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Prospects for studying continentalization and the origin of terrestrial ecosystems during the late Paleozoic

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The origin of terrestrial ecosystems during the Paleozoic is pivotal in the history of life on Earth. This is a fascinating case for testing hypotheses about how ecological novelty arises at the organismal, lineage, and community levels. In this paper, I review research on community assembly and change in deep time and discuss this work in the context of investigating the continentalization of ecosystems. The extensive study of large-scale Phanerozoic trends in taxonomic and autecological diversity, particularly in the marine realm, provides an important theoretical framework. However, the interactions between these trends and community-level properties such as stability and the species carrying capacity are not as well understood. The growing body of paleo-food web literature has returned ambiguous results, and it is not clear whether the bounds of community performance have shifted over time or not. Importantly, these studies are conducted either entirely in the marine realm or in the terrestrial realm, but not yet on communities representing the initial expansion of life into non-marine and, eventually, terrestrial habitats. Modern-day systems such as island colonization might provide some useful insights into continentalization in deep time, but are effectively instances of terrestrial ecosystems being reproduced using extant terrestrial taxa, not terrestrial ecosystems developing *de novo*. The timeline of Paleozoic continentalization as currently understood is reviewed. Although the process was already underway, the Late Paleozoic (Devonian–Permian) emerged as a key interval for the study of continentalization. Food web modeling methods and hypotheses are discussed. Although challenging, going forward, this area of research has great potential to address questions of relevance to paleontologists, neontologists, and ecologists alike.

KEYWORDS

early tetrapods, paleoecology, food web, terrestrialization, continentalization, Paleozoic, water land transition, community ecology

1 Introduction

The origin of terrestrial ecosystems during the Paleozoic is pivotal in the development of the global biosphere (Knoll and Bambach, 2000). Research has focused on the chronology of terrestrialization across taxa and its impacts on the Earth system (Knoll and Bambach, 2000; Sahney et al., 2010b; Vecoli et al., 2010; Kenrick et al., 2012; Lenton et al., 2016) and is deeply tied to work on large-scale changes in the taxonomic and autecological diversity of marine organisms (Sepkoski et al., 1981; Jablonski and Sepkoski, 1996; Bambach et al., 2007). Over the last two decades, advances in computing have spurred greater comparative investigations of fossil ecosystems as distinct from the sum of their components. Current issues include: the relationship between taxonomic diversity and ecosystem structure (Dunne et al., 2008; Blanco et al., 2021; Banker et al., 2022); whether ecological communities evolve and are subject to selection (Roopnarine and Angielczyk, 2016; Roopnarine et al., 2019); and the applicability of ecosystem assembly rules (DiMichele et al., 2023b). Most of the effort has gone into the marine or terrestrial realms, while the process of continentalization and the origin of terrestrial ecosystems remain understudied in this regard (Spiridonov and Eldredge, 2024). The aims of this paper are: 1) to review the paleontological and macroecological perspectives on community assembly and 2) to discuss continentalization and the origin of terrestrial communities during the Paleozoic as useful examples for study, with a special focus on the Late Paleozoic and the incorporation of vertebrates into terrestrial ecosystems.

Marine species diversity is commonly portrayed as increasing over the course of the Phanerozoic (Sepkoski et al., 1981; Sepkoski, 1993; Bambach et al., 2004; Bush and Bambach, 2004; Bush et al., 2004), with a sharp increase from the Cretaceous onwards. This biodiversity has also been divided into distinct taxonomic associations in the marine realm—Cambrian, Paleozoic, and Modern—each of the latter two arising after a mass extinction (End-Ordovician and End-Permian, respectively) (Sepkoski et al., 1981). The occupation of marine ecospace, i.e., the number of niches filled, and the breadth of ecospace, i.e., the number of possible niches, have also been described as increasing over the Phanerozoic along similar lines (Vermeij, 1977; Bambach et al., 2007; Patzkowsky and Holland, 2007; Klug et al., 2010, 2010; Villéger et al., 2011; Bush and Novack-Gottshall, 2012; Mondal and Harries, 2016), although there are complexities at smaller spatiotemporal scales. Parts of this interpretation have been challenged as a product of sampling, biotic, and/or tectonic biases in the fossil record (Raup, 1976; Cherns and Wright, 2000; Alroy et al., 2001, 2008; Peters and Foote, 2001; Wall et al., 2009; Zaffos et al., 2017).

Similar correlated increases in species diversity and ecological diversity have been described for tetrapods (Sahney et al., 2010b), suggesting that the pattern of increase might be general for Phanerozoic life. Spatiotemporally distinct taxon associations of terrestrial vertebrates, e.g.,faunachrons or assemblage zones, have been described at various scales, such as the Cenozoic of the Americas (Flynn et al., 1984; Pascual and Jaureguizar, 1990) or the Permo-Triassic of South Africa (Viglietti et al., 2022) and Russia (Olson and Chudinov, 1992; Golubev, 2000; Schneider et al., 2020; Shishkin et al., 2023c). However, thus far, there are no terrestrial analogues for the marine Sepkoski faunas.

If indeed Phanerozoic ecosystems have been assembled from an increasingly large pool of increasingly ecologically diverse species, then understanding the structure of these ecosystems and how they have changed is crucial to understanding the evolution of their component lineages. It is these patterns of species–species ecological interaction that, in conjunction with species–environment interactions, create the evolutionary environment in which species exist at any given time (Valen, 1973; Stenseth and Smith, 1984; Hubbell, 2001; Roopnarine, 2012; Solé, 2022; Spiridonov and Lovejoy, 2022).

2 Ecological assembly rules through time

If we consider the structure of ecosystems as important for understanding the evolution of taxa, the questions then follow of whether and how ecosystems in deep time were different from those in the Modern: were they subject to the same processes of assembly, network interactions, and energy flow (DiMichele et al., 2004)?

Primary productivity has increased over geologic time (Crockford et al., 2023), and it is possible that nutrient availability has increased during the Phanerozoic in particular (Assine et al., 2018; Wang et al., 2020). Increased energy consumption by marine organisms is inferred from the fossil record: the Cambrian rise in bioturbation and the metazoan morphological diversity (Droser et al., 2002; Marshall, 2006; Briggs, 2015; Darroch et al., 2021); the Devonian increases in morphologies for active predation and nektonic swimming (Novack-Gottshall, 2007; Klug et al., 2010); and evidence of increased predation intensity during the Mesozoic (Vermeij, 1977; Kelley and Hansen, 2001; Huntley and Kowalewski, 2007; Finnegan et al., 2011; Buatois et al., 2016). Presumably, this increased energy consumption by marine organisms corresponded with the increased consumption by marine communities (through some combination of bottom-up and top-down effects). Within such a hypothesis of dynamically changing ecological assembly processes over time, organismal identity and traits become more important for understanding past ecosystems (Banker et al., 2022).

