changes in relative abundance (Pimm, 1979; Drossel and McKane, 2003; Stouffer et al., 2012), and fail to capture changes in community functioning and structure (Strogatz, 2001; Roopnarine et al., 2009). In addition, neontological data preceding invasions are rare, making changes in community structure difficult to quantify (David et al., 2017). Geohistorical archives and fossils are the most obvious and widely accessible records of past ecosystem conditions predating human activities on decadal-to-millennial timescales, and can provide information on the long-term impact of invasive species, as well as pre-invasion conditions (Jackson et al., 2001; Willis and Birks, 2006; Willis et al., 2007; Kidwell, 2013; Dietl et al., 2015; Tyler and Schneider, 2018). Therefore, paleocommunities present suitable opportunities to test hypotheses about the effects of invasion on benthic marine paleocommunity structure and functioning in an ancient ecosystem, on evolutionary timescales.

Deglaciation caused sea level to rise during the Late Ordovician, connecting previously isolated shallow Laurentian epicontinental seas (Patzkowsky and Holland, 1997; Holland and Patzkowsky, 2007; Malizia and Stigall, 2011), facilitating an influx of > 75 nonnative genera, including mollusks, arthropods, brachiopods, and cephalopods, from the surrounding basins into the Cincinnati arch via larval dispersal (Holland, 1997; Stigall, 2012, 2023; Stigall and Fine, 2019; Stigall et al., 2019; Little and Brett, 2025). This well-known event spanned approximately seven million years, occurring in several pulses during the Richmondian Stage (~445 Ma) (Foerste, 1917; Patzkowsky and Holland, 1996, 2007; Holland, 1997; Holland and Patzkowsky, 2007; Stigall and Fine, 2019), and is classified as a coordinated invasion due to the concurrent immigration of multiple species groups from one geographic area to another from which they were previously isolated by geographical barriers (Stigall, 2019). The Richmondian Invasion is thought to have led to differential survival of various taxa, restructured community gradients, increased niche partitioning, increased taxonomic and ecological diversity within communities, and depressed speciation (Holland and Patzkowsky, 2007; Malizia and Stigall, 2011; Tyler and Leighton, 2011; Brame and Stigall, 2014; Stigall and Fine, 2019), which may have contributed to complete ecosystem restructuring (Patzkowsky and Holland, 1996, 1997, 2007; Dudei and Stigall, 2010; Stigall, 2010, 2012; Malizia and Stigall, 2011). However, previous studies have focused primarily on changes in taxonomic abundance or richness, i.e., community composition (but see, Forsythe and Stigall, 2023; Kempf et al., 2020), which does not necessarily equate to structural or functional change (Bambach et al., 2007; Bush et al., 2007; Bush and Bambach, 2011). As invaders can succeed at any trophic level, changes in trophic structure are frequently observed (Byrnes et al., 2007; Gido and Franssen, 2007; Romanuk et al., 2009; Comte et al., 2017; David et al., 2017). Trophic roles reflect key aspects of species ecological functions, and shifts in trophic roles can alter overall functional diversity and community dynamics. Here we quantify and examine these trends in functional diversity in response to the Richmondian Invasion.

Functional diversity, the number and types of functions performed by organisms in a community (Díaz and Cabido, 2001), influences ecosystem dynamics, stability, productivity, and functioning (Tilman et al., 1997; Hooper et al., 2005). Functional diversity may also be a better predictor of ecosystem stability and health than species richness (Tilman et al., 1997; Charvet et al., 2000; Hulot et al., 2000; Díaz and Cabido, 2001; Heemsbergen et al., 2004; Hooper et al., 2005; Norling et al., 2007; Schleuter et al., 2010; Cadotte et al., 2011; Mouillot et al., 2011; Villéger et al., 2011; Bellwood et al., 2012; Naeem et al., 2012; Lefcheck and Duffy, 2015) thus it is increasingly utilized today in ecosystem monitoring and management to assess anthropogenic effects (Burnham, 1993; Bremner, 2008; Garaffo et al., 2018; Rand et al., 2018; Durant and Otto, 2019; Liu et al., 2019). Functional diversity has also been used to examine the effects of both invasions (e.g., Britton-Simmons, 2006; Shuai et al., 2018; Renault et al., 2022) and extinction (e.g., Petchey, 2000; Buisson et al., 2013). However, these studies are typically limited in temporal and spatial scale and have traditionally focused on commercial fishery data (e.g., Steele, 1991; Villéger et al., 2010; Buisson et al., 2013; Stuart-Smith et al., 2013; Toussaint et al., 2016; Shuai et al., 2018), with few studies of benthic invertebrates (e.g., Bremner et al., 2003). Functional diversity can be measured using a widely applied quantitative trait-based approach assessing unique combinations of functional traits known as Functional Entities (FEs) (Villéger et al., 2008, 2011; Mouillot et al., 2011, 2013; Magneville et al., 2022). Traits are measurable properties of organisms describing their morphology, physiology, and behavior (McGill et al., 2006; Violle et al., 2007, 2014), making them useful in many aspects of modern ecology and conservation management as they are linked to ecosystem processes, and can be used to assess whole-ecosystem functioning (Tilman et al., 1997; Hooper et al., 2005; McGill et al., 2006; Bremner, 2008). Many traits can be readily obtained for fossil species, for example living habit or feeding type, characteristics that are associated with ecosystem processes such as nutrient cycling, sediment transport, productivity, and trophic support (Walker, 1992; Loreau, 2004; Bambach et al., 2007; Bush and Bambach, 2011; Bush and Novack-Gottshall, 2012). Biological traits can also be studied across taxonomic groups and over large geographic scales, as traits are independent of taxonomic affiliation and can be shared by organisms from phylogenetically distant groups (Doledec and Bernhard, 1994; Charvet et al., 2000;

Usseglio-Polatera et al., 2000; Statzner et al., 2001; Bremner et al., 2006).

Benthic marine ecosystems in the Ordovician present an ideal system for the application of trait-based approaches, as benthic macroinvertebrates dominated the paleocommunity, which was devoid of large predatory fish and other vertebrate predators (Servais et al., 2009; Villéger et al., 2011; Harper et al., 2015). Macrobenthic faunas strongly influence biogeochemistry, e.g., fluxes of carbon and oxygen, as well as nutrient cycling and decomposition of dead organic matter (Officer et al., 1982; Snelgrove et al., 1997; Snelgrove, 1998; Austen et al., 2002; Norling et al., 2007). They contribute to biogeochemical processes through activities such as feeding, burrowing, and tube building, thereby helping to maintain the structure and functioning of ecosystems (Kristensen et al., 2012; Ortega-Cisneros et al., 2017; Zhang et al., 2020). Burrowing organisms, for example, can alter sediment conditions, resuspend fine particles in the water column, change grain size distributions, oxygenate sediments, and increase the sediment water content (Rhoads, 1974; Meadows and Meadows, 1991; Constable, 1999; Norling et al., 2007). In addition, burrowing facilitates the transport of buried organic matter and nutrients, bringing them to the surface and promoting decomposition and supporting benthic communities (Rhoads, 1974; de Wilde, 1991; Aller and Aller, 1998; Constable, 1999; Anderson et al., 2013). Given the importance of benthic macroinvertebrates in biogeochemical cycles in the Ordovician, we examined seven common functional traits in these animals that are linked to ecosystem processes and that can be readily described for fossil taxa: tiering in relation to the substrate, feeding habit, motility/degree of attachment, structural robustness, trophic rank, vision, and body form.

