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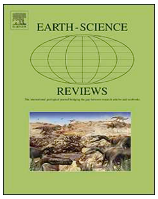

Ecological persistence, incumbency and reorganization in the Karoo Basin during the Permian-Triassic transition

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ABSTRACT

The geological persistence of biotic assemblages and their reorganization or destruction by mass extinctions are key features of long-term macroevolutionary and macroecological patterns in the fossil record. These events affected biotic history disproportionately and left permanent imprints on global biodiversity. Here we hypothesize that the geological persistence and incumbency of paleocommunities and taxa are maintained by patterns of biotic interactions that favour the ecological persistence and stable coexistence of interacting species. Equally complex communities produced by alternative macroevolutionary histories, and hence of different functional structure, may support less stable species coexistence, and are therefore less persistent. However, alternative communities with the same functional structure as a persistent paleocommunity, but variable clade richnesses, tend to be as or more stable than observed palecommunities, thus demonstrating that geological persistence is not the result of constrained patterns, or ecological locking. Numerically modeled food webs for seven tetrapod-dominated paleocommunities spanning the traditionally-recognized Permian-Triassic boundary in the Karoo Basin of South Africa, show that incumbency before the Permian-Triassic mass extinction was maintained by a dynamically stable, community-level system of biotic interactions, thereby supporting the hypothesis. The system's structure was lost through successive extinction pulses, and replaced initially by a rich but geologically ephemeral Early Triassic fauna, which itself was replaced by a novel Middle Triassic community with renewed incumbency. The loss of persistence and incumbency, therefore, did not result simply from the extinction of species; instead the largest declines were accompanied by the addition of new species to the system in the earliest aftermath of the event. We therefore further hypothesize that ecological reorganization and evolutionary innovation in the wake of mass extinctions play key roles in the destruction of highly stable, preexisting systems of biotic interaction. In the case of the Karoo Basin paleocommunities, we estimate that a return to stable interactions, and thus incumbency, was achieved in approximately 4–17 Ma.

1. Introduction

The compositional stability, or persistence, of biotic assemblages at multiple levels of the taxonomic and ecological hierarchies is a major feature of the Phanerozoic fossil record (Dimichele et al., 2004). In the marine realm, the most encompassing of these assemblages are Sepkoski's marine evolutionary faunas, but multiple lower levels of organization have been proposed, including Boucot's Ecological Evolutionary Units (EEUs) (Boucot, 1983; Sheehan, 1996), and subdivisions at yet finer stratigraphic and geographic scales (Bambach and Bennington, 1996). Similar attempts have been made to partition Phanerozoic terrestrial biotas into major assemblages, often with different macroevolutionary properties, including studies of plants (Niklas et al., 1983; Niklas and Tiffney, 1994; Cleal and Cascales-Miñana, 2014), insects (Labandeira and Sepkoski, 1993), tetrapods (Benton, 1985a, 1985b; Sahney et al., 2010), and even community-level trophic structures (Olson, 1966). More recent work has focused on identifying important shifts in diversification and extinction patterns without attempting to define major assemblages (e.g., Condamine et al., 2016; Cascales-Miñana and Cleal, 2014). Nevertheless, the idea of significant shifts in composition and abundance, such as the replacement of communities dominated by archaic synapsids by communities comprising early members of more modern lineages following the Permo-Triassic mass extinction (e.g., Fraser and Sues, 2010; Sookias et al., 2012; Benton et al., 2014; Padian and Sues, 2015; Simões et al., 2018) retains a pervasive influence on our understanding of the evolution of

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terrestrial ecosystems.

The division of the Phanerozoic biota into compositionally consistent sub-units is motivated by the geological persistence of specific clades, the greater abundance (numeric dominance) of specific clades, and the types of paleocommunities featuring and often dominated by those clades. The causes of this macroevolutionary incumbency remain debated, but it has been attributed variously to differential rates of speciation (Rosenzweig and McCord, 1991), the resistance of incumbents to the evolution or invasion of ecologically similar competitors (Vermeij and Roopnarine, 2013), constraints of biotic interactions (Roy, 1996; Morris et al., 1995), competitive superiority (Hallam and Wignall, 1997), environmental fidelity and tracking (Dimichele et al., 2004), and purely stochastic phenomena (Gould and Calloway, 1980). Regardless, a broadly recognized fact is that transitions between these biotic units are marked by changes of incumbency, either by the extinction of incumbent clades or their loss of dominance. Jablonski (2001) noted that incumbent clades are often removed, or their incumbency undone, by mass extinctions, and Sheehan (1996) proposed extinction as the mechanism underlying the ecological reorganizations that take place during the transitions between EEUs. Thus, complementary to compositional stability at the highest ecological and macroevolutionary levels is the consistent removal of incumbents by mass extinctions, and the subsequent reorganization of ecological communities or their replacement by ecologically novel systems. The prevalence of such transformations, and the replacement of previously successful incumbents, have given mass extinctions an effect on history disproportionate to their relatively minor contribution to the total number of Phanerozoic extinctions (Marshall, 1998; Hull et al., 2015).

In this paper we propose a new hypothesis to explain incumbency, compositional stability, and the reorganizations that take place at the end of macroevolutionary biotic units. We propose that compositional stability is maintained by specific patterns of biotic interactions that arise among coexisting and coevolving clades. The patterns of biotic interaction, however, do not act as constraints. Instead, compositional stability is maintained because those patterns of interaction promote both the ecological persistence and ecologically stable coexistences of the species involved, rendering low likelihoods that significant macroevolutionary changes will yield alternative patterns of interaction that would improve either persistence or coexistence. We show, using a well-documented series of terrestrial paleocommunities from the Karoo Basin of South Africa, spanning the Permian-Triassic mass extinction (PTME), that incumbency and compositional stability prior to the mass extinction were maintained by a community-level structure of biotic interactions. The structure's loss through successive waves of extinction resulted in an Early Triassic community in which reorganization could have significantly improved species persistence and coexistence. By the Middle Triassic, however, this recovery stage was replaced by a community in which significant innovation and reorganization would have been disadvantageous, thereby forming the basis for renewed incumbency. We argue that the apparent stability of the pre-PTME ecosystem, its subsequent loss, and replacement, resulted from the influence of community-level structure and dynamics on species evolution and survival. To test the hypothesis, we examine the Karoo system prior to, during, and after the PTME and make three predictions. First, there should have been a low likelihood of macroevolutionary change prior to the mass extinction. Second, that likelihood should have increased significantly after the mass extinction. And finally, recovery from the mass extinction would have been marked by an ecological transformation to a new type of paleocommunity, characterized by renewed compositional stability and incumbency.

Our hypothesis implies an association between a community's interspecific biotic interactions, and both long term species persistence and stable coexistence in the community. The manner in which interactions are structured in a community certainly plays a role in the stability of the community, and Roopnarine and Angielczyk (2015) established that the paleocommunities considered here had significantly greater local stabilities (ability of a system in equilibrium to return to equilibrium after minor disturbance) than equivalently rich, but randomly structured communities. The basis for the difference between the paleocommunities and random communities is the manner in which species are partitioned along dimensions of ecological function and habitat, the trophic relationships among the resulting partitions, and the species richnesses of the partitions, which we refer to collectively as the paleocommunity's structural complexity. Such partitioning is a level of organization within a community above species, and it constrains both the number and types of interactions possible within the community. However, the number of ways in which a set of unique species can be partitioned is beyond astronomical for even communities of modest diversity. Therefore, if compositionally stable paleocommunity types arise purely by chance, they would be unlikely to persist on geological timescales because environmental heterogeneity and change, as well as evolution, would be overwhelmingly likely to result in alterations that would degrade their stability. Mechanisms by which such communities could persist include: ecological superiority, where species within persistent paleocommunities were exceptionally resistant to the evolution or invasion of ecologically innovative taxa; constraint, where species evolution and other macroevolutionary changes were limited within those paleocommunities; and path dependence, where the initial historical stages of a developing paleocommunity would constrain its future compositional options. The observed transitions between community types could also occur if previous tolerance to a broad range of environmental conditions was overwhelmed by environmental changes or variance. Such tolerance, however, cannot explain the lack of significant macroevolutionary change or stability of community types during the intervals between transitions.

Two components are necessary to discriminate among, or determine the relative contributions of one or more of these mechanisms to the observed sequence of Karoo Permian-Triassic paleocommunities. The first component is a model of the relationship between the biotic interactions of the community, and species persistence and stable coexistence. Here we define persistence as the duration of a species in a community before local extinction occurs, and stable coexistence as the ability of species to coexist indefinitely in the absence of external perturbations. Species in an assemblage may form a persistent community only if the species remain feasible under conditions of interspecific competition and predation, even in the absence of external influences. Population growth rates and the strengths of interspecific interactions are two factors that determine the fraction of the assemblage for which this is true. For the remainder of this paper, we will refer to the levels of persistence and stable coexistence within a paleocommunity as its global stability (Chen and Cohen, 2001).