On the other hand, some modeling of Cenozoic communities has found that the occupation pattern of niches or guilds can persist despite species extinction and turnover, suggesting that organismal interactions have a stronger control on ecosystem structure than organismal traits (Fraser and Lyons, 2020; Blanco et al., 2021; Whittingham et al., 2024b). These results support the hypothesis that fossil ecosystems are best understood not as groupings of species autecologies but rather as sets of interactions. The taxonomic identity and particular traits of organisms are deemphasized in favor of their niche or functional role within the community (Roopnarine, 2012). The origin of new functional roles, such as herbivory, could have large effects on ecosystem "fitness" (Roopnarine and Angielczyk, 2012; Angielczyk et al., 2020); alternatively, the dynamics inherent to sufficiently-sized networks might have greater importance (Dunne et al., 2002, 2004, 2008). If communities are emergent entities in this way, it is possible that not only do species co-evolve within communities but that the communities themselves undergo selection and evolve (Bambach, 2001; Roopnarine and Angielczyk, 2016; Roopnarine et al., 2019).

Significantly, the ecosystems spanning the continentalization of life have not yet been analyzed in this way. This is quite understandable, given the challenges of the fossil record. However, continentalization in deep time presents a unique opportunity to study ecological assembly rules: the expansion of life into fully novel habitats—beginning with non-marine waters and eventually leading to land—entailed numerous organismal adaptations, the origin of functional roles, and the construction of unprecedented ecosystems in a manner arguably not seen since.

3 Modern models for continentalization?

Ideally, it should be possible to find at least partial Modern analogues for deep-time continentalization. There are three such potential analogues: disturbance (such as that of a volcanic eruption), glacier retreat, and island colonization (Thornton, 2007; Crisafulli and Dale, 2018; Cauvy-Fraunié and Dangles, 2019; Ficetola et al., 2024; Khelidj et al., 2024).

DiMichele and colleagues recently made direct comparisons between recovery following disturbance and the evolution of the first terrestrial floras (DiMichele et al., 2023b). In both cases, the initial plant colonizers were morphologically simple and formed fast-propagating and taxonomically and functionally homogenous floras. Competition was primarily intraspecific. These were then replaced by floras that were progressively more architecturally complex and taxonomically diverse. Within these more complex floras, interspecific interactions (including competition) became more significant, creating a more interconnected and resilient community. Similar successional patterns are seen in the aftermath of the glacier retreat (Cauvy-Fraunié and Dangles, 2019; Ficetola et al., 2024; Khelidj et al., 2024).

Island colonization events differ from both post-disturbance and post-glacier retreat community assembly events in terms of spatial dynamics. Islands are isolated from their mainlands by water bodies that constitute dispersal barriers that colonizers must cross. This requirement of dispersal biases the set of organisms that can colonize. Islands are also limited in area and are generally small, while a glacier retreat can expose large areas on a continental scale relatively quickly (in geological terms). A general pattern of succession and community assembly can be drawn from several extensively researched case studies (Thornton, 2007). Airborne dispersal is primary for both plants and animals. Early colonists depended on airborne or waterborne food sources until a fully terrestrial local community was established. The extinction rates of resident species were initially high, but those species that successfully became established persisted even as the community expanded (Heatwole, 1981).

The order of succession/colonization is, at high taxonomic/ecological levels, the same between the above three scenarios and the fossil record of continentalization, with microorganisms preceding macroorganisms. There were non-marine microfossils ~1,000 Ma (Strother et al., 2011), and geochemical signals have been used to infer the presence of unspecified, presumably microscopic, terrestrial photosynthetic organisms from ~850 Ma (Horodyski and Knauth, 1994; Knauth and Kennedy, 2009). Terrestrial plant fossils have been known from the Late Ordovician onwards (Edwards and Wellman, 2001; Raymond et al., 2006; Steemans et al., 2009; Kenrick et al., 2012; Xue et al., 2018), although, again, earlier origins for land plants have been proposed (Clarke et al., 2011). Body fossils indicate that arthropod terrestrialization was underway by the Middle Silurian (~430 Ma), and fully terrestrial arthropods had evolved by the Late Silurian (Dunlop, 1996; Dunlop and Selden, 2013; Waddington et al., 2015). Hypotheses of a Cambrian radiation of terrestrial arthropods have been proposed on the basis of molecular clock studies (Tihelka et al., 2022). Arthropods appeared to have expanded onto land directly from the ocean without passing through freshwater environments first. During this "intertidal phase," they likely played an important role in the transfer of marine nutrients into the terrestrial community, as is the case with early arthropod island colonizers in the Modern (Thornton, 2007). The timing and the process of vertebrate terrestrialization are highly contentious and will be discussed later.

4 Limits to modern models

However, there are several major differences between Modern systems of disturbance and colonization and continentalization in the fossil record. Biotic (re)colonization of disturbed areas, previously glaciated areas, and islands can be extremely rapid, on the order of decades for community establishment (Thornton, 2007). In contrast, the invasion of land was protracted across hundreds of millions of years across the Late Precambrian to the Middle Paleozoic. This difference in timing highlights the differences in the biological and ecological problems that need to be solved. In the three Modern scenarios, the foremost problem an organism must solve is that of arriving to the area in question. In cases of disturbance or glacier retreat, this is relatively easy as the distance is small and the climatic/physical barriers minimal. Some heat- or drought-resistant organisms can survive disturbance and persist in place. As discussed, islands are more isolated, but they still draw from a regional pool of colonists at varying scales. In all three cases, the organisms are already adapted to terrestrial life broadly and the new area falls within their habitat parameters (at the very least). Organisms can thus (re)establish and form ecological communities quickly.

In contrast, the greatest problem for organisms during terrestrialization in deep time was adapting to life on land in the first place. This process differed between major clades, although osmotic control and body support were common problems for both plants and animals (Markey and Marshall, 2007b; Clack, 2012; Standen et al., 2016; Lemberg et al., 2021; Tihelka et al., 2022). For vertebrates, terrestriality required extensive modifications to the locomotor and sensory systems, with corresponding neurological and behavioral changes (Clack, 2009; Esteve-Altava et al., 2019; MacIver and Finlay, 2022). In contrast, changes to the feeding system were comparatively modest before, during, and well past the origin of both limbs and terrestriality (Markey and Marshall, 2007b; Anderson et al., 2013; Neenan et al., 2014; Witzmann, 2016; Lemberg et al., 2021; Werneburg, 2024). The components of continental ecosystems had to be created through adaptation and cladogenesis on the scale of millions of years, rather than tens or hundreds, with the correspondingly slow assembly of continental ecosystems.

5 The unrepeatability of the past

In a review of plant and animal transitions between marine, freshwater, and terrestrial habitats, Vermeij and Dudley (2000) found that such transitions were rare overall, but not equally distributed: terrestrial–marine transitions are rarer than the reverse; most marine-terrestrial and terrestrial-marine transitions proceeded via freshwater; and marine–freshwater and terrestrial–freshwater transitions were more common than transitions between marine and freshwater (in either direction) via freshwater (Vermeij and Dudley, 2000). The discrepancy is particularly pronounced in limbed tetrapods, which have repeatedly become secondarily aquatic as far back as the Pennsylvanian (deBraga and Reisz, 1995; Nuñez Demarco et al., 2018) or even earlier (Ahlberg, 2018; Herbst and Hutchinson, 2018).