How species are distributed among functional entities has important consequences for ecosystem functioning, as a loss of species does not always equate to a loss of functions. Invading taxa may be accommodated within pre-existing functions, add new functions, or alter the distribution of species among functional entities. High functional redundancy, when multiple species perform similar functions in an ecosystem (Mouillot et al., 2011, 2013, 2014; Villéger et al., 2011), can provide insurance toward maintaining functional diversity despite species loss, thereby providing greater resilience to disturbance (Naeem, 1998). Conversely, vulnerable functional entities with low redundancy are maintained by only a few or lone species (Bremner, 2008). When invaders arrive in a region, they may perform new functions not represented in the recipient community, adding functions and increasing functional diversity (Hoehn et al., 2008; Novotny et al., 2010; Matsuzaki et al., 2013; Cavalcante et al., 2022). However, if invaders replace native species or alter the environment, thus potentially decreasing functional diversity, functional homogenization may occur (Cavalcante et al., 2022). Homogenization is frequently associated with invasion in conjunction with increasing generalist species, particularly when invasive species are translocated from nearby regions. Species are considered translocated when they are introduced outside their native geographic range but remain within the same broader biogeographical zone, establishing in areas where they did not historically occur. Translocation is a distinct process from the introduction of an exotic species, which originated in an entirely different biogeographical zone and subsequently dispersed into a new region, for example in ballast water (Matsuzaki et al., 2013; Cavalcante et al., 2022). Translocated invasive species are often more functionally similar to native species, as these generalists tend to have biological traits related to higher tolerances for environmental variation and greater dispersion, leading to homogenization (Marr et al., 2013; Zeni et al., 2020; Cavalcante et al., 2022). During the Richmondian, invaders originated from nearby regions (Stigall, 2023) with similar oceanographic conditions in that they were likely hydrologically homogenous, warm and subtropical, and consisted of a shallow carbonate platform, and may therefore be considered translocated. In addition, changes in niche overlap and morphological character displacement have both been observed during the Richmondian Invasion, suggesting that invaders performed functions similar to those of native taxa and that species became more generalized (Dudei and Stigall, 2010; Stigall, 2010, 2012; Malizia and Stigall, 2011; Tyler and Leighton, 2011; Forsythe and Stigall, 2023), which may have caused an increase in functional redundancy, reduced functional vulnerability, or functional homogenization. The invasion is also thought to have increased the number of species present in the basin (Patzkowsky and Holland, 1996; Holland and Patzkowsky, 2007; Malizia and Stigall, 2011; Bauer and Stigall, 2014; Stigall, 2019; Brett et al., 2020; Kempf et al., 2020; Forsythe and Stigall, 2023), but whether increases in species richness due to invasion translate into expansions of functional space, and if so, how this may vary over time as invasion progresses and as well as spatially, across the geographic region remains poorly documented (Matsuzaki et al., 2013; Milardi et al., 2019). It is possible that functional diversity increased if invaders added new functions. However, if these new functions were performed by only a few species, functional redundancy may have decreased, or increased ecosystem vulnerability.

Here we employ whole community assessment, using macroinvertebrates to quantify changes in functional diversity across the Richmondian Invasion in the Cincinnati Arch and identify potential changes in ecosystem structure during the Late Ordovician across six 3rd order stratigraphic sequences. Using biological trait analyses, this study aims to (1) determine whether the invasion restructured paleocommunities through time, (2) assess the relationship between species richness and functional diversity across the invasion, and (3) characterize the tempo and mode of any potential changes in functional diversity across the invasion. Late Ordovician ecosystems are suitable analogues to the modern Antarctic, as both are dominated by suspension feeders and lack durophagous predators (Aronson and Blake, 2001; Arntz et al., 2005; Gili et al., 2006; Aronson et al., 2007). Thus, this study may also have important implications for understanding the long-term impacts of current Antarctic invasions on functional diversity and community stability (Aronson and Blake, 2001; Gili et al., 2006).

2 Geological setting

During the Late Ordovician (Katian), the Cincinnati region was in the Southern subtropics at ~20-23°S (Hatfield, 1968; Jin et al., 2013), and a warm epicontinental sea covered most of the continent of Laurentia (Brett et al., 2020). The strata during this 7.5 million-year interval are well-known for their immense number of invertebrate fossils, including corals, bryozoans, brachiopods, mollusks, trilobites, and echinoderms, in addition to a well-established sequence stratigraphic framework, which has been recently revised (Patzkowsky and Holland, 1996, 1997; Brett and Algeo, 2001; Holland, 2008; Meyer and Davis, 2009; Babcock et al., 2014; Aucoin and Brett, 2015; Brett et al., 2020). These lithologic units can be classified into six depositional environments based on water depth: peritidal (including supratidal and intertidal), lagoon, shoal, shallow subtidal, deep subtidal, and offshore. The sequence stratigraphic framework includes eight 3rd order shoaling upward depositional sequences (Brett et al., 2020). Overall, these sequences exhibit a gradual shallowing-upward progression due to infilling of the basin from the Taconic highlands to the east (Holland, 1993; Holland et al., 2001); however, the direction and magnitude of environmental change within sequences is comparable (Stigall, 2014). Here we examine paleocommunities from six of the eight sequences, C2 through C7, which include the Richmondian Invasion (C5 peak invasion) and multiple laterally adjacent depositional environments along a carbonate ramp (Supplementary Figure S1). We exclude the C1 sequence (Edenian), which predates the invasion (Maysvillian and Richmondian) and represents a deeper-water environment that is not present in the younger strata. Similarly, the youngest sequence, C8, is excluded here as it occurs after the invasion concluded and represents an overall shallower environment.

3 Material and methods

3.1 Methods

To identify changes in functional diversity in response to invasion, we compared the types and number of unique combinations of functional traits, or Functional Entities (FEs), as well as the distribution of species richness within FEs. A comprehensive list of all macroinvertebrate species for each of the six sequences was compiled using the Paleobiology Database and the following museum collections: the Cincinnati Museum Center, the Karl E. Limper Geology Museum at Miami University (Oxford, Ohio), Indiana University, and the University of California Museum of Paleontology. Species nomenclature was carefully checked and revised if necessary. Species were assigned to sequences based on the geologic Formations and Members from which they were collected using the framework of Brett et al. (2020). The following seven traits were assigned to each species to create FEs (Supplementary Table S1): tiering (e.g., infaunal, semi-infaunal, epifaunal, etc.), feeding type (e.g., carnivore, herbivore, grazer, etc.), motility (motile, passive sessile attached, sessile unattached), structural robustness (unprotected, protected), trophic rank (e.g., autotroph, primary consumer, etc.), vision (blind, sighted), and body form (e.g., rectangular, branching, etc.). When multiple processes are shaping a community, they will likely be reflected differently in the overall trait composition of the community (Lefcheck et al., 2015). Thus, including multiple traits can provide an overall representation of functional diversity of the community. This is particularly relevant when considering large geographic regions and temporal spans, where functional diversity would be influenced by multiple factors (Lefcheck et al., 2015). In this study, this is further complicated by the simultaneous evaluation of multiple types of organisms (i.e., phyla, classes, etc.), as the same ecological function may be represented by different traits across taxonomic groups (Luza et al., 2023). Thus, including a variety of traits and trait types is necessary to capture functional diversity in this multitaxic paleocommunity. Traits were assigned by consulting online databases (Paleobiology Database, Polytraits, Encyclopedia of Life, WoRMS, SealifeBase, and Biotic), as well as an extensive literature review (Supplementary Table S2).