The second component is a framework within which to assess the proposed mechanisms. Here we develop a counterfactual approach, comparing paleocommunities to hypothetical alternative macroevolutionary histories of the paleocommunities, asking "what if" questions as a means for understanding: (1) how distinct the global stabilities of observed paleocommunities are from hypothetical alternatives of equal richness, and in some cases equal structural complexity; and (2) the likelihood that an observed paleocommunity would have remained compositionally stable, thereby rendering its taxa incumbent, rather than embark on a new macroevolutionary trajectory. We also examine a second set of comparisons, those among the paleocommunities themselves. Defining community global stability as the fraction of species that could persist under different demographic and ecological parameters allows us to question whether relative paleocommunity stability varied through the P-Tr interval. It is expected that less diverse and complex communities might be more stable because of the decreased numbers of biotic interactions, but the lowest diversity/complexity communities in our dataset were also either those that were affected by the PTME, or that represent the early stages of the aftermath in the Early Triassic. Thus, what sort of community would have resulted from a combination of intrinsic dynamics and the unusual environmental and evolutionary conditions that likely prevailed during the end Permian and Early Triassic?

The remainder of the paper is organized as follows. First we summarize the currently accepted understanding of the paleocommunities and PTME in the Karoo Basin. The data and methods used to test the hypothesis of stability and incumbency are presented next, followed by results of applying the methods to the Permian-Triassic Karoo Basin sequence of paleocommunities. Finally, we discuss the implications of the results, evaluate the incumbency-biotic interactions hypothesis, consider caveats and limitations of the models and analyses presented here, and discuss directions for future work.

1.1. The Permo-Triassic extinction in the Karoo Basin

The PTME is the largest mass extinction recorded in Earth's history: approximately 81% of marine species (Stanley, 2016) and about 89% of terrestrial tetrapod genera (Benton et al., 2013) became extinct during the event. Since the 1990's, the geologic record of the South African Karoo Basin has been a focal point for research on the Permo-Triassic transition in the terrestrial realm. The rocks of the Beaufort Group are highly fossiliferous (Nicolas and Rubidge, 2009, 2010; Smith et al., 2012), comprising a nearly continuous record of community evolution from the middle Permian to the Middle Triassic (Rubidge, 1995, 2005; Day et al., 2015; Rubidge et al., 2013, 2016). In this paper, we focus on the PTME, which occurred at the end of the Changhsingian Stage, although there is strong evidence that the Beaufort group also preserves a record of the terrestrial end-Guadalupian extinction event (e.g., Retallack et al., 2003; Day et al., 2015; Lucas, 2017; Rey et al., 2018), and the methods we develop here could be applied to that event as well. Work on the PTME in the Karoo has included database- and literature-based studies (King, 1991; Irmis and Whiteside, 2012; Irmis et al., 2013; Fröbisch, 2013, 2014; Codron et al., 2017), as well as a great deal of field-based research encompassing vertebrate paleontology, paleobotany, palynology, ichnology, biostratigraphy, geochemistry, geochronology, and stratigraphy and sedimentology (e.g., Smith, 1995; MacLeod et al., 2000; Ward et al., 2000, 2005; Smith and Ward, 2001; Hancox et al., 2002; Retallack et al., 2003; Schwindt et al., 2003; Steiner et al., 2003; De Kock and Kirschvink, 2004; Gastaldo et al., 2005, 2014, 2015; Smith and Botha, 2005; Botha and Smith, 2006; Coney et al., 2007; Tabor et al., 2007; Gastaldo and Rolerson, 2008; Pace et al., 2009; Botha-Brink et al., 2014; Neveling et al., 2016; Viglietti et al., 2016).

The most frequently cited scenario for the PTME in the Karoo posits that the traditional biostratigraphically defined Permo-Triassic boundary (PTB), at the top of the *Daptocephalus* Assemblage zone (sensu Viglietti et al., 2016), is contemporaneous with the boundary in the marine realm, and that rapid warming and drying of climates, and potential associated plant die-offs, were the primary drivers of the extinction of tetrapods (e.g., Ward et al., 2000, 2005; Benton and Newell, 2014; Smith and Botha, 2005; Rey et al., 2016; MacLeod et al., 2017; Viglietti et al., 2018b). Further elaboration of the scenario has resulted in the recognition of a phased extinction with an initial minor loss of diversity and changes in abundances of taxa near the boundary of the lower and upper *Daptocephalus* assemblage zones, and three more significant pulses of extinction close to the PTB (Smith and Botha-Brink, 2014; Viglietti et al., 2016, 2018b) (Fig. 1). Recovery from the event, at least in terms of taxonomic diversity, has been hypothesized to have been relatively rapid (Smith and Botha, 2005; Botha and Smith, 2006), with the Early Triassic *Lystrosaurus* Assemblage Zone having about two-thirds the number of tetrapod species as the upper *Daptocephalus* zone (Roopnarine et al., 2018). Complete ecological recovery from the event likely took longer (Roopnarine et al., 2007; Irmis and Whiteside, 2012; Roopnarine and Angielczyk, 2012, 2015, 2016).

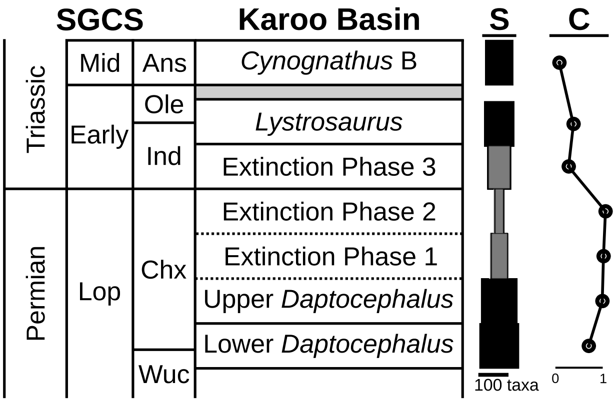


Fig. 1. Stratigraphic position of each Karoo Basin paleocommunity, its taxon richness (S), and taxon continuity (C, calculated as the fraction of vertebrate genera that have persisted from the previous community). Communities are shown with equal thicknesses for convenience; their real temporal durations varied (see text for details). Extinction phases 1 and 2 are sub-intervals of the upper *Daptocephalus* Assemblage Zone, and are therefore distinguished with dotted lines. Epoch abbreviation, Lop - Lopingian. Stage abbreviations: Wuc - Wuchiapingian; Chx - Changhsingian; Ind - Induan; Ole - Olenikian; Ans - Anisian.

Although this scenario has become a key part of our understanding of how the PTME affected tetrapod-dominated terrestrial communities (Benton and Newell, 2014), it has been the subject of several criticisms over the past decade. Challenges to the scenario include difficulties defining a consistent PTB using litho- and biostratigraphic data; geochronological and paleomagnetic data that suggest the traditional Permo-Triassic boundary in the Karoo is not contemporaneous with the boundary defined in the marine realm; alternative interpretations of sedimentary environments and continuity of deposition through the interval in question; the nature of environmental and floral changes through the interval; and questions about whether the faunal turnover between the *Daptocephalus* and *Lystrosaurus* assemblage zones meets the criteria necessary to be considered a mass extinction (Gastaldo et al., 2005, 2009, 2014, 2015; Tabor et al., 2007; Gastaldo and Rolerson, 2008; Lucas, 2009, 2017; Pace et al., 2009; Prevec et al., 2010; Neveling et al., 2016; Li et al., 2017). Useful summaries of these criticisms can be found in Gastaldo et al. (2017) and Neveling et al. (2016). The nature of the analyses and results presented in this paper do not allow us to directly address the debate on topics such as the nature of environmental changes across the traditionally-recognized PTB. However, they do provide insight into the question of whether the transition between the paleocommunities represented by the *Daptocephalus* and *Lystrosaurus* assemblage zones in the Karoo was anomalous, i.e., consistent with an event that was of greater scale and significance than background extinction and faunal turnover. We consider a larger, mass extinction-scale event likely based on several lines of evidence, including: 1) the near complete loss of *Daptocephalus* zone tetrapods during the transition to the *Lystrosaurus* zone (Smith et al., 2012; Fröbisch, 2013; Smith and Botha-Brink, 2014; Viglietti et al., 2016, 2018b); 2) altered growth patterns and life histories among Early Triassic tetrapods (Huttenlocker and Botha-Brink, 2013, 2014; Huttenlocker, 2014; Botha-Brink et al., 2016); 3) use of burrowing behavior as a means to escape presumably unfavourable environmental conditions (Botha-Brink, 2017); 4) significant changes in relative abundance, evenness, and beta diversity across the boundary (Irmis and Whiteside, 2012; Irmis et al., 2013; Brocklehurst et al., 2017); and 5) significant changes in community structure and function after the proposed extinction (Roopnarine et al., 2007, 2018; Roopnarine and Angielczyk, 2012, 2015, 2016).