If, then, terrestrial–aquatic transitions are easier for organismal lineages than the reverse given that terrestriality requires a previous aquatic stage (either marine or non-marine), would we expect there to be an analogous directionality during the initial continentalization of ecosystems? Previous research has indicated that, during biotic invasions, invaders that persist do so via either outcompeting incumbents in the receiving community or filling unoccupied ecospace (Patzkowsky and Holland, 2007; Dudei and Stigall, 2010; Stigall, 2019; Kempf et al., 2020). If the source and receiving habitats are different, invaders might face additional competitive disadvantage due to the lack of suitable adaptations. For the earliest land colonizers, interspecific competition would initially have been low and had a negligible or small role in the taxic (low barrier to invasion) or structural (little or no forced ecospace overlap) composition of ecosystems. These colonizers adapted to increase their fitness in the new environment and became terrestrial residents. As additional organisms made the water–land transition (invaded), competition assumed a greater role that drove further terrestrial adaptation. At some hypothetical point during continentalization, the competitive barrier to invasion became a limiting factor; on the other hand, the cost of returning to the water was lower, although not uniform across lineages (Vermeij and Dudley, 2000).

In summary, just as secondarily aquatic organisms are constrained by a history of terrestrial existence, so might there be forms of continental ecological communities (especially terrestrial ones) that can only have existed in the geologic past. If that is the case, then Modern systems are insufficient as models. Testing this hypothesis, then, requires the extensive study of fossil data.

6 Terrestrialization and continentalization in the Devonian–Carboniferous

Plants and animals were present on land before the Devonian (Kenrick et al., 2012; Kraft et al., 2019; Pšenička et al., 2021; Buatois et al., 2022; Tihelka et al., 2022). However, it is during the Devonian that the terrestrial fossil record improved drastically (Edwards et al., 2018; Xue et al., 2018; Shen et al., 2020; Gess and Prestianni, 2021; Ţabără et al., 2021; Buatois et al., 2022), and these increased data enable us to better understand the emerging terrestrial biosphere. The Rhynie Chert community from the Early Devonian of Scotland preserves a continental community of microorganisms (nematodes), plants (lycopsids and extinct tracheophytes), aquatic invertebrates (e.g., branchiopods and notostracans), and terrestrial invertebrates (e.g., trigonotarbids, opiliones, and myriapods) distributed across multiple trophic levels. Based on the coprolite contents and mouthpart morphology, the terrestrial invertebrates included detritivores, fungivores, and predators (Habgood et al., 2003; Dunlop and Garwood, 2018). This community existed within a volcanic spring environment (Trewin, 1992). If continental communities were restricted to such environments in the Early Devonian, the community from the Gilboa Forest in New York (Shear et al., 1984, 1987; Norton et al., 1988; Shear and Bonamo, 1988; Stein et al., 2012) indicates that such limitations had been overcome by the Middle Devonian time (Givetian).

By the Middle Devonian, progymnosperms and lycopsids had diversified and repeatedly developed shrub and leaf habits (Stein et al., 2007, 2012; Berry and Marshall, 2015; Gensel et al., 2020), leading to the formation of wetland forests and woodlands (Greb et al., 2006; Gensel et al., 2020). Here, terrestrial plants both created new microhabitats and a growing resource pool for terrestrial invertebrates. The advent of root systems in the Devonian (Morris et al., 2015; Xue et al., 2016; Stein et al., 2020, 2020; Wang et al., 2019) facilitated the establishment and the persistence of these communities: roots made plants more physically stable, increased the available nutrients through increased rock weathering, and increased the spread and density of the terrestrial biosphere by extending further underground. Terrestrial trigonotarbid–opilione–myriapod–scorpion assemblages are known from these habitats across the remainder of the Devonian (Parent and Cloutier, 1996; Cressler et al., 2010; Gess, 2013). The evolution of seed reproduction in the Middle Devonian (Gerrienne et al., 2004, 2005) enabled the expansion of terrestrial floras onto less waterlogged sediments during the Late Devonian (Greb et al., 2006; Cressler et al., 2010; Linkies et al., 2010; Gensel et al., 2020).

The increase in Devonian flora also affected aquatic organisms, both continental and marine. Increased organic matter and phosphorous runoff (Wang et al., 2020), as evidenced by the Devonian coastal plankton blooms and corresponding anoxic events (Joachimski and Buggisch, 1993; Algeo and Scheckler, 1998; Boyer et al., 2021). These blooms would have drawn marine organisms (chiefly vertebrates and eurypterids) closer to the shoreline and into non-marine environments. The physical stabilization of sediment by roots increased the persistence of riverbanks and shorelines. These littoral habitats could then be used as sites for reproduction (Gueriau et al., 2016; Olive et al., 2016; Gess and Whitfield, 2020; Piñeiro et al., 2024) and/or feeding on others doing the same before returning to the ocean. Eventually, some of these transients adapted to life in these non-marine habitats as residents. The Devonian–Carboniferous increase in the abundance and diversity of non-marine microinvertebrates such as ostracods was particularly important in providing an expanding prey base for secondary consumers (Bennett et al., 2012). This transition to non-marine environments would be the antecedent for the transition to terrestrial environments in vertebrates (Vermeij and Dudley, 2000; Buatois et al., 2022).

The timing and process of vertebrate terrestrialization is currently contentious (King et al., 2011; Pierce et al., 2012; Mansky and Lucas, 2013; Ahlberg, 2018, 2024). Tetrapodomorph fishes had begun invading non-marine environments early in their evolutionary history and are common components of such brackish and freshwater assemblages from the Middle Devonian onward (Gray, 1988; Cressler et al., 2010; Sallan and Coates, 2010; Swartz, 2012; Schultze, 2013; Zhu et al., 2017; Laurin, 2024). Sedimentological and isotopic evidence suggests that a panderichthyid tolerance for variable salinity was maintained by tetrapods well into the Carboniferous (Laurin and Soler-Gijón, 2001, 2010; Gogáin et al., 2016; Bennett et al., 2017; Goedert et al., 2018; Laurin, 2024). Current phylogenies agree that panderichthyid (=elpistostegalian) tetrapodomorphs comprise the immediate outgroup to limbed tetrapods (Swartz, 2012; Cloutier et al., 2020; Stewart et al., 2022), although it is unclear whether they are a clade or a grade (a series of successive sister groups). The traditional ecological interpretation of panderichthyids has been as shallow-water aquatic predators, their well-developed, jointed fins being used to push against the substrate and navigate around obstacles (Shubin et al., 2006; Clack, 2012; Stewart et al., 2019). The dorsal shift in orbit placement and the increase in orbit size in panderichthyids and Devonian tetrapods relative to more conventionally “fish-shaped” tetrapodomorphs (e.g., *Eusthenopteron*) suggest an increasing role for vision in these animals, particularly vision through air (MacIver et al., 2017). Predation across the water–land interface as a learned behavior—sans morphological adaptation—has been documented in Modern catfish (Cucherousset et al., 2012). A similar behavior by panderichthyids and the earliest tetrapods might have been part of the changing neuroecology during the origin of tetrapods (MacIver and Finlay, 2022). Nevertheless, there is little “hard” evidence for vertebrates as “resident” components of terrestrial food webs by the end of the Late Devonian. That said, there are hypotheses that posit terrestrial locomotion for both panderichthyids and Devonian tetrapods (Ahlberg, 2018, 2024). The substantial (Warren and Wakefield, 1972; Rogers, 1990; Stössel, 1995; Niedźwiedzki et al., 2010; Stössel et al., 2016; Qvarnström et al., 2018) and growing (Ahlberg, 2024) Devonian trackway record attributed to tetrapod trackmakers remains temporally disjunct from the body fossil record, but represents a tantalizing—if ambiguous—additional source of data.