We first evaluated the distribution of species among FEs using the three traits which are most widely applied to invertebrate fossils: tiering, feeding, and motility (Bambach et al., 2007; Bush and Bambach, 2011; Bush and Novack-Gottshall, 2012). This approach represents a more conservative estimate of functional diversity, allows for straightforward comparisons with other paleoecological studies, employs traits that are well-studied in paleoecology and therefore likely to be the most reliably assigned, and are commonly available in various databases (e.g., the PBDB). To quantitatively assess the distribution of species across FEs, we employed all seven traits to calculate the mean number of species per FE, functional redundancy (the number of species divided by the number of FEs), functional vulnerability (the percentage of FEs with only one species), and functional over-redundancy (the percentage of species that fill FEs above the mean functional redundancy) for each assemblage (Schleuter et al., 2010; Mouillot et al., 2014). Functional metrics were calculated as follows (Mouillot et al., 2014), where if S is the total number of species in the assemblage, FE is the total number of functional entities, n_i is the number of species in a functional entity (FE), then functional redundancy (FR, Equation 1), functional vulnerability (FV, Equation 2), and functional over-redundancy (FOR, Equation 3) can be expressed by the equations below:

$$\mathrm{FR} = \frac{\sum_{i=1}^{\mathrm{FE}} n_i}{\mathrm{FE}} = \frac{S}{\mathrm{FE}} \tag{1}$$

$$\mathrm{FV} = \frac{\mathrm{FE} - \sum_{i=1}^{\mathrm{FE}} \min(n_i - 1, 1)}{\mathrm{FE}} \tag{2}$$

$$\mathrm{FOR} = \frac{\sum_{i=1}^{\mathrm{FE}} [\max(n_i, \mathrm{FR}) - \mathrm{FR}]}{S} \tag{3}$$

In addition, for each sequence we also assessed the number of new FEs, or FEs not present in the previous sequence, the number of FEs lost, or FEs present in the previous sequence that are no longer present, and persistent FEs, or FEs that were also present in the previous sequence. The relationships between the number of species and measures of functional diversity were assessed using simple linear regression. To assess changes in the distribution of species among functional entities across the invasion, the initial number of species per FE prior to the invasion in C2 was compared with the distribution during the main phase of the invasion in C5, and the resultant post-invasion community in C7 using a pairwise Spearman's Rank Correlation. The mean number of species per functional group was compared across sequences using a Kruskal-Wallis test. All analyses were performed in R version 4.3.0 (R Core Team, 2023) and functional diversity metrics were calculated in R using the mFD package (Magneville et al., 2022).

4 Results

A comprehensive list of 1,272 macroinvertebrate species across the six sequences was compiled with 2,321 occurrences from the Paleobiology Database and 77,180 museum specimens from localities in Ohio, Kentucky, and Indiana (USA) (Figure 1).

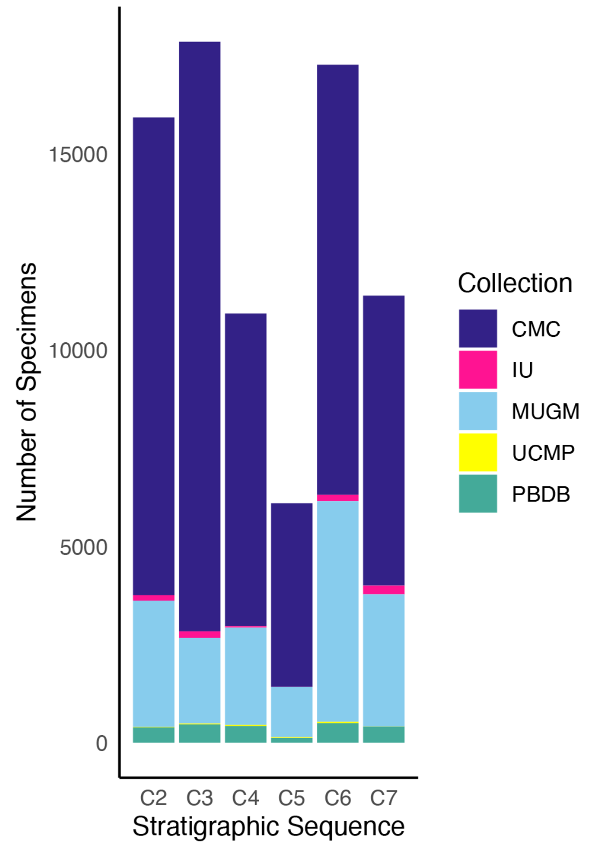

FIGURE 1
Dataset composition. Number of individuals per stratigraphic sequence from both Paleobiology Database (PBDB) and museum collections, including the Cincinnati Museum Center (CMC), Indiana University (IU), the Karl E. Limper Geology Museum (MUGM), and the University of California Museum of Paleontology (UCMP). The total dataset across all six sequences consisted of 77,180 specimen occurrences and 1,272 species.

Within these six stratigraphic sequences, the number of species was the lowest in C5 (167 species), and highest in C7 (442 species), and overall, included species from 10 phyla (Figure 2): Annelida, Arthropoda, Brachiopoda, Bryozoa, Chordata, Cnidaria, Echinodermata, Hemichordata, Mollusca, and Porifera. Seven traits were assigned to all 1,272 species (Figure 3).

When employing only the three most widely used fossil traits (motility, feeding, and tiering), the total number of occupied FE's across all six sequences was 23, and varied from 19-22. The largest number of occupied FEs occurred during C2 (preceding the main phase of the invasion), C5 (during the main phase of the invasion), and C7 (subsequent to the main phase of the invasion), all with 20 or 22 FEs (Figure 4). C3 and C6 had the lowest with 19 occupied FEs. Although C7 had the highest number of species (442), it also had the highest number of vulnerable FEs (4), which were occupied by only one species. C6 only had one vulnerable FE, whereas C2, C3, C4, and C5 had two to four (Figure 4). Most functions persisted across sequences, particularly at the pelagic and epifaunal tiers. However, in C2, the infaunal tier had seven FEs occupied and three that were vulnerable, occupied by only one species. By C7 there were only four FEs occupied with only one vulnerable. In the epifaunal tier, mostly the same FEs were consistently occupied until C7. Additionally, in C7 two epifaunal functional entities were occupied by a single species, one new FE, not seen before the invasion and one FE refilling from pre-invasion: sessile unattached grazer/herbivore/scraper (new) and passive suspension feeder (returning). During the invasion, the infaunal motile predator FE was occupied densely in C4, but the number of species slowly decreased to one in C6, and the entity was unoccupied in C7. The mean number of species per functional entity did not differ significantly across sequences ($\chi^2 = 2.29$, $p = 0.81$).