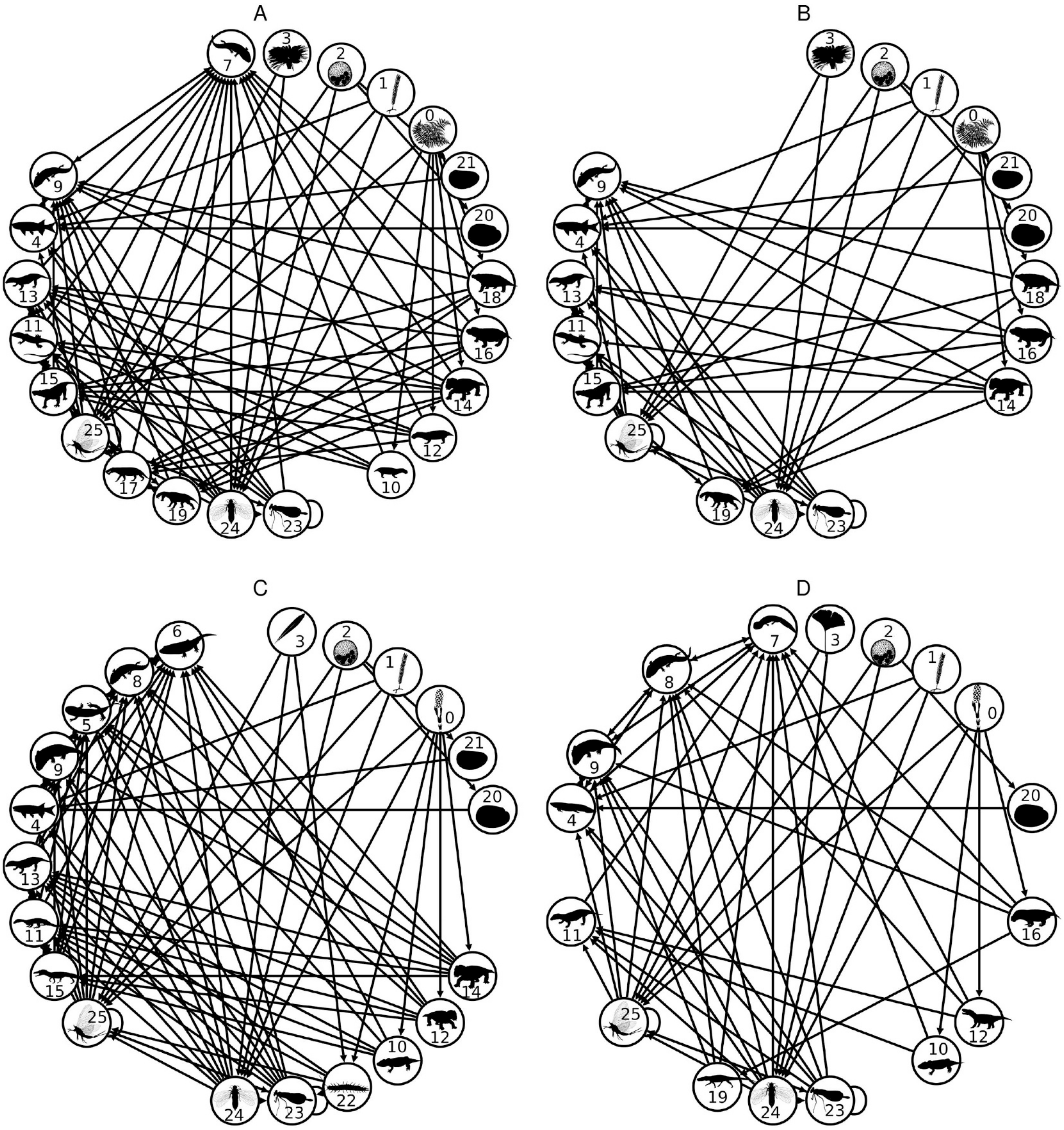


Fig. 2. Guild level community networks of four paleocommunities: A - late Permian lower *Daptocephalus* Assemblage Zone; B - late Permian Phase 1 of the extinction; C - Early Triassic *Lystrosaurus* Assemblage Zone; D - Middle Triassic *Cynognathus* Assemblage Zone B. Guilds are represented as network nodes, with representative taxon silhouettes. Network edges or links point in the direction of energy transfer, or prey-predator relationships. Guild numbers correspond to guilds listed in Appendix ATable A.1. (Most silhouettes adapted from Phylopic; see Appendix ATable A.2 for sources and attribution.)

2. Materials and methods

2.1. Paleocommunity reconstruction

The paleocommunity data and biostratigraphic framework used here were documented recently (Roopnarine et al., 2018), and represent a modification of data presented in previous work (Angielczyk et al., 2005; Roopnarine et al., 2007; Roopnarine and Angielczyk, 2012, 2015, 2016), so we present a brief summary only (Fig. 2). The biostratigraphic framework generally follows that of Viglietti et al. (2016, 2018b), where the latest Permian prior to onset of the mass extinction is divided into two assemblage zones, the lower and upper *Daptocephalus* assemblage zones (lDAZ and uDAZ, respectively) (Fig. 1). The two zones were formerly united as the single *Dicynodon* Assemblage Zone, and both are taxon rich, comprising 138 and 117 species respectively in our models (see below, and Appendix ATable A.1 for explanation). The interval of the uDAZ immediately preceding the Permian-Triassic transition is further sub-divided into two extinction phases, Extinction Phases I (Ph1) and II (Ph2), in accord with the stepped pattern of extinction reported by Smith and Botha-Brink (2014). Ph1 is marked by the significantly biased extinction of small body-sized amniotes and large amniote carnivores (Roopnarine and Angielczyk, 2015; Roopnarine et al., 2018), and reduced the uDAZ to 58 species. The second phase, Ph2, further reduced richness to 31 species, the lowest richness of the sequence. In our analyses we therefore consider the end Permian to consist of three successive units: the uDAZ unaffected by extinction, followed by extinction phases I and II. Similarly, the earliest Triassic unit (Ph3; Fig. 1) comprises a few surviving species from the Permian Ph2, and several new taxa that were likely immigrants from biogeographic regions neighboring the Karoo Basin, and is distinguished here from the conventional Early Triassic *Lystrosaurus* Assemblage Zone (LAZ), which includes all taxa in Smith and Botha-Brinks's (2014) LAZ, except for five taxa indicated to have become extinct in the earliest Triassic (*Promoschorhynchus, L. curvatus, Tigrisuchus, Proterosuchus, Progalesaurus*). The final unit is the Middle Triassic *Cynognathus* Assemblage Zone. Here we restricted the vertebrates to those assigned to *Cynognathus* Assemblage subzone B (CAZ) (Roopnarine et al., 2018), the best sampled of Hancox et al.'s (2002) threefold subdivision of the complete assemblage zone (Smith et al., 2012). The underlying and presumably older subzone A, and the overlying subzone C, are both poorly sampled in comparison to subzone B (Neveling, 2004; Smith et al., 2012), and we therefore focus here on subzone B as representative of the best-documented discrete community in the Karoo Basin from the time period represented by the *Cynognathus* zone.

Despite the controversy surrounding the timing and nature of the Permo-Triassic extinction in the Karoo (see below), we consider the use of Smith and Botha-Brink's (2014) phased extinction model justified for two reasons. First, it represents the most finely resolved model of tetrapod faunal turnover available for the basin (resting on the assumption that stratigraphic ranges of taxa have been accurately documented). Second, as we have argued elsewhere (Roopnarine et al., 2018), our model results can provide insight into whether the changes in community composition, structure, and function are similar to those expected by chance (e.g., through preservational bias or poor documentation of stratigraphic ranges) or if they seem unlikely to have arisen through stochastic processes. Even if the extinction phases are eventually shown to be incorrect, comparisons between our lower *Daptocephalus* AZ and our post-extinction *Lystrosaurus* AZ will still provide insight into the transition between two widely-recognized faunal assemblages. A complete list of all tetrapods included in the assemblage zones examined here can be found in Roopnarine et al.'s (2018) Supplementary Data, Table S1.

The following rules for paleocommunity reconstruction were applied uniformly to all the assemblage zones. The paleocommunities were partitioned into a total of 26 guilds (Appendix ATable A.1), where a guild is herein defined as a group of species utilizing the same resources in similar ways (Yodzis, 1989) and sharing other properties such as habitat, body-size ranges, and predators, e.g., “large amniote carnivores”, or “very small carnivores/insectivores”. Species richness of each guild varies among the communities, and guilds may be vacant if appropriate species are missing from the community. Our set of guilds includes four primary producer guilds, and both terrestrial and aquatic invertebrates and vertebrates. An important difference between the food webs analyzed here and those used in our previous studies lies in the treatment of plant guilds. Previous studies examined the effects of disruption of primary productivity, and plants were therefore represented by units of production, not taxa. Here, plant guilds are represented as taxa, but each guild has a richness of one. This is necessary because the current nature of paleobotanical systematics (i.e., parataxonomies for different organs) does not allow estimates of guild richness that are comparable to those for animals. Therefore, we assume plant species within a guild to be effectively neutral (Hubbell, 2001), and treat them as a single population, resulting in producer guild richnesses of one.