The End-Devonian mass extinction (EDME), also known as the Hangenberg event, included mass extinctions of marine and non-marine vertebrates (Sallan and Coates, 2010) and terrestrial plants (Myrow et al., 2014; Silvestro et al., 2015; Marshall, 2020; Marshall et al., 2020). There are earliest Mississippian tetrapod trackways (Mansky and Lucas, 2013; Lucas, 2019), but no body fossil evidence for tetrapod terrestriality (Lennie et al., 2021; Long et al., 2025). Terrestrial arthropod assemblages during the Tournaisian were similar to their Late Devonian counterparts in both taxonomic composition and trophic structure (Clarkson, 1985; Mansky and Lucas, 2013; Otoo et al., 2018). The Visean East Kirkton fauna represents a key biota within the context of continentalization. In addition to a more species-rich arthropod fauna (although still only composed of predators and detritivores), the East Kirkton community includes the oldest terrestrial tetrapod body fossils (Milner and Sequeira, 1993; Smithson et al., 1993; Ruta and Clack, 2006; Ruta et al., 2020). This makes East Kirkton the oldest terrestrial vertebrate assemblage at the time of writing (Clarkson et al., 1993). The lack of similar assemblages of terrestrial tetrapods elsewhere in the Mississippian (even from the Scottish Midland Valley succession, despite years of determined search) suggests that terrestrial tetrapods remained relatively rare until at least the Early Pennsylvanian. The Serpukhovian Loanhead community, also from the Scottish Midland Valley succession, contains primarily aquatic vertebrates alongside a much smaller number of likely semi-aquatic tetrapods (Smithson, 1985) and is much more representative of the Mississippian tetrapod communities (Godfrey, 1988; Schultze and Bolt, 1996; Snyder, 2006; Bolt and Lombard, 2010; Clack, 2012; Otoo et al., 2018, 2021).

There is trace fossil evidence of invertebrate herbivory on liverworts by the Middle Devonian (Labandeira et al., 2014), but traces of arthropod herbivory on living vascular plant tissue (folivory) appeared in the Late Mississippian (Iannuzzi and Labandeira, 2008). The latter is closely tied to the Carboniferous radiations of insects, in particular blattodeans, orthopterans, and palaeodictyopterans, that took advantage of expanding terrestrial floras (Grimaldi and Engel, 2005; Donovan et al., 2023). These radiations are primarily recorded in a few exceptionally preserved Pennsylvanian entomofaunas, such as Joggins (Bashkirian), Mazon Creek (Moscovian), and Carrizo Arroyo (Gzhelian) (Rowland, 1997, 1997; Shabica and Hay, 1997; Rasnitsyn et al., 2004, 2015; Grimaldi and Engel, 2005; Falcon-Lang, 2006; Falcon-Lang et al., 2006; Clements et al., 2019; Burke et al., 2024). Fossil coleopterans first appeared in the Early Permian, although they might also be part of these Carboniferous radiations (Kirejtshuk and Nel, 2013; Kirejtshuk et al., 2014; Beutel et al., 2019; Schädel et al., 2022; Boudinot et al., 2023).

Although body sizes generally remained small during the Early Pennsylvanian (Bashkirian–Moscovian), terrestrial tetrapods expanded into both fossoriality (Maddin et al., 2011; Pardo et al., 2015; Mann et al., 2019, 2021a) and scansoriality (Mann et al., 2021b). From the Mississippian through the end of the Early Pennsylvanian, the set of terrestrial tetrapods was taxonomically skewed toward “lepospondyls” (especially “microsaurs”) and total group amniotes (Hook and Baird, 1986, 1993; Clarkson et al., 1993;

Milner and Sequeira, 1998, 2011; Falcon-Lang, 2006; Stimson et al., 2013; Mann et al., 2020). The phylogenetic status and affinities of Lepospondyli and its various putative subclades are topics of active debate among early tetrapod specialists (Ruta and Coates, 2007; Pardo et al., 2017; Clack et al., 2019; Marjanović and Laurin, 2019; Mann et al., 2023b; Pardo, 2023; Igielman, 2024; Smithson et al., 2024), but beyond the scope of this paper.

During the Late Pennsylvanian (Kasimovian–Gzhelian), tetrapods began adapting for omnivory and, later, herbivory (Beerbower et al., 1992; Mann et al., 2023a; Ponstein et al., 2024). The advent of tetrapod herbivory greatly increased the influence of tetrapods on plants (Brocklehurst et al., 2020) and compounded the structural changes to food webs induced by insect herbivory. The upper limit of terrestrial tetrapod body size among herbivores and predators increased markedly around this time (Brocklehurst and Brink, 2017). It is during the Late Pennsylvanian that crown amniote lineages began returning to the water (deBraga and Reisz, 1995; Nuñez Demarco et al., 2018), although the specifics are disputed (Romer, 1974; Canoville and Laurin, 2010; Felice and Angielczyk, 2014; Laurin and Piñeiro, 2017; Nuñez Demarco et al., 2018). Thus, by the end of the Pennsylvanian, the fundamental components of terrestrial vertebrate ecosystems appeared to have been in place: multitaxic, architecturally diverse floras; terrestrial invertebrate primary and secondary consumers; and vertebrate primary and secondary consumers.

7 The Late Paleozoic origin of terrestrial vertebrate ecosystems

Olson proposed a scenario for the development of terrestrial vertebrate communities during the Permian (Olson, 1952, 1966, 1971, 1977). He defined a terrestrial (vertebrate) community as one for which the energy base is terrestrial primary productivity. Olson began with (at the time) the oldest known communities with terrestrial vertebrates. These communities were still considered aquatic (but still continental) as aquatic primary activity forms the energy basis of the community, conveyed to terrestrial organisms via predation on semi-aquatic and aquatic organisms. Olson developed this characterization of "type I" communities based primarily on observations of lowland redbed communities from the Late Pennsylvanian/Early Permian of the Southwestern United States (Carpenter, 1970; Olson, 1971, 1977; Fracasso, 1980; Rowland, 1997; Krainer and Lucas, 2004; Schneider et al., 2004; Lucas et al., 2005, 2010; Huttenlocker et al., 2018). Among these, tetrapod herbivores were greatly outnumbered by predators. Terrestrial insects were the primary terrestrial herbivores.