When considering all seven traits, the total number of FEs for all sequences combined was 57. Within sequences, the number of FEs was the lowest in C5 with 33, and highest in C2 with 45. Twenty-six FEs were lost more than once across the invasion, while 9 FEs that were present in either C2 or C3 did not return. Overall, 24 FEs persisted across the entire invasion. Furthermore, 7 FEs lost in C3-C4 were reoccupied in C6 or C7, and 14 new FEs arose. Overall, the two functional entities with the greatest number of species were FE 1 (epifaunal, sessile attached, protected, branching, blind, primary consumer, suspension feeder), and FE 2 (epifaunal, sessile attached, protected, massive, blind, primary consumer, suspension feeder), both of which were populated almost exclusively by bryozoans. Applying a linear regression, the number of species per sequence predicted the number of FEs (F = 10.7; $r^2 = 0.66$; $p = 0.03$), functional redundancy (F = 43.6; $r^2 = 0.90$; $p = 0.003$) and over-redundancy (F = 28.7; $r^2 = 0.85$; $p = 0.006$), but not vulnerability (F = 0.07; $r^2 = -0.23$; $p = 0.79$). Functional redundancy started high and was somewhat similar from C2 to C3 (Figures 5, 6), then decreased substantially from C3-C5, followed by a sharp increase in C6 and C7, with values higher than prior to the invasion. Functional over-redundancy followed a similar trend with incremental decreases from C2 to C5, then increasing in C6 and C7. Interestingly, functional vulnerability was decoupled from the other metrics, including number of species, decreasing in C4

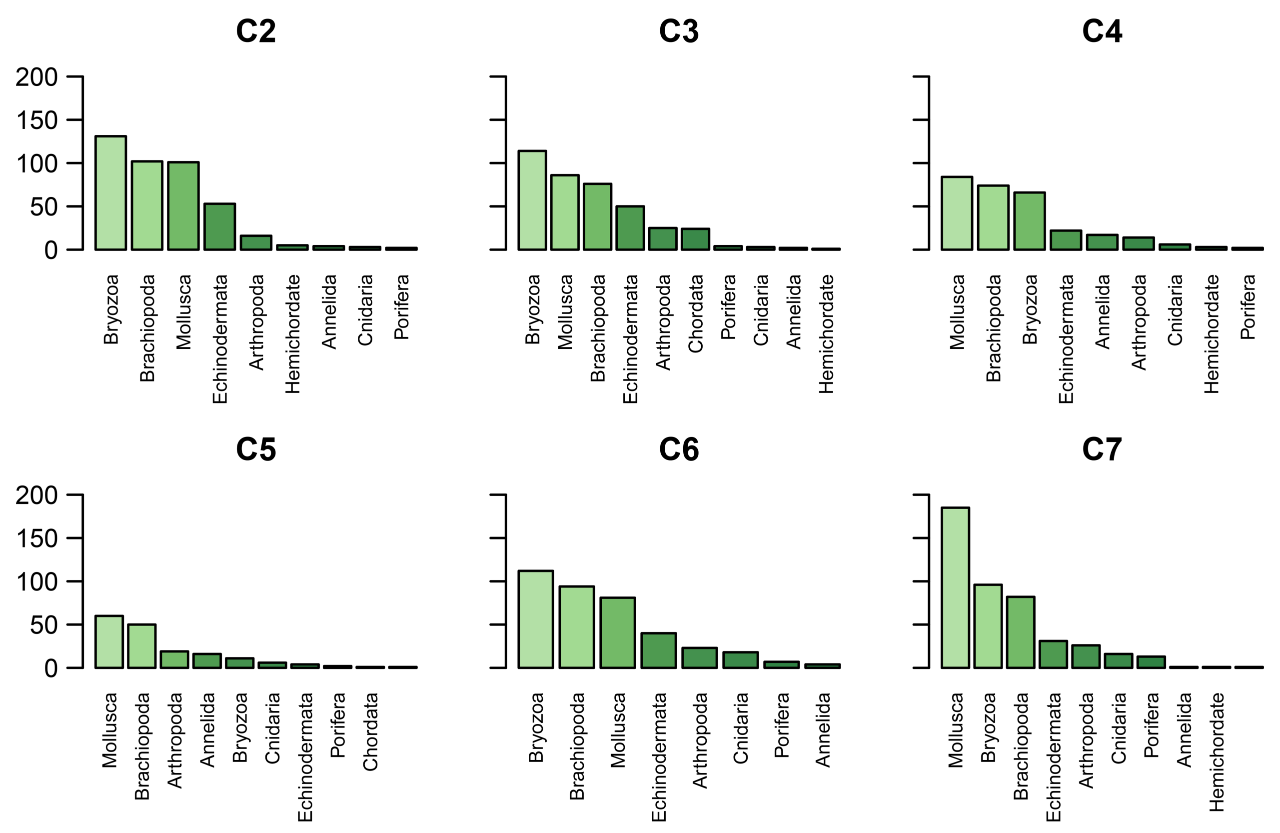

FIGURE 2
Number of species per Phylum for each stratigraphic sequence. Brachiopods dominated collections in abundance across all six, however in species diversity, the richest phyla were Bryozoa and Mollusca.

through C6, and increasing notably in C7. C2 had 31% vulnerable functional entities, while C3 had 33% (Figure 5). C4 had 35 functional entities, only 25% of which were vulnerable, and C5 had the lowest number of functional entities (33), 24% of which were vulnerable. During C6, we begin to see an increase back to pre-invasion functional entity numbers (37) and the lowest vulnerability (8%). The proportion of functional entities increased again in C7, but did not return to pre-invasion levels (45 in C2), with 29% FV. Four FEs present in C2 were lost and never returned (FE 39, 46, 49, and 53; see Supplementary Tables S3, S4 for FE descriptions), and two were unique to C7 (FE 52 and 55).

The distribution of species among functional entities, assessed by comparing the rank order of the number of species per FE, was significantly correlated prior to and during the main phase of the invasion, between C2 and C5 (Spearman's Rho = 0.65, $p < 0.01$; Figure 7), as well as prior to and subsequent to the invasion, between C2 and C7 (Spearman's Rho = 0.65, $p < 0.01$; Figure 7). The mean number of species per functional entity did not differ significantly across sequences ($\chi^2 = 5.5$, $p = 0.36$). In addition, the number of new FEs remained consistent, but was marginally higher in C6 and C7, while the number of lost FEs steadily declined (Figure 6). While the number of persistent FEs remained consistent across the invasion with a steady increase (C3-C7), the number of new FEs increased from C4 to C6 and the number of lost FEs decreased consistently throughout the invasion (C3-C6).