2.2. Ages of the Karoo Basin paleocommunities

Absolute paleocommunity ages are of interest because they provide insight into the timing of the loss of, and return to incumbency during and after the PTME. The ages of the fossil vertebrate assemblages of the Beaufort Group (Karoo Basin) were long based only on biostratigraphic correlations (e.g., Rubidge, 1995, 2005), but over the past decade, radiometric dates have become available that calibrate the ages of many of the Permian biostratigraphic assemblages (Coney et al., 2007; Fildani et al., 2007, 2009; Rubidge et al., 2013; Day et al., 2015; Gastaldo et al., 2015; Neveling et al., 2016). However, direct radiometric ages of the Triassic assemblage zones (i.e., the *Lystrosaurus* and *Cynognathus* assemblage zones) remain unavailable (although see Viglietti et al., 2018a). The boundary between the *Daptocephalus* Assemblage Zone and the *Lystrosaurus* Assemblage Zone has long been considered to mark the PTB in the Karoo Basin. Our assertion that the upper and lower *Daptocephalus* Assemblage Zone communities date from the late Permian is based on Viglietti et al.'s (2018b) synthesis of litho- and biostratigraphic data with the radiometric dates reported by Rubidge et al. (2013) and Gastaldo et al. (2015). In that work, the Lower *Daptocephalus* Assemblage Zone (lDAZ) encompasses much of the Wuchiapingian and potentially part of the lower Changhsingian stages, with the Upper *Daptocephalus* Assemblage Zone (uDAZ) comprising the remainder of the Changhsingian. Even if Viglietti et al.'s (2018a) framework proves to be chronologically incorrect, the results reported by Gastaldo et al. (2018) would still place the *Daptocephalus* Assemblage Zone in the late Permian, although they would shift the entire assemblage backwards in time such that the upper part of the zone would be early Changhsingian in age.

Smith and Botha-Brink (2014) did not explicitly calibrate their three extinction phases to the geological timescale, but they noted that phases 1 and 2 (Ph1 and Ph2) occurred below their placement of the PTB, whereas Phase 3 (Ph3) was located above the boundary. They also speculated about the duration of the phases based on estimates of sediment accumulation rates. Viglietti et al. (2018a) agreed that Ph1 and Ph2 fall within the upper Permian (i.e., in the uDAZ), while Ph3 occurs in the Lower Triassic. If their placement of the beginning of extinction Ph1 close to Gastaldo et al.'s (2015) radiometric date of 253.48 Ma is correct, and their PTB is correctly placed relative to the boundary in the marine realm, this would imply that the changes in richness and faunal composition observed during these extinction phases occurred over a period of about 1.5 Ma. However, we regard this result as preliminary, pending further investigation of the placement of the PTB in the Karoo Basin (e.g., Gastaldo et al., 2017), additional radiometric dating, and refinement of the placement of the extinction phases relative to dated strata.

As traditionally defined (i.e., roughly corresponding to the faunal assemblage of the Katberg Formation; see e.g. the stratigraphic range chart in Botha and Smith, 2006), the *Lystrosaurus* Assemblage Zone (LAZ) community is near-universally regarded as Early Triassic in age. If the first appearance of the genus *Lystrosaurus* is used to define the LAZ and equivalent biostratigraphic units (e.g., Lucas, 2010), then the biostratigraphic subdivision begins in the upper Permian with the first appearance of *Lystrosaurus* L. *maccaigi*. In our work, we consider L. *maccaigi* to be part of the late Permian DAZ community, and consider the LAZ to be exclusively Early Triassic in age. L. *maccaigi* has also been reported from the Fremouw Formation of Antarctica, and Fröbisch et al. (2010) have suggested that the fauna there bears similarities to the LAZ. Until recently, age estimates for the (Triassic portion of) LAZ have been based on biostratigraphy only, with no direct radiometric controls. Viglietti et al. (2018b) reported a population of detrital zircons from the lower Katberg Formation, strata assigned to the LAZ, with an age of 250 ± 5 Ma. This result is consistent with an Early Triassic age for the LAZ, but in the context of this study we consider the result preliminary for three reasons: 1) The large confidence intervals raise the possibility that the age of the sampled Katberg strata could range from late Permian to Middle Triassic; 2) Strata from the underlying Balfour Formation, considered to be late Permian in age, also produced detrital zircons of this age; and 3) Viglietti et al. (2018b) did not locate their samples in measured stratigraphic sections, so the exact correlation between their sampled horizons, extinction Ph3 and the LAZ (as used here) is uncertain.

Radiometric dates are currently unavailable for strata of the Burgerdorp Formation, which comprises the *Cynognathus* Assemblage Zone (CAZ). Subzone B, on which we focus here (Roopnarine et al., 2018), is by far the best sampled part of the zone (Smith et al., 2012), and represents the “classic” CAZ that has been recognized for over a century. Based on biostratigraphic correlations, the age of Subzone B is generally thought to be Anisian (see reviews in Lucas, 1998, 2010; Hancox, 2000; Hancox and Rubidge, 2001; Neveling, 2004; Rubidge, 2005). However, recently recovered radiometric dates from basins that have been biostratigraphically correlated with the CAZ have raised questions about its age. Ottone et al. (2014) reported a date of 235.8 ± 2 Ma for the Rio Seco de la Quebrada Formation (San Rafael Basin, Argentina), which would imply a Late Triassic (Carnian) age for the *Cynognathus* B and/or C subzones (also see Marsicano et al., 2016 for further discussion). In contrast, Liu et al. (2017) recovered a radiometric date of 243.53 Ma for Member II of the Ermaying Formation (Ordos Basin, China), whose *Sinokannemeyeria* Fauna has been correlated with Subzone C of the CAZ. This Anisian age is much more in keeping with traditional age estimates for the CAZ.

Resolving the age of Subzone B of the CAZ is beyond the scope of this paper, but the recent radiometric dates from Argentina and China help to provide some constraints on the time over which the observed faunal and ecological changes occurred. Subzone A of the CAZ is generally considered to be late Early Triassic (Olenkeian) in age (e.g., Hancox et al., 1995; Hancox, 2000; Neveling, 2004; Rubidge, 2005; Lucas, 2010; Gower et al., 2014). If correct, this would imply a maximum age of about 247–248 Ma for the overlying Subzone B, depending on the exact placement of the boundary between the subzones. The minimum age for Subzone B can be set in the range of about 243 to 235 Ma, although its actual age is likely slightly older than these dates because the radiometrically dated strata correlate at least in part with the overlying Subzone C.

2.3. Alternative macroevolutionary histories

Tests of the incumbency-biotic interactions hypothesis depend on the comparison of paleocommunities to hypothetical, or alternative macroevolutionary histories, which we describe here. Given a community richness of *S* species, the manner in which those species are partitioned among guilds is a result of the evolutionary histories of the species and the lineages to which they belong, and the history of the community. Furthermore, given that closely related species are more likely to share ecological properties than not, then the number of species within a guild is partly a function of diversification processes of clades within a guild, in addition to truly novel ecological innovations and taxon immigration. It should be noted that having two or more closely related taxa within a single guild does not run counter to expectations that those species might evolve divergently as a result of interspecific competition. Species within guilds may prey, and be preyed upon by similar or the same species, but resource overlap is not expected to be complete, a property reflected in our method of modeling biotic interactions (see below).

Communities that differ in the evolutionary and coevolutionary histories of their taxa can therefore be of equal structural complexity, yet have different partitionings of species richness, guild richnesses, and interactions between guilds. The set of structurally varying communities that can be derived from *S* species thus represents the set of all possible alternative histories of an assemblage of that size. We utilize this set to test our hypothesized dependence of compositional stability and incumbency on paleocommunity structure. We restrict our selection to a subset of the "alternative histories" whose members can be ordered by being increasingly constrained to be consistent with the structure of the observed paleocommunity (Fig. 3). The subset itself comprises four variants of the observed paleocommunity structure: (1) unstructured communities with no guilds and thus no complexity above the level of interspecific interactions (Model 1; Fig. 3); (2) communities with structural complexity equal to that of the observed paleocommunity but differing patterns of guild richnesses and interactions (Model 2; Fig. 3); (3) communities with structural complexity and pattern equal to that of the observed paleocommunity but differing guild richnesses (Model 3; Fig. 3); (4) and communities structurally consistent with the observed paleocommunity (Fig. 3). Model 1 encompasses the set of random networks associated with *S* nodes. Models 2–3 encompass communities in which *S* is partitioned into the same number of guilds as the paleocommunity, but the associations or interactions among guilds varies, as does the number of species per guild. Model 2 communities have patterns of guild interactions which differ from the observed paleocommunity and, using Gould's (1990) metaphor, may be thought of as histories that could result from replaying the tape of the ecosystem's history at a high macroevolutionary level. The results are communities of equal species richness and functional diversity, but which differ structurally from the observed paleocommunity. Model 3 retains the same pattern of guild interactions inferred for the observed paleocommunity, but the number of species per guild varies. Model 3 communities would be those where rates of diversification varied within guilds, leading to communities that differ from the observed paleocommunity only in the richnesses within guilds, but not in functional structure.