Type III communities overlapped with type I communities in time, but developed in upland, rather than lowland, settings. The communities were based on terrestrial primary productivity, which supported insect herbivores that were, in turn, preyed upon by small tetrapods. Olson considered type III communities to be rare (in large part due to the lack of favorable preservational conditions), but suggested that the Early Permian Fort Sill and the Middle Permian Mezen, Shikhovo-Chirki, and Belebei assemblages from Russia could represent type III communities (Olson, 1962, 1966, 1971). Olson variously hypothesized that the Middle Permian "caseid chronofauna" assemblages—so named for the overwhelming abundance of herbivorous caseids—were type II or type III communities (Olson and Beerbower, 1953; Olson, 1958, 1962, 1966, 1971).

Over the course of the Permian, type I and type III communities were replaced by "fully" terrestrial type II communities. The increased diversity of tetrapod herbivores created the necessary terrestrial food source to effectively reduce the dependence of terrestrial predators on aquatic or semi-aquatic prey, thereby shifting the energy base for the community to terrestrial primary productivity. Olson hypothesized that type II communities developed various combinations of type I and type III communities approximately by the Middle Permian. Olson's first clear examples of type II communities are pareiasaur–therapsid assemblages from the Late Permian of Russia (Olson and Chudinov, 1992; Golubev, 2000; Benton et al., 2004; Tverdokhlebov et al., 2005; Shishkin, 2022a, b) and South Africa (Olson, 1965, 1966, 1971; Damiani, 2004; Day, 2013; Sidor et al., 2013; Fröbisch, 2014; Brocklehurst et al., 2017; Groenewald et al., 2019; Day and Rubidge, 2021; Prevec et al., 2022; Viglietti et al., 2022; Ronchi et al., 2023). Since the Late Permian, type II of various taxonomic compositions have gone on to dominate the terrestrial portion of the continental biosphere (Olson, 1966).

Substantial data have been added since Olson's articulation of the above hypothesis. East Kirkton approximates a small type III community, albeit one based mostly on the exploitation of detritus rather than living plant matter (Clarkson et al., 1993). Such "pseudo-type III" communities might have been relatively common during the terrestrialization of arthropods (e.g., Gilboa) and tetrapods at least through the Early Pennsylvanian. New data from Richards Spur (=Fort Sill) (Anderson and Reisz, 2003; Anderson et al., 2009; Modesto et al., 2018b; Brink et al., 2019; deBraga et al., 2019; Gee et al., 2019; Gee, 2020; Hannibal and May, 2020), Bally Mountain (Fox and Bowman, 1966; LeBlanc et al., 2015; Goss, 2023), and Bromacker (Berman et al., 2000, 2014; Eberth et al., 2000) localities indicate the presence of type II communities in the Early Permian. In all three, tetrapod herbivores were a dominant component, chiefly captorhinomorphs (Richards Spur and Bally Mountain) or diadectids (Bromacker). Dental morphologies support high-fiber herbivory in both groups by the Early Permian (Hotton et al., 1997; Ponstein et al., 2024). The composition of these assemblages suggests that type II communities were present by the Early Permian and were less tied to the evolution of mammal-line tetrapods than Olson supposed.

At the same time, data from South America are difficult to interpret. Although records of Early Permian captorhinids (Cisneros et al., 2020), Middle Permian therapsids (Langer, 2000; Cisneros et al., 2012), and Late Permian temnospondyls (Piñero et al., 2007) suggest similar faunal turnover to that observed in Russia and South Africa (Cisneros et al., 2012), it is not clear that the same was the case for changes in community structure. For example, the Early Permian dvinosaur–captorhinid fauna from the Parnaíba Basin of Brazil (Iannuzzi et al., 2018; Cisneros et al., 2020; Marsicano et al., 2021; Richter et al., 2022) could represent a partially preserved type I or type II community, or another form of organization entirely.

Under Olson's hypothesis, the change in community structure, either through transformation or replacement, was gradual rather than catastrophic. However, he did suggest that older community structures could reemerge:

> "Later, during the Triassic, new versions of type I appeared once more. With the development of birds and mammals, the chances of such communities were reduced. Type I, however, is approximated in some of the largely fish-based communities that exist in subtropical swamp regions. The assemblages of the Florida Everglades, in their unmodified form, depart only moderately from this type of community." (Olson, 1966, p. 296).

The aberrance of the Early Triassic continental biosphere in the aftermath of the End-Permian mass extinction (EPME) is well attested (Benton et al., 2004; Roopnarine et al., 2007, 2018, 2019; Irmis and Whiteside, 2012; Roopnarine and Angielczyk, 2012, 2015; Whiteside et al., 2015; Huang et al., 2021; Viglietti et al., 2022; Hoffman et al., 2023; Rey et al., 2023; Shishkin et al., 2023a, 2023; Pinheiro et al., 2024). In southern Africa, food web modeling found that Early Triassic communities were more unstable and vulnerable to collapse than those prior to the EPME (Roopnarine et al., 2007, 2018; Roopnarine and Angielczyk, 2012). The Early Triassic communities were greatly depleted in terrestrial herbivores and enriched in small terrestrial predators. Taxonomically, these communities were dominated by multiple clades of aquatic and terrestrial temnospondyls (Damiani and Rubidge, 2003; Roopnarine et al., 2007; Mehmood et al., 2025). Intense competition among predators, predation pressure on insect prey, and a lack of herbivores created a boom-and-bust dynamic in the community. These communities might represent type III communities, or a (partial) recapitulation of the type I structure (Huttenlocker, pers. comm.; Irmis, pers. comm.). In either case, it is possible that instability was a feature of these community structures that contributed to their marginalization by type II communities. Alternatively, these could represent dysfunctional, "incomplete" type II communities that have had their terrestrial component temporarily pared back by extinction, or type III communities alongside their aquatic counterparts/ components. It is possible, then, that mass extinctions generally might not only degrade the structure of preexisting communities but also temporarily allow otherwise marginal forms of organization to proliferate.

8 Methods and hypothesis testing

Testing hypotheses of community-level selection and competition will be an important step toward reconciling paleontological and ecological modeling perspectives on the uniformity of processes over geologic time. Categorizing the autecology of fossil species—which is necessary to constraining their possible ecological interactions for the purpose of modeling (Bartley et al., 1993)—has been done across numerous studies, most of which focused on marine invertebrates (Bambach et al., 2007; Novack-Gottshall, 2007; Sahney et al., 2010b; Mondal and Harries, 2016; Reeves et al., 2020; Whalen et al., 2020). The categorical approach must necessarily balance precision (the ability to capture the autecology of a taxon) and breadth (the ability to be applied to taxa across space and time) and is best suited for larger datasets and cases in which autecology is difficult to infer from available data.