5 Discussion

The Richmondian Invasion, which involved more than 75 taxa invading during several pulses throughout C3-C6, resulted in only minor changes to functional diversity by C7. There was a slight contraction in functional entities in C7 and high species richness, though a more notable reduction of species occurred in C5. Although C5 is considered the main phase of the invasion, with the largest influx of immigrants, invaders began to arrive as early as C3 (Malizia and Stigall, 2011; Bauer and Stigall, 2014; Stigall, 2019; Brett et al., 2020; Kempf et al., 2020; Forsythe and Stigall, 2023). During C5, the number of species decreased notably, with 249 fewer species than C2. Early invaders in C3 and C4 could possibly have triggered a cascade effect, known as an invasion meltdown, as small numbers of invading taxa can create more opportunities for subsequent invaders to be successful (Ricciardi and Simberloff, 2025). In addition, many invaders may have either been unsuccessful initially and did not become fully established until after C5, and/or the loss of incumbents increased as the invasion intensified. This pattern may be the result of incumbents being outcompeted by invaders (Tyler and Leighton, 2011; Forsythe and Stigall, 2023), particularly where invaders and incumbents occupied the same functional space as invading species became integrated into the community. The former is consistent with the repeated introduction of invasive species today, as invasions are dynamic but

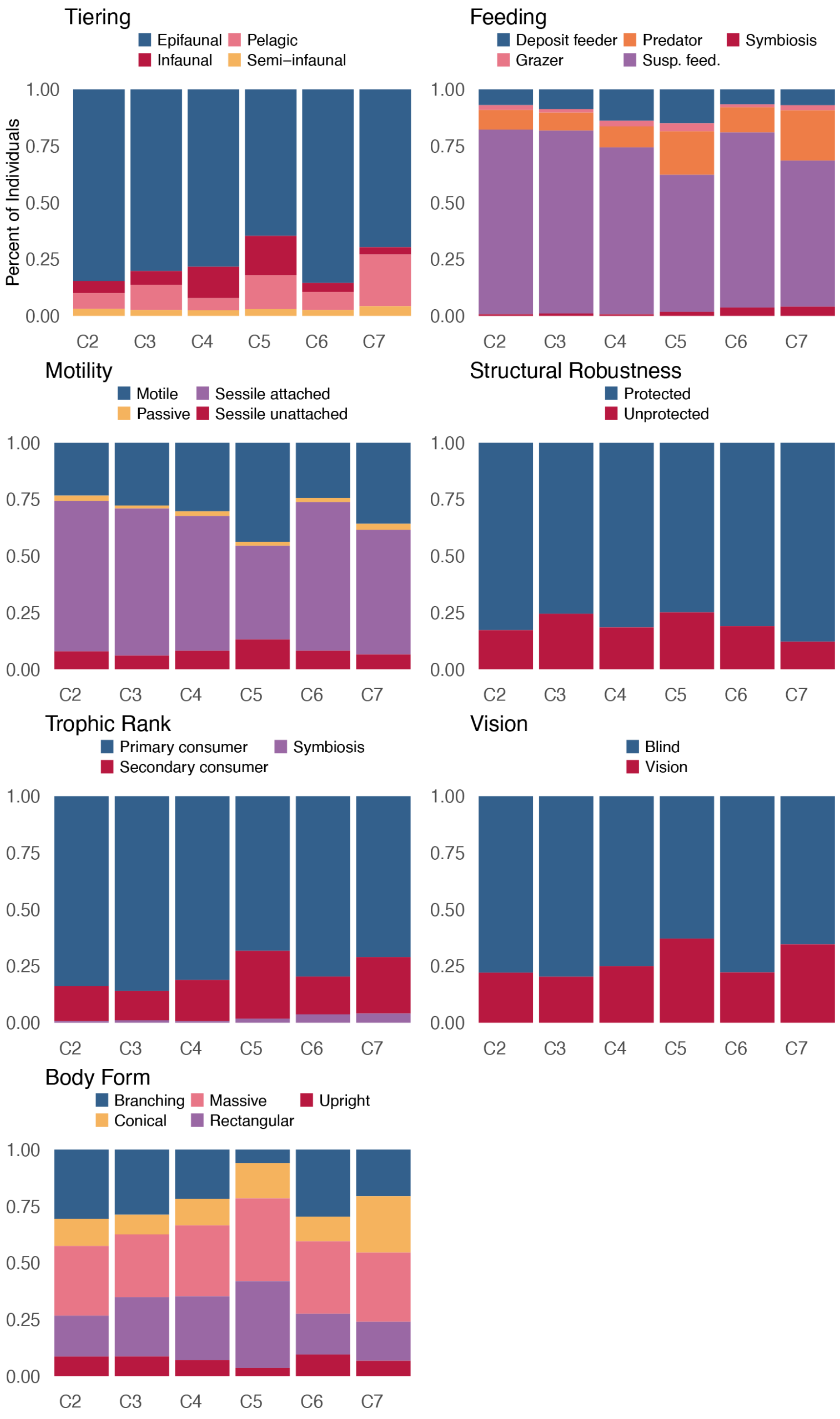

FIGURE 3
Functional traits. Proportion of species in each sequence for assigned categories for each of the seven traits examined.

often transient disruptions, typically requiring frequent invasions to become established and ultimately assimilate into a community (Vermeij, 1996; Zenni and Nunez, 2013; David et al., 2017). Established invaders should consist of self-sustaining populations that no longer depend on repeated re-introduction to persist and overcome any competitive advantages of incumbency (Vermeij, 1996), which we propose occurred in C6, after the main invasion phase. C7 would therefore represent the integrated community, where invaders have forged new ecological links with incumbents and perhaps maintained older ones with one other (Vermeij, 1996).

When considering only the three most commonly used and reliable fossil traits, changes in functional diversity were minimal,