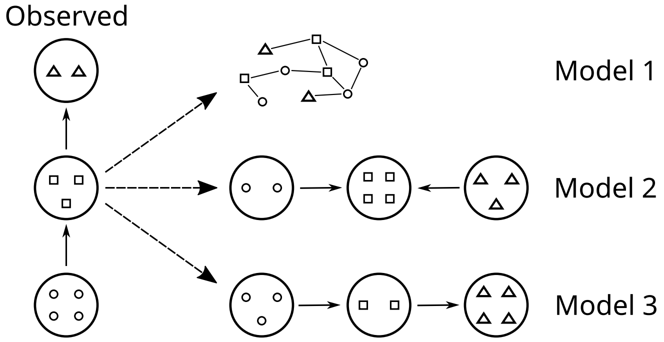


Fig. 3. Derivation of alternative model communities from an observed, or real paleocommunity. Observed: large circles represent guilds, symbols within represent species within guilds, and solid arrows between guilds indicate trophic interactions between guild members. The example paleocommunity therefore comprises three guilds, in which species interactions would be structured linearly between guilds (food chains). Model 1: a random food web of equal species richness, but no hierarchical guild structure, and therefore lower complexity. Model 2: alternative community of equal complexity (same number of species, guilds, and interactions), but in which guild richnesses and interactions have been altered. Model 3: alternative community of equal complexity and guild structure, but in which guild richnesses have been altered.

2.4. Paleocommunity stability

Global stability, or the persistence and indefinite stable coexistence of species within the observed paleocommunity or any of the alternative models, depends on the outcomes of biotic interactions among the species, as dictated by the complex structure of the community. We modeled patterns of interspecific interactions using model food webs with topologies constrained to conform to the topology of the paleocommunity or alternative models. Food webs were constructed from a guild-level structure (also referred to as a "metanetwork"; Roopnarine et al., 2007; Roopnarine, 2018; Roopnarine and Dineen, 2018; Roopnarine et al., 2018) by first selecting species stochastically from within guilds and assigning to each, predators and prey within the constraints of guild linkages. The number of interspecific interactions of a species was determined randomly by assuming that the overall distribution of the number of prey per consumer (in-degree distribution) within a trophic guild or partition is hyperbolic, as commonly observed in modern food webs (Dunne et al., 2002; Roopnarine et al., 2007; Williams, 2010; Roopnarine, 2018). We used a mixed exponential-power law distribution, $P(k)$ (Roopnarine, 2018), which has been shown to compensate statistically for trophic interactions that are lost during the fossilization of a food web (Roopnarine and Dineen, 2018).

$$P(k) = e^{-k/\varepsilon} \tag{1}$$

where

$$\varepsilon = \exp[(1-\gamma)\ln(M/\gamma)] \tag{2}$$

γ is a power law exponent (2.5 for all simulations conducted here; see Roopnarine et al. (2007)) and M is the total species richness of all guilds that are prey to the one to which the species under consideration belongs. This link or interaction parameterization of all S species yields a food web topology that is consistent with the higher-level topology of the observed paleocommunity or alternative model. The repeated stochastic generation of such species-level networks (SLNs) from guild-level networks accounts for both the uncertainty of reconstructing fossil biotic interactions, as well as the spatial and temporal variation expected in the topologies of real communities (Roopnarine, 2018). Each paleocommunity and its associated alternative models were therefore represented by ensembles of model food webs whose topologies were constrained by the complex structures of their parent metanetworks.

The stability of a paleocommunity or alternative model is here described by the global stabilities of its ensemble of model food webs. We therefore simulated the population dynamics of species within a food web, measuring global stability as the fraction of original species richness still persisting after a pre-specified interval of simulation time. Population dynamics were simulated with a discrete-time equation, which for a single species takes the form

$$X(t+1) = X(t)e^{R[1-X(t)]} \tag{3}$$

where R is the net reproductive rate of the population, that is, the number of individuals with which an individual is replaced reproductively per generation. Eq. (3) is a form of the Ricker equation (Ricker, 1954), with the carrying capacity of the population standardized to one, and yields a discrete approximation of logistic growth. Interspecific interactions are introduced into the system as a modification of population size for each generation (Sinha and Sinha, 2005),

$$X^*(t) = X(t)\left(1 \pm \sum_{i=1}^{S-1} \sigma_i Y_i(t)\right) \tag{4}$$

where σ is the per capita interaction strength between species X and Y. σ is positive if X preys on Y, negative if Y is a predator of X, and zero otherwise. The total effect of interspecific interactions on X may be positive or negative, dependent upon the signs of the interactions, and the population sizes of the species with which X interacts. The population growth of X, so modified by trophic interactions as X^*, is now formulated by substituting Eq. (4) into Eq. (3), yielding

$$X(t+1) = X^*(t)e^{R[1-X^*(t)]} \tag{5}$$

The dynamics of all populations in the community are subsequently modeled with a system of equations of the form of Eq. (5). The use of a discrete system, rather than a system of ordinary differential equations, maintains mathematical tractability and computational feasibility as S increases to dozens or hundreds of species.

2.5. Model comparison

Community stability is affected by several properties and variables including S, the connectance or density of interactions, and average interaction strength. The stability of randomly connected networks declines as any of these parameters increases (May, 1972; Sinha and Sinha, 2005), but real community networks are both observed and theoretically expected to respond differently because in general link density in food webs is sparse (Martinez, 1992), and interactions tend to be relatively weak (Paine, 1980; McCann et al., 1998). Two of these variables, S and connectance, are fixed in our comparison of paleocommunities and alternative models. The alternative models to which an observed paleocommunity is compared have the same S as the paleocommunity, and the species level networks or food webs (SLNs) generated for each model are constrained to have the same number of interactions as those generated for the paleocommunity. The third variable, interaction strength, is a factor in species population dynamics ($\pm\sigma$ in Eq. (4)), and with population net reproductive rate R and the pattern of interspecific interactions, determines species persistence and stable coexistence, and hence global stability. Therefore, in order to understand the effect of patterns of biotic interactions on global stability, we examined paleocommunity and model community dynamics under fixed ranges of R and σ. In other words, R and σ were controlled, leaving patterns of biotic interactions as the only property varying among models and observed paleocommunities. R for all species in a food web was fixed at the same value, and simulations were performed over a range of one to four, in increments of 0.1. The strengths of both positive and negative interactions in a food web were drawn individually and stochastically from a uniform distribution, ranging from greater than zero to one (Roopnarine and Angielczyk, 2015). Interaction strength was varied over all simulations by scaling the drawn interactions from a minimum of 0.02 (2% of drawn strength) to one. The parameter space of the simulations thus consisted of R, and scaled negative and positive interactions, with simulations performed at particular parameter combinations or coordinates, $(R, -\sigma, +\sigma)$. Combining the ranges of each parameter at the incremental resolutions outlined in the previous statement yields a total of 77,500 parameter coordinates. Each coordinate was simulated 30 times, that is, 30 SLNs (food webs) were generated for each paleocommunity and the three alternative models at each parameter coordinate, yielding a total of 9.3 million simulations per paleocommunity analysis. Each simulation of a SLN was performed for 10,000 time steps, during which time Eq. (5) was iterated for all species in the community. Global stability was measured as the number of species extant at the end of the simulation, that is, the set of species that persisted and were coexisting.

Alternative model SLNs were created from manipulations of SLNs derived from the observed paleocommunity being tested. Model 1 SLNs were generated by assigning interactions from the observed paleocommunity SLN randomly to pairs of species. Model 1 SLNs therefore had the same number of species, biotic interactions and interaction strengths as the paleocommunity SLN, but no higher level structure, i.e., functional partitioning into guilds. Model 2 SLNs were generated by randomly manipulating the guild memberships of species, and the interactions between guilds. Model 2 SLNs therefore had the same number of species, biotic interactions, interaction strengths, guilds, and guild interactions as paleocommunity SLNs, but the number of species within guilds, and the patterns of interactions between guilds (and hence species), could differ from the observed paleocommunity. Finally, Model 3 SLNs were created from observed paleocommunity SLNs by random manipulation of the numbers of species within guilds, but conservation of the total number of species, the total number of interactions, and the patterns of interactions between guilds.

Each observed paleocommunity was compared to the alternative models at each parameter coordinate, measuring the difference in the richness of persistent species, or global stability, as $\overline{\Delta Se} = \overline{Se}(\text{paleocommunity}) - \overline{Se}(\text{model})$, or the difference of the mean global stabilities given the number of simulations at each coordinate. Because the paleocommunity and alternative model are each represented by 30 simulations at each coordinate, simulation results were compared using coordinatewise two-tailed z-tests, yielding comparisons where paleocommunity global stability was significantly less or greater than that of the alternative model ($\text{probability}(\Delta Se \neq 0)$, $\alpha = 0.05$), or did not differ. Model results and comparisons were then visualized as in Fig. 4, with visualizations serving as the basis of assessing the relative stabilities of the alternative models in comparison to the observed paleocommunities. Finally, the comparisons were made among the paleocommunities themselves, using this same statistical approach, to assess the effect of the PTME and aftermath on the inferred stability of the ecosystem.