Once species autecologies have been established, the paleoecological community can be reconstructed from the fossil assemblage (Behrensmeyer, 1982; Bartley et al., 1993; Flessa, 2001). A paleoecological community can be analyzed as either a collection of the autecologies of its component organisms or as a network of interactions such as a food web (Dunne et al., 2008; Mitchell et al., 2012; Roopnarine and Angielczyk, 2015; Chevrinais et al., 2017; Codron et al., 2017; Roopnarine et al., 2018). When modeling the community as a food web, species–species feeding interactions can either be specified by the user (Dunne et al., 2004, 2008; Cortés and Larsson, 2023) or drawn stochastically from a set of possible interactions (Roopnarine, 2009; Mitchell et al., 2012; Roopnarine et al., 2018, 2019; Kempf et al., 2020; Huang et al., 2021, 2023). Both methods allow for model simplification, either through the collapsing of species with identical specified feeding relationships into trophic species or the collapsing of species with identical potential feeding relationships into guilds, respectively. The structure of the community can then be described, usually with ordinations and network statistics (Dunne et al., 2008; Chevrinais et al., 2017; Roopnarine et al., 2018; Banker et al., 2022), and compared to other communities in a dataset. Standard metrics include connectance, link density, and network trophic position (Table 1).

Communities can be compared based not only on their structure and composition but also on their community-level (=emergent) properties. (Global) stability combines persistence (i.e., how long a species continues in a community before going extinct) with stable coexistence (i.e., the ability of species to coexist without external disruption) and can be expressed as the faction of species that can persist different conditions (Chen and Cohen, 2001). Resistance to perturbation is another metric (Roopnarine, 2009), which captures the proportion of species in the community that become extinct (populations decrease to zero) in response to perturbation (usually loss of primary productivity). Roopnarine et al. recently developed a method to compare the stability between both observed communities (those modeled on fossil data) and computer-generated communities of similar species richness but different trophic structure to test for community-level selection for stability (Roopnarine et al., 2019). Community-level properties are key to the question of whether or not (paleo)ecological communities evolve (Eldredge, 1985; Jablonski and Sepkoski, 1996; Bambach, 2001; Spiridonov and Eldredge, 2024).

TABLE 1 Network statistics commonly calculated for food web studies. Formulae and explanations drawn from Banker et al., 2022.

Metric	Symbol	Calculation	Explanation
Connectance	C	$C = \frac{L}{G^2}$	C is connectance, L is the number of guild interactions, and G is the number of guilds.
Link density	D_i	$D_i = \frac{L}{G}$	D_i is the link density of guild i.
Network trophic position	ntp_i	$\mathrm{ntp}_i = 2 + \frac{1}{r_i}\sum_{j=1}^{S} a_{ij} l_j$	r_i represents the number of prey species of i and $a_{ij} = 1$ if j consumes species i and is otherwise 0. l_j is the shortest path length of species j to the primary producer level. Primary producers have an ntp of 1.

An attempted synthesis of hypotheses of the changes in community properties and structure during Paleozoic continentalization is presented in Figures 1 and 2 (sources for graphics are presented in Tables 2 and 3). It can be divided into two phases: the first defined by the terrestrialization of plants and arthropods and the second defined by the terrestrialization of vertebrates (tetrapods). Possible community-level properties for selection are conceptually united as "performance." More precise estimations are made here below.

The first phase (Figure 2) was underway by the Ordovician and began with the colonization of land by plants, fungi, and arthropods. The terrestrial–terrestrial species feeding interaction strengths were initially outweighed by those of terrestrial–aquatic feeding interactions and, as during island colonization (Heatwole, 1981; Thornton, 2007), turnover was high and the stability of the terrestrial food web was likely low. Increased adaptation to the terrestrial environment continued until stable food webs could persist and replicate across the landscape. Arthropod exploitation of terrestrial detritus, fungi, and plants (Labandeira, 1997; Labandeira et al., 2014) was key in establishing a trophic guild of a fully terrestrial primary consumers. Interspecific competition increased (Vermeij and Dudley, 2000; DiMichele et al., 2023b), as did co-evolution: morphological evidence suggests that, by the Middle Devonian, terrestrial plants had developed chemical defenses against invertebrate herbivory (Labandeira et al., 2014). The Middle Devonian Gilboa assemblage represents the form of the oldest terrestrial community and the culmination of this first phase.

The second phase (Figure 2) began when the effect of vertebrate feeding across the water–land interface started to exert a significant effect on terrestrial food webs, reintensifying the aquatic–terrestrial interactions and effectively "de-terrestrializing" terrestrial communities by more fully integrating them with aquatic

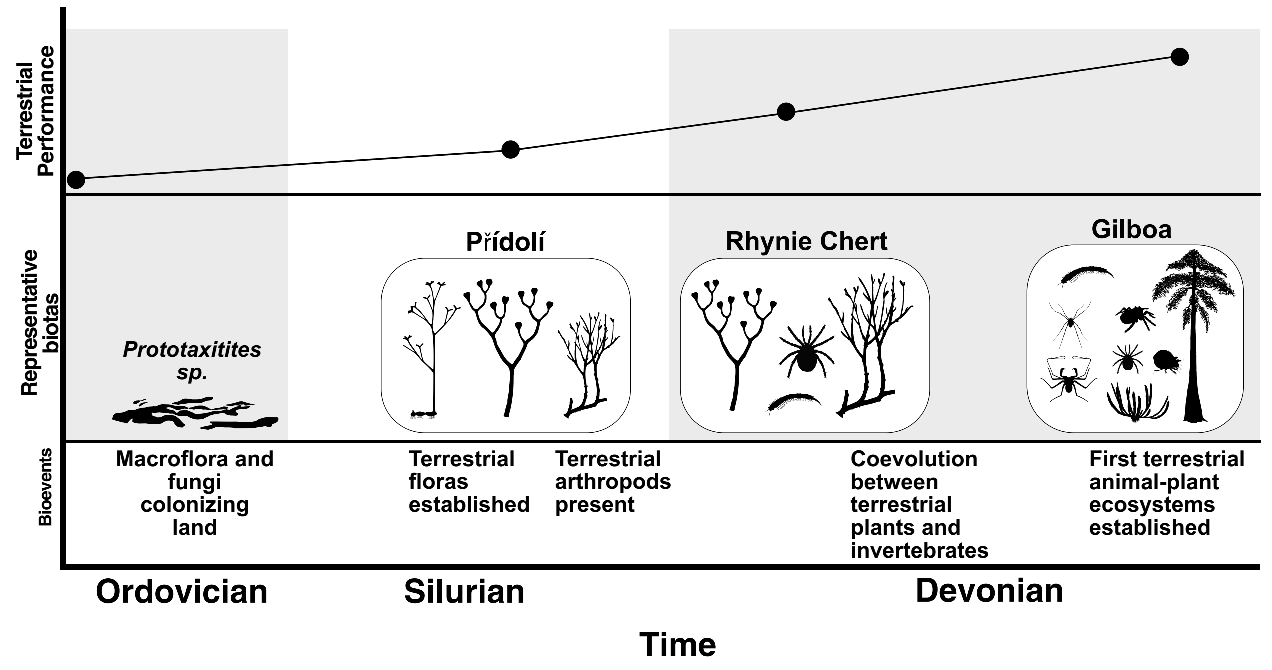

FIGURE 1
Hypothetical community performance curve during the origin and early development of terrestrial communities during the Ordovician–Devonian. Representative faunas are represented by silhouettes of component organisms (or analogues/equivalents): Přídolí (Libertín et al., 2018; Kraft et al., 2019; Pšenička et al., 2021), Rhynie Chert (Dunlop and Garwood, 2018; Long et al., 2024), and Gilboa (Shear et al., 1984, 1987; Norton et al., 1988; Shear and Bonamo, 1988; Stein et al., 2007, 2012, 2021). Silhouettes from PhyloPic. Individual contributors are listed in Table 2.