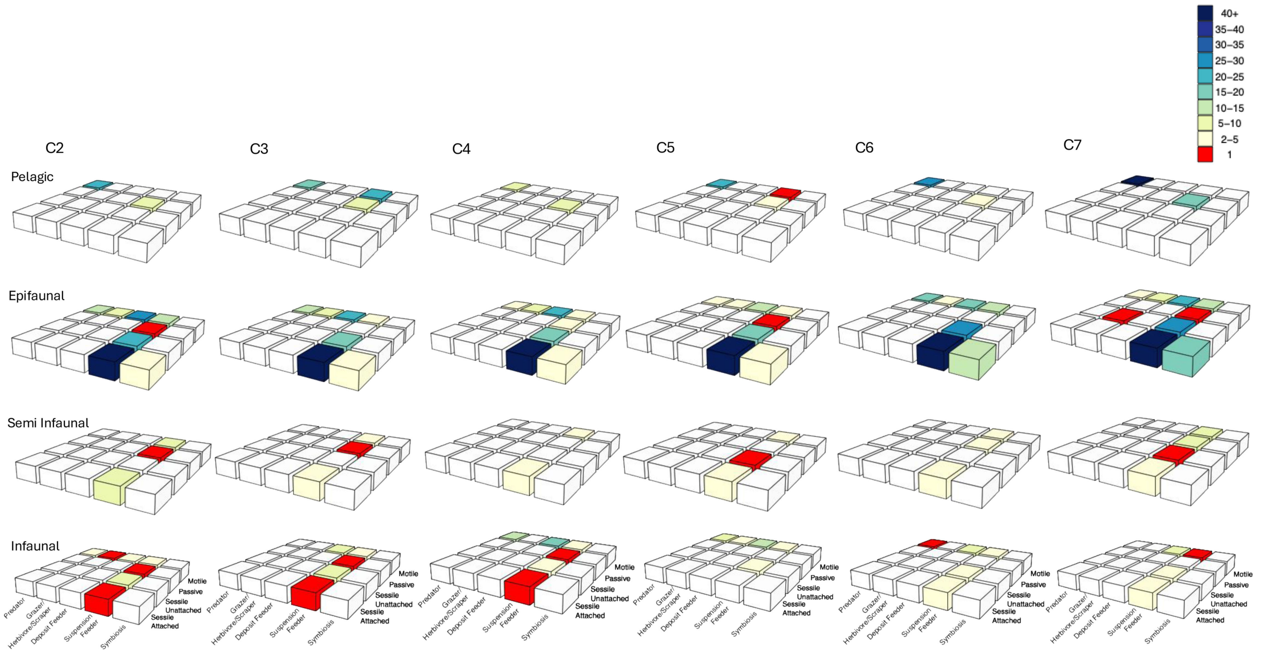

FIGURE 4
Functional space. When constrained to three functional traits commonly used in invertebrate paleoecology (tiering, feeding, and motility), there are few differences between the pre-invasion C2 community and C7 post-invasion community. Each cube represents a unique Functional Entity (FE). The color scale corresponds to species richness per FE, with red representing vulnerable functions.

and it is difficult to detect the nuances of novel functions. The resultant post-invasion community (C7) differed from the pre-invasion community only with the addition of two new vulnerable functional entities populated by a single species, one existing functional entity becoming vulnerable, one functional entity lost, as well as an increase in the number of species within existing functions. These findings suggest that the inclusion of more traits may be critical for detecting changes in functional diversity. Future studies should explore the potential effects the number of traits and trait modalities employed may have on the measurement of functional diversity.

When considering all seven traits, the number of functional entities, functional redundancy, and over-redundancy all corresponded to changes in the number of species. The number of functional entities declined from 45 in C2 (416 species) prior to the invasion to 33 in C5 (167 species) during the main invasion (Figure 6). The number of functional entities increased in C6 and C7 to 41 FEs but did not return to pre-invasion levels despite an increase in the number of species, and the invasion thus ultimately marginally reduced functional richness. That is, despite the strong relationship between the number of species and the number of functional entities, the resulting community in C7, even after ~1.5 m.y. (from C4-C7), and the addition of 26 species, still had fewer functions relative to the pre-invasion community. Ecological processes relating to invasion had a strong effect on community structure on evolutionary timescales, suppressing the existing relationship between species richness and functional diversity. Overall, the number of species declined by ~60% between C2 to C5 whereas the number of FEs only declined by ~27%, and only 3 FEs present in C2 were lost, and the total number of FEs was reduced by only 4 with one additional FE gained during the invasion but not lasting into C7. The low species richness in C5 is unlikely to be an artifact of undersampling, as C5 had a large sample size of > 6,000 individual occurrences and 164 species, which is fewer species relative to other sequences. In addition, lower species diversity in C5 has been observed in other studies, despite including the main phase of the invasion (Aucoin and Brett, 2015).

The number of species in C5 relative to the other sequences was to some extent, the result of the revised sequence stratigraphic framework, which placed a sequence boundary within a formation. As the majority of locality information associated with specimens only included the formation name, and not the member, it was not always possible to resolve this stratigraphically, which led to the exclusion of a large number of specimens. Taphonomic biases are unlikely to have produced the observed differences in functional diversity, as fossils yield reasonable estimates of functional diversity across multiple types of marine invertebrates in shallow marine environments despite their varied preservation potential. Furthermore, the functional fidelity of the diversity indices employed here (e.g., number of functional entities, redundancy, over-redundancy, and vulnerability) is high (Tyler and Kowalewski, 2025). The minor changes in functional diversity observed here may, however, reflect the methodology itself, as functions are context dependent, and are affected by the other functions present, and the position of the function within the food web (Banker et al., 2022). Therefore, we recommend that future studies

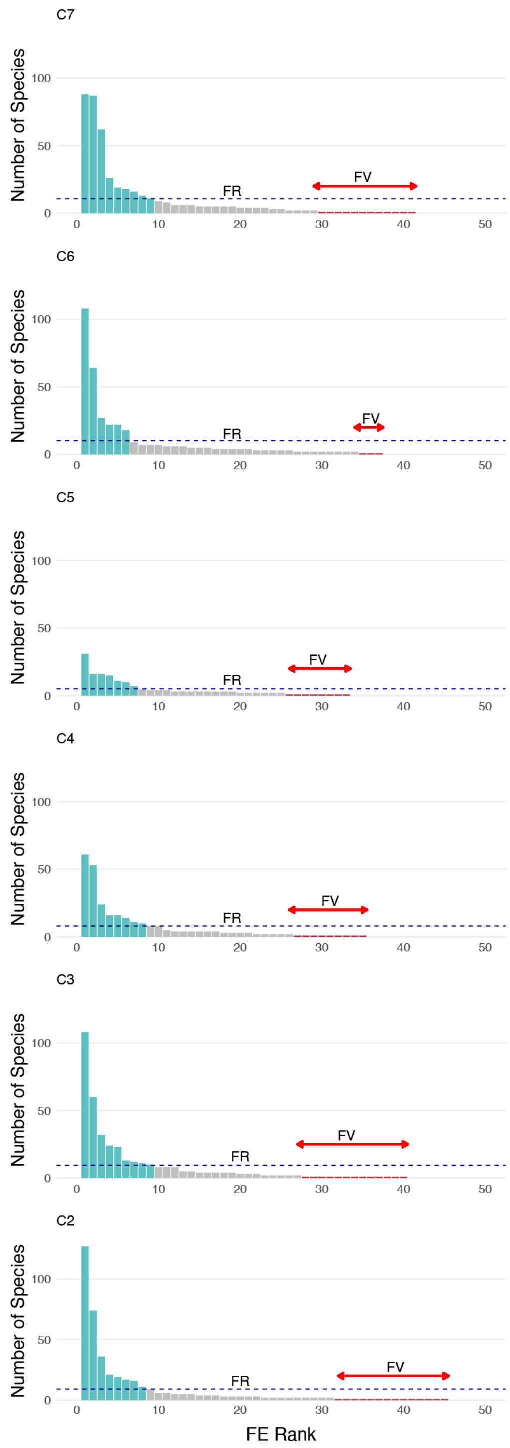

FIGURE 5
Functional diversity per stage. The ranked distribution of species among FEs highlights changes in Functional Vulnerability (FV), Functional Redundancy (FR), and Functional Over Redundancy (FOR) for C2 - C7. Red bars indicate FEs with only one species, and FV is thus represented by the width of the red arrows. The dashed line marks the FR, or the number of species divided by the number of FEs. Green bars are over-redundant FEs with more species than mean functional redundancy.

investigating changes in functional diversity include additional information on trophic position and interactions, i.e., examine food webs.