3. Results

3.1. Population and community dynamics

Population sizes, X in Eq. (5), are functions of the net reproductive rate R, both positive and negative interspecific trophic interactions ($\pm\sigma$ in Eq. (4)), and normalized carrying capacity. R is the sole determinant of a population's dynamics in single species models, with the complexity of the dynamics increasing as R increases. The dynamics

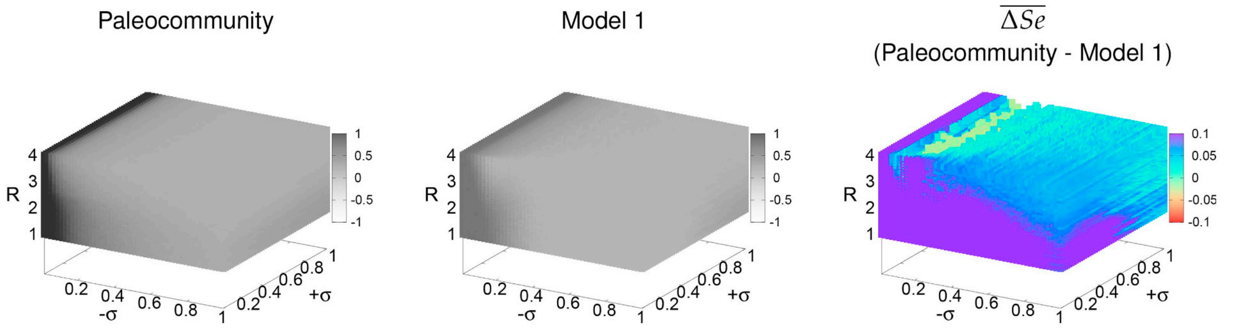


Fig. 4. Visualization of paleocommunity and model stability, using the lower *Daptocephalus* Assemblage Zone as an example. Axes represent ecological model parameters: R - net reproductive rate, $-\sigma$ - negative interaction strength, $+\sigma$ - positive interaction strength. Global stability Se, the number of stably coexisting species expressed as a fraction of total species richness S, is coloured at each parameter coordinate ($R, -\sigma, +\sigma$), as indicated by the grayscale spectra of the paleocommunity and Model 1. The statistically significant differences between the paleocommunity and the alternative model, $\overline{\Delta Se}$, are illustrated on the far right. The lower and upper ends of the colour spectrum indicate $\overline{\Delta Se} \leq -0.1$ and $\overline{\Delta Se} \geq 0.1$ respectively. Coordinates at which there is no significant difference, i.e. $\overline{\Delta Se} = 0$, are uncolored.

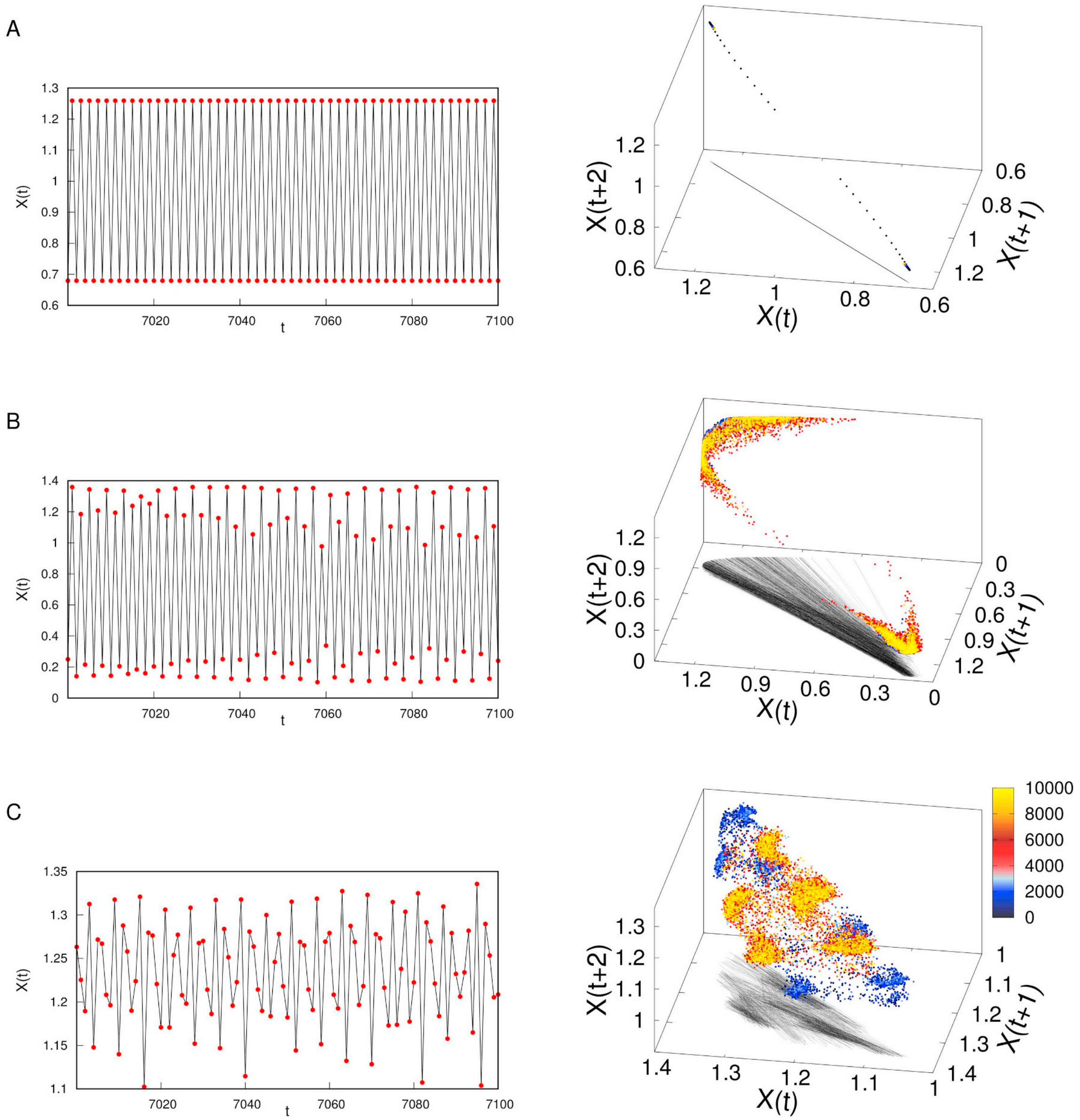


Fig. 5. Population trajectories (left) and phase plots (attractors) (right) of taxa from the lower *Daptocephalus* Assemblage Zone (lDAZ), illustrating three types of dynamics at $R = 2$, and both $-\sigma$ and $+\sigma = 0.1$. A - stable oscillation or limit cycle of a freshwater bivalve. B - quasi-periodic oscillation of a freshwater fish. C - chaotic dynamics of an omnivorous insect. Colour bar illustrates time step (t) out of $T = 10{,}000$ total steps. Left plots show a subset of T, with t ranging from 7000 to 7100. Lines projected at base of attractor plots trace the trajectories for the t subsets.

undergo a series of transitions typical of other discrete population growth models, such as the discrete logistic map, transitioning from an initial stable point equilibrium ($R \approx \leq 2$), to stable oscillations, quasi-periodicity, and finally chaos (at $R = 2.692$) (May, 1974). Population trajectories of the communities and models simulated here were representative of an array of empirically and theoretically expected forms, including stable point equilibria, stable limit cycles, quasi-periodic cycles, and chaos (Fig. 5). Quasi-periodic and chaotic trajectories were confirmed by estimation of largest Lyapunov exponents (Rosenstein et al., 1993). The transition from simple to complex dynamics, including chaos, generally occurs at values of R as low as 2.0, which is below the expected value of 2.692 for a single species system. This highlights the fact that the major sources of complex dynamics in rich, multi-species communities are not necessarily species-specific characteristics, i.e. R. Instead, they are generated by complicated asynchronous interspecific impacts, i.e., the time scales on which species affect each other are spectra of the lengths of the multiple pathways of interaction that connect them, and hence are functions of community size and complexity.

All communities and alternative models exhibited May-Wigner transitions (Wigner, 1967; May, 1972; Sinha and Sinha, 2005), where species persistence, or the fraction of species populations that do not become extinct (Se), is inversely related to the number of species (S), the connectance or density of interspecific interactions, and the average strength of those interactions (Fig. 6). Given that the method for generating interspecific interactions was uniform for all the paleocommunities and alternative models, and that all were subjected to the same range of interaction strengths, the major expected source of variation among paleocommunities is S, which reached a minimum during the PTME.