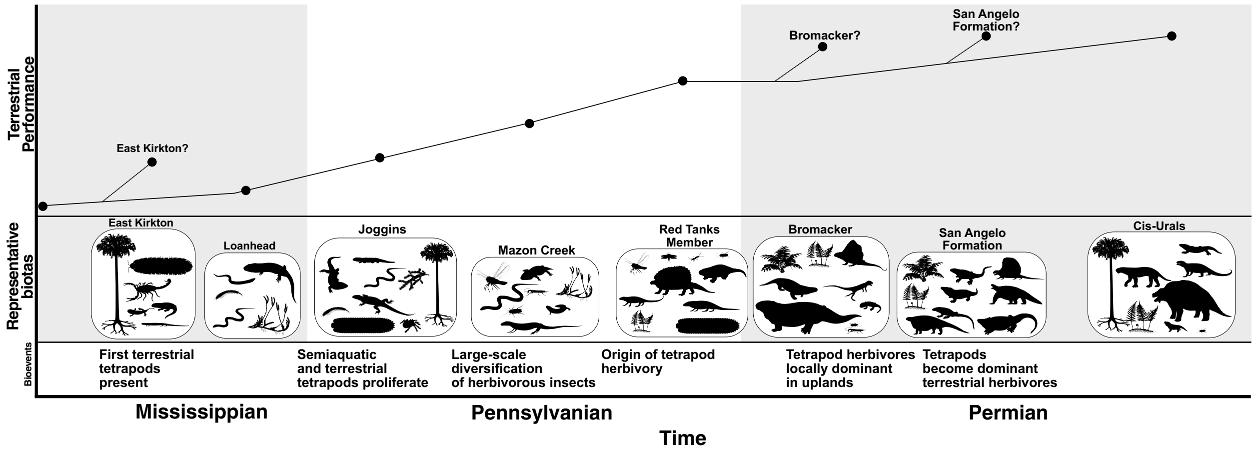

FIGURE 2
Hypothetical community performance curve during the origin and early development of terrestrial communities during the Mississippian–Permian. Representative faunas are represented by silhouettes of component organisms (or analogues/equivalents): East Kirkton (Clarkson et al., 1993), Joggins (Falcon-Lang, 2006; Falcon-Lang et al., 2006; Mann et al., 2020), Mazon Creek (Shabica and Hay, 1997; Mann and Gee, 2019; Mann et al., 2021a, b), Red Tanks Member (Rowland, 1997; Hannibal et al., 2004; Harris et al., 2004; Rasnitsyn et al., 2004; Schneider et al., 2004), Bromacker (Berman et al., 2000, 2014; Eberth et al., 2000), San Angelo Formation (Olson and Beerbower, 1953; Olson, 1966, 1971; Sidor and Hopson, 1998), and Cis-Urals (Olson, 1962, 1966; Tverdokhlebov et al., 2005; Naugolnykh et al., 2022). Silhouettes from PhyloPic. Individual contributors are listed in Table 3.

communities. This phase was preceded by the invasion of non-marine settings by vertebrates and was arguably a continuation of such. Effects on stability depend on hypotheses of tetrapod terrestrialization (see *Section 6*), particularly the role of miniaturization. Larger aquatic tetrapods would have been resistant to terrestrial predation and thus represent destabilizing pressure on the terrestrial sub-community. Small aquatic tetrapods, as prey for terrestrial predators (Mansky and Lucas, 2013), would have a stabilizing effect by transferring biomass from the aquatic to the terrestrial sub-community. This phase probably began sometime in the Late Devonian or the earliest Mississippian, but body fossil evidence has yet to be found. Regardless, it was well underway by the middle Mississippian (Clarkson et al., 1993; Garza et al., 2025), from which point on body size diversity was such that tetrapods exerted both effects to varying degrees across faunas. The stability and species carrying capacity of the terrestrial sub-community increased as terrestrial herbivorous insects diversified in the middle–late Pennsylvanian.

TABLE 2 Credits for the silhouettes used in Figure 1.

Taxon	Fauna	PhyloPic creator
Prototaxites sp.	N/A	Public domain
Horneophyton lignieri	Přídolí	Peter Coxhead
Cooksonia pertoni	Přídolí	Ville Koistinen
Rhynia gwynne-vaughanii	Přídolí	Griensteidl, T. Michael Keesey
Palaeotarbus jerami	Rhynie	Public domain
Sottyxerxes multiplex	Rhynie Chert	Qohelet12
Archaeopteris sp.	Gilboa	Falconaumanni, T. Michael Keesey
Palaeotarbus germaini	Gilboa	Gareth Monger
Palpatores sp.	Gilboa	Gemma Martínez-Redondo
Oribatula tibialis	Gilboa	Birgit Lang
Phrynoidea sp.	Gilboa	Gemma Martínez-Redondo
Psilotum complanatum	Gilboa	Public domain

The silhouettes used in multiple faunas are credited with the first fauna in which they appear.

By the Early Permian, both of Olson's type I and type II communities were present. Their relative community-level performance at that time is difficult to assess, in part due to the environmental differences between the two. The diversification of tetrapod herbivores almost certainly had a stabilizing effect, as seen in the natural experiment of their preferential removal in the EPME and scarcity in the protracted post-extinction recovery (Roopnarine et al., 2007, 2018, 2019; Roopnarine and Angielczyk, 2015). What does appear to be the case is that, by the middle Permian, terrestrial communities had (re)emerged as distinct from aquatic communities that contained semi-aquatic and/or terrestrial species. The apparent replacement of type I communities by type II communities in environments occupied by the former in the middle and late Permian, subsequent the global success of type II communities, and the marginalization of type I communities are consistent with type II communities being more stable and/or having a greater carrying capacity.

9 Conclusions

The origin of terrestrial ecosystems during the Paleozoic, part of the broader phenomenon of continentalization during this time, was a crucial episode in the development of the Earth's biosphere. Since the middle 20th century, the pre-Permian fossil and geobiological records have improved dramatically (Clarkson et al., 1993; Coates et al., 2008; Knauth and Kennedy, 2009; Cressler et al., 2010; Clack, 2012; Kenrick et al., 2012; Gensel et al., 2020; Pšenička et al., 2021). Advances in biomechanics (Markey and Marshall, 2007a; Rayfield, 2007; Brainerd et al., 2010) and ecological modeling (Chen and Cohen, 2001; Dunne et al., 2002; Roopnarine, 2009; Villéger et al., 2011; Slatyer et al., 2013) have greatly expanded our capacity for reconstructing the ecology of fossil organisms and communities, respectively. Much of the incorporation of these techniques into paleontology is the result of increasing interdisciplinary and international collaboration.