Although the largest number of invaders is thought to have arrived in C5, the number of new FEs only slightly increased overall from C4 to C6. A modest increase of seven new FEs did not occur until after the main invasion phase, following invader establishment in C6. Invaders, therefore, may have largely occupied preexisting functional entities early on, and had similar traits to native species, as is common for translocated species today (Marr et al., 2013; Zeni et al., 2020; Cavalcante et al., 2022), as few new functional entities arose from C3-C6 across what is believed to include the main phase of the invasion. Similarly, functional redundancy and over-redundancy increased notably in C6 and again in C7. As invaders arrived, they were not only occupying preexisting functional entities but were also likely outcompeting functionally equivalent incumbents, leading to species replacement within existing functional roles (Tyler and Leighton, 2011; Forsythe and Stigall, 2023). Future work identifying which species are invasive and the proportions of invaders within each functional entity is needed to test whether invaders were outcompeting functionally equivalent incumbents, decreasing the number of species within those entities, or determining which specific invaders were contributing entirely new functions. Functional redundancy and over-redundancy may positively affect community stability and resilience to disturbance (Biggs et al., 2020), suggesting that the invasion led to less stable and resilient communities during C5. This is consistent with previous studies, which found that post-invasion, communities were moderately less stable (Kempf et al., 2020). The number of functions, and aspects of redundancy, may therefore be more strongly impacted by invader establishment, as opposed to their initial arrival. Interestingly, as the invasion progressed, functional entities were lost across sequences, and the largest loss of functions occurred between C5 and C6. The establishment of invaders may therefore pose the greatest threat to functional diversity, promoting the loss of functions. However, lost FEs steadily declined during the arrival and early establishment (C3-C5), suggesting that preserving functional diversity may require monitoring and possibly removing early, rare, or transient invasive species when invasion is caught early enough.

Functional vulnerability was highest in C2 to C3 when early invaders entered the basin. However, vulnerability decreased in C4, and continued to decrease until C6, before increasing in C7. Functional vulnerability is indicative of the proportion of functions that are at risk of being lost, as these functional entities only contain one species. If that single species is affected by stressors present, e.g., competitive exclusion or new predators, and goes extinct, then that function is also lost. Increasing species richness may therefore reduce vulnerability, if this results in adding species to species-poor functions (McWilliam et al., 2018). Vulnerability decreased across the invasion from C3 to C6 (and was lowest in C6), while few new functions appeared, and the number of species decreased from C2 to C5. In addition, 10 vulnerable FEs across the C3-C6 interval were later

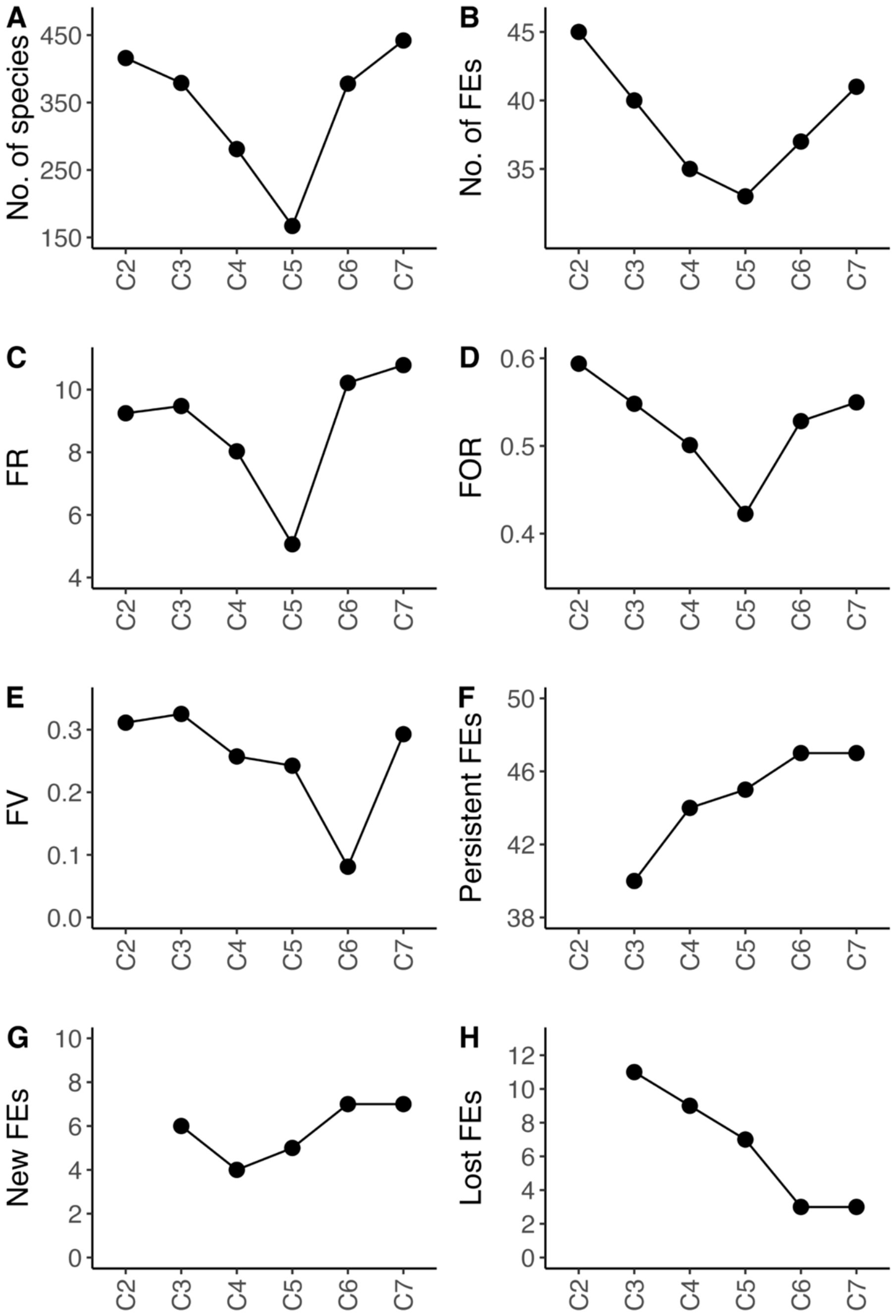

FIGURE 6
Functional metrics. The number of species **(A)**, Functional Entities (FEs) **(B)**, Functional Redundancy (FR) **(C)**, Functional Over-Redundancy (FOR) **(D)**, Functional Vulnerability (FV) **(E)**, persistent FEs or the number of FEs also present in the previous sequence **(F)**, new FEs or the number of FEs not present in the previous sequence **(G)**, lost FEs or the number of FEs from the previous sequence that are no longer present **(H)** for each sequence.