3.2. Model comparisons

The comparisons of each paleocommunity to alternative models were visualized throughout the $(R, -\sigma, +\sigma)$ parameter space as three dimensional heat maps (Figs. 7 and 8). Each point in a map's parameter space represents a statistically significant difference ($p < 0.05$) between the simulations of the paleocommunity and those of an alternative model, at a particular parameter coordinate. Colours indicate whether the paleocommunity is more or less globally stable than the model, and the magnitude of the difference, that is, differences between paleocommunity and model richnesses at the end of 10,000 time steps. The ends of the colour spectrum include differences greater than or equal to 0.1S ($\geq$10% differences of richess). Points at which the paleocommunity and an alternative model do not differ are uncoloured. For example, the comparison of the lower *Daptocephalus* Assemblage Zone (lDAZ) to alternative Model 1, in which the communities are unstructured and have no complexity above the level of interspecific interactions, is illustrated in Fig. 4 and the lowest row of Fig. 7. The lDAZ is significantly more stable than Model 1 throughout the parameter ranges as indicated by the cooler (bluer) colours. There is a narrow region, bounded by $R > 3.5$ and negative interaction strength, $-\sigma$, ranging between 0.2 and 0.3, where Model 1 produces SLNs more stable than the lDAZ. Warm colours, that is the declining difference between the observed paleocommunity and Model 1, increase as interaction strengths increase. Testing the model comparisons at each parameter coordinate, and visualizing significant differences, shows both the very nonlinear dependence of community dynamics on population dynamics and interactions, and details of how the alternative models differ from the observed paleocommunity.

We also used two summary measures to describe overall differences between paleocommunities and models (Fig. 9). First is the frequency at which a paleocommunity, under any given combination of parameters, will be more stable than an alternative model. This is expressed as an estimate of the probability that a SLN, or paleo-food web that is structurally consistent with the observed paleocommunity would be more stable than an alternatively structured food web, under the same ecological circumstances (Figs. 6 and 7). We denote this probability estimate as $\theta = \#\,(\Delta Se > 0)/N$, where ΔSe is the significant difference between the stability of the paleocommunity and an alternative model at a given parameter coordinate, and N is the total number of parameter coordinates. θ in other words is the fraction of simulations where the paleocommunity is significantly more stable than an alternative model. The second measure describes the overall magnitude of ΔSe, calculated as the mean value for a set of comparisons, $\overline{\Delta Se} = \sum (\Delta Se > 0)/N$. Values of $\overline{\Delta Se} > 0$ indicate that overall, the paleocommunity would have been more stable than the alternative model.

Several trends are apparent within the results for each paleocommunity during the Permian (Fig. 6). First, the distinction between the observed paleocommunity and the models decreases from Models 1 to 3, as the models become more structurally complex (relative to Model 1) and similar to the paleocommunity. The declining values of θ and $\overline{\Delta Se}$ from Model 1 to Model 3 of each paleocommunity capture this trend. Second, whereas Models 1 and 2 are more stable than the paleocommunity only at high parameter values, or not at all (Ph1 and Ph2; $\theta = 1$), Model 3 exhibits greater stability in a heterogeneous

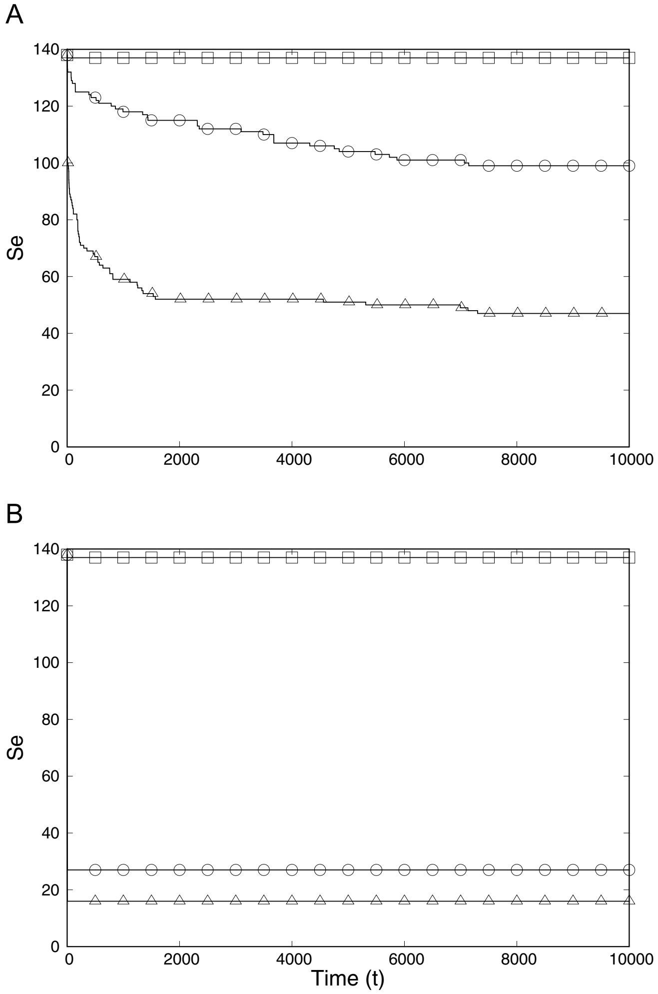
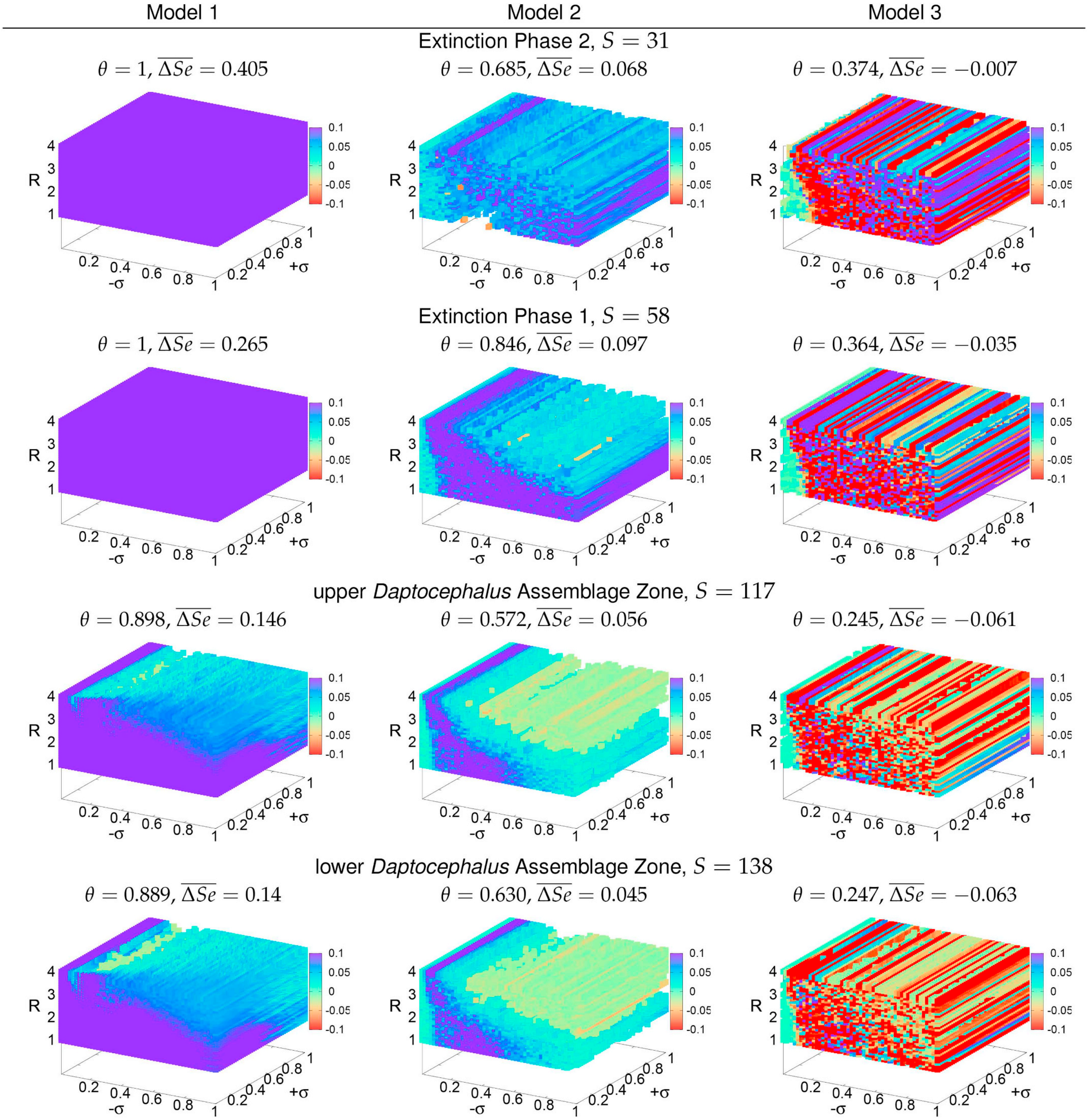


Fig. 6. Relationships between global stability (Se) and the parameters R and interaction strengths. Plots show Se trajectories of single simulations of the lower *Daptocephalus* Assemblage Zone (lDAZ) paleocommunity for 10,000 time steps (T). A - Simulations with interaction strength ranges fixed, varying between zero and 0.1, but with variable R. Squares, $R = 2$; circles, $R = 3$; triangles, $R = 4$. B - Simulations with R fixed at two, positive interaction strengths ranging up to 0.1, but negative interaction strengths scaled to range as: squares, $-\sigma[0 - 0.1)$; circles, $-\sigma[0{,}0.5)$; and triangles, $-\sigma[0,1)$. Symbols are plotted every 500 time steps.