Substantial data gaps and analytical challenges remain. Hypotheses of early tetrapod terrestrialization remain complicated by the incongruity between the body fossil and trackway records (Ahlberg, 2018; Long et al., 2025). While much more is now known from previously understudied regions, such as South America (Piñeiro et al., 2003, 2012; Piñero et al., 2007; Cisneros et al., 2012, 2015, 2020; Abrantes et al., 2016, 2019; Araújo et al., 2016; Iannuzzi et al., 2018), Southern Europe (Matamales-Andreu et al., 2022), China (Jun et al., 2014; Chen and Liu, 2020; Huang et al., 2021), and Africa (O'Keefe et al., 2005; Damiani et al., 2006; Steyer et al., 2006; Smiley et al., 2008; Sidor, 2013; Sidor et al., 2013, 2021, 2023; Tsuji et al., 2013; Smith et al., 2015; Turner et al., 2015; Peecook et al., 2017, 2021; Modesto et al., 2018a; Roopnarine et al., 2018), we still know much less about these areas during the Paleozoic than their North American and European counterparts. Reinvestigation of the latter in the context of current dating and stratigraphic schemes (Smith, 1974; Clack et al., 2016; Naugolnykh et al., 2022; Viglietti et al., 2022; Garza et al., 2025) is also warranted. This knowledge deficit hampers attempts to understand the temporal and geographic distributions of not only taxa but also forms of the ecological structure. This paper has focused on animals, especially tetrapods, but there is a pressing need to integrate the fossil records of vertebrates, invertebrates (both micro- and macroinvertebrates), and plants (Bartley et al., 1993; Falcon-Lang, 2006; Falcon-Lang et al., 2006; Iannuzzi and Labandeira, 2008; Sahney et al., 2010a; Stimson et al., 2013; van Hoof et al., 2013; Labandeira et al., 2014; Clack et al., 2016; Kearsey et al., 2016; Dunne et al., 2018; Schachat et al., 2018b, 2018; Bennett et al., 2021; Buatois et al., 2022; Whittingham et al., 2022, 2024; DiMichele et al., 2023a, 2023; Whittingham, 2023; Knecht et al., 2024).

Current community modeling methods have been applied to individual faunas (Dunne et al., 2008; Chevrinais et al., 2017) or biotic crisis intervals (Sidor et al., 2013; Roopnarine and Angielczyk, 2015; Roopnarine et al., 2018, 2019). Recent large-scale biogeographic datasets (Brocklehurst and Fröbisch, 2018; Brocklehurst et al., 2018; Pardo et al., 2019) could represent the foundation of comparative analyses that could test hypotheses such as those of Olson (Olson, 1952, 1966, 1971), Romer (Romer, 1958, 1974), and others (Sahney et al., 2010a; Mansky and Lucas, 2013; Ahlberg, 2018; Lucas, 2019) about the ecological context for evolutionary events and the development of communities themselves. Such investigations are work- and data-intensive, but have proven highly informative and

TABLE 3 Credits for the silhouettes used in Figure 2.

Taxon	Fauna	PhyloPic creator
Lepidodendron sp.	East Kirkton	Eliana P. Coturel
Westlothiana lizzae	East Kirkton	Public domain
Balanerpeton woodi	East Kirkton	Scott Hartman
Eldeceeon rolfei	East Kirkton	Neil G. Pezzoni
Pulmonoscorpius kirktonensis	East Kirkton	Junn111
Arthropleura sp.	East Kirkton	Timothy Bertelink
Lycopodium clavatum	Loanhead	Public domain
Aistopoda	Loanhead	Public domain
Adelospondylus watsoni	Loanhead	Dmitry Bogdanov
Caerorhachis bairdi	Loanhead	Dmitry Bogdanov
Arthropleura sp.	Joggins	Jun
Dendrerpeton acadianum	Joggins	Dmitry Bogdanov
Lycopodium clavatum	Joggins	Mason McNair
Hylonomus lyelli	Joggins	Nobu Tamura, T. Michael Keesey
Leiocephalikon problematicum	Joggins	Daeng Dino
Protorothyris archeri	Mazon Creek	Smokeybjb, T. Michael Keesey
Periplaneta americana	Mazon Creek	Thomas Hegna
Meganeura sp.	Mazon Creek	Public domain
Amphibamus grandiceps	Mazon Creek	Nobu Tamura
Grylloblatta campodeiformis	Mazon Creek	Public domain
Joermungandr bolti	Mazon Creek	Nix Illustration
Polypodium vulgare	Red Tanks Member	Public domain
Diasparactus zenos	Red Tanks Member	Dmitry Bogdanov
Planococcus citri	Red Tanks Member	Public domain
Stenodictya sp.	Red Tanks Member	Public domain
Ophiacodon sp.	Red Tanks Member	Public domain
Clepsydrops sp.	Red Tanks Member	Dmitry Bogdanov
Edaphosaurus pogonias	Red Tanks Member	Matt Celeskey
Marattia sp.	Bromacker	Mason McNair
Georgenthalia clavinasica	Bromacker	Dmitry Bogdanov
Eudibamus cursoris	Bromacker	Nobu Tamura

(Continued)

TABLE 3 Continued

Taxon	Fauna	PhyloPic creator
Seymouria baylorensis	Bromacker	Will Toosey
Diadectes sp.	Bromacker	Dmitry Bogdanov, Roberto Díaz Sibaja
Dimetrodon loomisi	Bromacker	Dmitry Bogdanov
Dimetrodon giganhomogenes	San Angelo Formation	Dmitry Bogdanov
Varanops brevirostris	San Angelo Formation	Dmitry Bogdanov
Varanodon agilis	San Angelo Formation	Dmitry Bogdanov
Labidosaurikos meachami	San Angelo Formation	Dmitry Bogdanov
Cotylorhynchus hancocki	San Angelo Formation	Dmitry Bogdanov
Cotylorhynchus sp.	San Angelo Formation	Dmitry Bogdanov, Roberto Díaz Sibaja
Cotylorhynchus sp.	San Angelo Formation	Jagged Fang Designs
Scutosaurus karpinskii	Cis-Urals	Public domain
Phthinosuchus sp.	Cis-Urals	CaptGo
Venyukovia prima	Cis-Urals	Dmitry Bogdanov
Sauroctonus parringtoni	Cis-Urals	Public domain
Chroniosuchus paradoxus	Cis-Urals	Dmitry Bogdanov

The silhouettes used in multiple faunas are credited with the first fauna in which they appear.

productive (Sidor et al., 2013; Roopnarine and Angielczyk, 2015; Roopnarine et al., 2018, 2019; Angielczyk et al., 2020). Future studies of deep-time continentalization can begin to test hypotheses about the universality of ecological rules, the interactions between ecological and evolutionary processes on multiple scales (Spiridonov and Eldredge, 2024), and more.

Author contributions

BKAO: Conceptualization, Writing – review & editing, Investigation, Writing – original draft.

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Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

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