occupied by additional species. That is, during this interval, many invasive species were occupying existing functions and thus increasing the number of species within previously vulnerable functions. Vulnerability returned to pre-invasion values in C7, as invaders became integrated into the recipient community. Overall, the decline in species richness was associated with the loss of functional entities, but did not necessarily increase the proportion of remaining functional entities classified as vulnerable (vulnerability was not significantly associated with species richness). During the peak of the invasion there may have been high incumbent extinction and turnover within the FEs most vulnerable, which outpaced the success or arrival of invaders with novel functions. That is, as the invasion intensified and invader populations became self-sustaining, vulnerability dropped, while the number of new FEs remained steady. Following the peak invasion, during integration, invaders may have begun to repopulate FEs previously occupied by incumbents or expand into novel FEs (7 FEs lost in C3-C4 were reoccupied in C6 or C7, and 14 new FEs arose). Changes in functional vulnerability

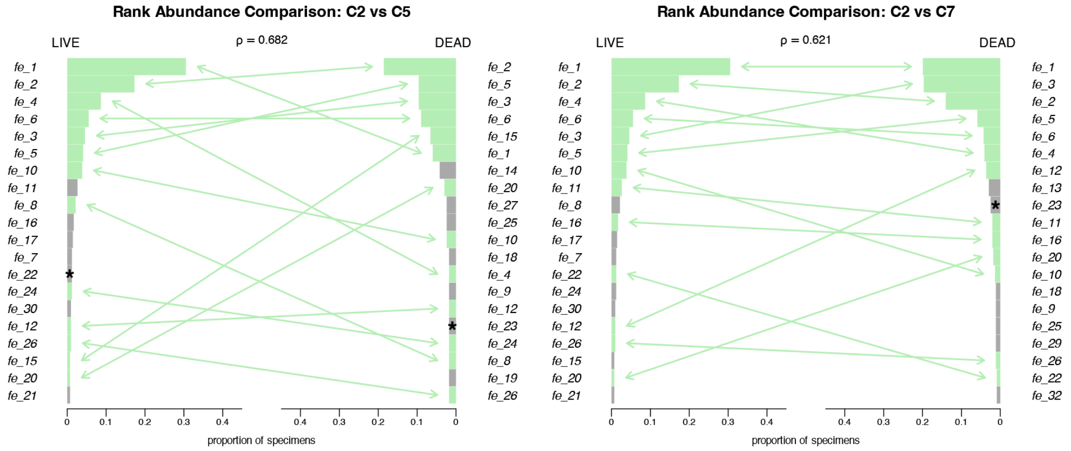

FIGURE 7
Rank abundance of unique functional entities. The proportional rank abundance of the number of species within functional entities in C2 and C7 (A, rho = 0.61, $p < 0.01$), and C2 and C5 (B, rho = 0.69, $p = 0.01$), and the majority of the 20 functional entities with the greatest number of species are present in both C2, and both C7 and C5 (green). Spearman's Rho is shown at the top of the figures.

may be the most notable aspect of changes in functional diversity with respect to invasions on evolutionary timescales, as opposed to species richness. It has also been suggested that a species richness threshold exists, above which functional redundancy counterbalances the buffering effect of species richness on vulnerability (Parravicini et al., 2014; Auber et al., 2022). Functional vulnerability may be dependent on spatial scale, as larger areas tend to contain more species (Pombo-Ayora et al., 2024) and the decoupling of vulnerability from redundancy may instead be an artifact of the spatial scale of this study. However, this would not alter the observed relative differences in vulnerability between sequences.

During the arrival phases of the invasion, in stages C3, C4 and C5, there were ecological changes as new functional roles were established or reestablished, species competed for the same resources, and new predators arrived. Following the invasion, regardless of the disruptions during arrival and establishment, the integrated post-invasion paleocommunity was functionally similar to the pre-invasion (C2) paleocommunity with respect to the number of functional entities, redundancy, over-redundancy, and vulnerability. When comparing the pre- and post-invasion communities, differences in functional redundancy (9.2 vs. 10.8, an increase of 14.8%), over-redundancy (0.59 vs. 0.55, -6.8%), and vulnerability (0.31 vs. 0.29, -6.5%) were relatively minor when comparing C2 to C7. In addition, 24 FEs persisted across the entire invasion, while only 3 FEs present in C2 were never occupied again, and the total number of FEs was reduced by only 4 (-8.8%). While there is no exact answer as to how significant having 4 fewer FEs was in this benthic marine ecosystem, it is useful to consider how species are distributed among the FEs, which has implications for community resilience to, and insulation from, disturbances. To have species more equally distributed among FEs should provide more redundancy and prevent functional loss. The distribution of species among FEs does not statistically differ from C2 to C7, and the overall loss of FEs is a modest 8.8% decrease (Figures 6, 7) with functional over redundancy and functional vulnerability having less than a 7% reduction pre- and post-invasion. Considering the amount of time, 7.5 million years, and the large number of species from multiple phyla (> 75 species) that invaded this basin, the species losses are not consistent with widespread community restructuring.

We propose that on evolutionary timescales, while invasion temporarily altered functional diversity, many aspects of functional diversity recovered, likely due to invaders occupying similar functional roles to incumbent taxa. However, 3 FEs present in C2 never returned, and the total number of FEs was reduced by 4. Although the number of species was correlated with the number of functions, it is notable that despite species richness recovering, functional diversity never returned to preinvasion levels. This suggests that conservation strategies relating to invasions should not rely solely on increasing the number of species to restore marine ecosystems, particularly in the Antarctic, which is most analogous to the Late Ordovician. In addition, conservation managers should consider whether the community being remediated is experiencing initial invader arrival, or if invaders have already become established. If the community is still experiencing the initial arrival of invaders and they are not yet established - the phase associated with the greatest loss of functions - conservation strategies should focus on preventing any additional loss of functional diversity by slowing or stopping invasion. However, if an ecosystem is in the establishment phase, it may be crucial to monitor the perseverance of preinvasion functions. For invasions already in the integration phase, conservation strategies should consider focusing on restoring and protecting functional diversity and redundancy, as opposed to increasing species richness.

6 Conclusions

Despite well-known substantial changes in community composition associated with the Richmondian Invasion, functional diversity was modestly affected and is not consistent with purported community restructuring. Various aspects of functional diversity returned to near pre-invasion (C2) levels, including the number of functional entities, functional redundancy, functional over-redundancy, and functional vulnerability. The C5 community was the most functionally different. However, neither the C5 nor C7 communities differed significantly from C2 in the distribution of species among functional entities. Throughout the invasion, we find that the arrival of invaders altered functional diversity, with a 27% decrease in the number of FEs between C2 and C5, but when comparing pre- and post- invasion communities, the invasion did not appear to substantially change the number of FEs, add many new functional entities, and invaders largely appeared to occupy pre-existing functional entities. There were subtle changes during the main establishment phase of the invasion; however, ultimately, functional redundancy returned to near pre-invasion levels. This suggests that, despite changes in community composition, the Richmondian Invasion may not have substantially restructured ecosystems, as few changes in various measures of functional diversity were observed.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

ME: Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing. RB: Conceptualization, Data curation, Investigation, Methodology, Software, Visualization, Writing – review & editing. SM: Data curation, Formal analysis, Writing – review & editing. AD: Conceptualization, Funding acquisition, Investigation, Supervision, Validation, Writing – review & editing. PR: Conceptualization, Investigation, Validation, Writing – review & editing. CT: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

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Conflict of interest

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