Model 1 Model 2 Model 3

Extinction Phase 2, $S = 31$

$\theta = 1, \overline{\Delta Se} = 0.405$ $\theta = 0.685, \overline{\Delta Se} = 0.068$ $\theta = 0.374, \overline{\Delta Se} = -0.007$

Extinction Phase 1, $S = 58$

$\theta = 1, \overline{\Delta Se} = 0.265$ $\theta = 0.846, \overline{\Delta Se} = 0.097$ $\theta = 0.364, \overline{\Delta Se} = -0.035$

upper *Daptocephalus* Assemblage Zone, $S = 117$

$\theta = 0.898, \overline{\Delta Se} = 0.146$ $\theta = 0.572, \overline{\Delta Se} = 0.056$ $\theta = 0.245, \overline{\Delta Se} = -0.061$

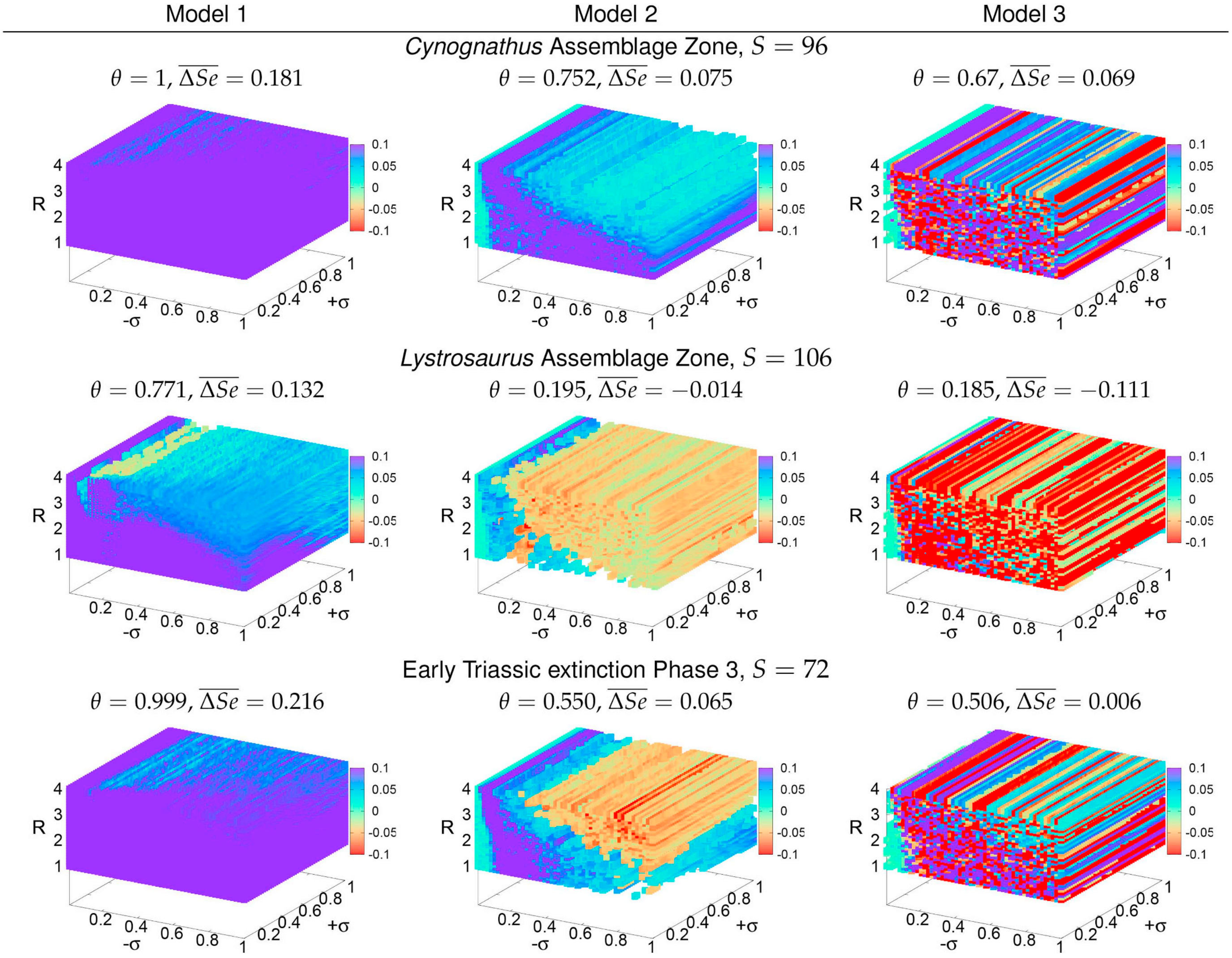
lower *Daptocephalus* Assemblage Zone, $S = 138$

$\theta = 0.889, \overline{\Delta Se} = 0.14$ $\theta = 0.630, \overline{\Delta Se} = 0.045$ $\theta = 0.247, \overline{\Delta Se} = -0.063$

Fig. 7. Global stability comparisons between Permian paleocommunities and Models 1, 2 and 3. Paleocommunities are arranged stratigraphically, with the earliest in the lowest row (see Fig. 1). S, paleocommunity species richness; θ, the proportion of simulations in which the paleocommunity is more stable than the model (ΔSe significantly greater than zero); $\overline{\Delta Se}$, average ΔSe of all simulations in a model comparison where ΔSe differs significantly from zero. Axes: $-\sigma$, negative interaction strength; $+\sigma$, positive interaction strength; R populations' net reproductive rates. Each plot illustrates 9.3 million model comparisons, and cooler colours indicate $\Delta Se > 0$.

distribution throughout the parameter space. θ is > 0.5 for all Models 1 and 2, meaning that the probability that a SLN from a real paleocommunity is more stable than an alternative model is greater than 50% of the parameter space (Fig. 8). The opposite is true for Model 3, where θ has a maximum Permian value of 0.374. Third, the paleocommunities become increasingly distinguished from Model 1 as time progresses, a trend already noted for the late Permian in the Karoo system (Roopnarine and Angielczyk, 2015). A similar trend occurs in the Model 2 comparisons where, although θ and $\overline{\Delta Se}$ do not increase monotonically, the more nuanced heat maps show that any parameter ranges which produce more stable model SLNs than the paleocommunity, essentially disappear during Phases 1 and 2 of the PTME. Conversely, the proportion of more stable SLNs produced by Model 3 increases during the PTME.

The Early Triassic third phase of the PTME, Ph3, comprised survivors from the Permian Karoo Basin ecosystem, and presumed immigrants from neighboring regions (Bernardi et al., 2018). Like preceding Permian communities, the Ph3 community would have been



Model 1 Model 2 Model 3

Cynognathus Assemblage Zone, $S = 96$

$\theta = 1, \overline{\Delta Se} = 0.181$ $\theta = 0.752, \overline{\Delta Se} = 0.075$ $\theta = 0.67, \overline{\Delta Se} = 0.069$

Lystrosaurus Assemblage Zone, $S = 106$

$\theta = 0.771, \overline{\Delta Se} = 0.132$ $\theta = 0.195, \overline{\Delta Se} = -0.014$ $\theta = 0.185, \overline{\Delta Se} = -0.111$

Early Triassic extinction Phase 3, $S = 72$

$\theta = 0.999, \overline{\Delta Se} = 0.216$ $\theta = 0.550, \overline{\Delta Se} = 0.065$ $\theta = 0.506, \overline{\Delta Se} = 0.006$

Fig. 8. Global stability comparisons between Triassic paleocommunities and Models 1, 2 and 3. Paleocommunities are arranged stratigraphically, with the earliest in the lowest row (see Fig. 1). See Fig. 7 for explanations of symbols, labels and plots.

significantly more stable than any equivalent Model 1 unstructured communities, and generally so relative to Model 2 communities, except under conditions of higher R and negative interaction strengths ($-\sigma$). The latter condition is similar to pre-PTME communities (lDAZ and uDAZ), but in Ph3 the stable Model 2 communities would be even more stable relative to the observed paleocommunity than prior to the PTME. Ph3 also differs from Permian communities in the Model 3 comparison, where now the probability that the Ph3 community would be more stable than a Model 3 community is greater than the probability of being less stable ($\theta = 0.506$, $\overline{\Delta Se} > 0$) (Fig. 9). The succeeding *Lystrosaurus* Assemblage Zone (LAZ) is similar to the pre-PTME in its comparison to Models 1 and 3, but is uniquely less stable than Model 2 ($\theta = 0.195$, $\overline{\Delta Se} < 0$). This contrasts strongly with the Middle Triassic *Cynognathus* Assemblage Zone (CAZ), which is significantly more stable than all the alternative models.

Comparisons between successive paleocommunities reveal a progressive change of increasingly stable paleocommunities through the late Permian (Fig. 10). There is very little difference between the pre-PTME lDAZ and uDAZ paleocommunities, but the initiation of the PTME, that is, the transition from the uDAZ to Ph1, is marked by both the first dramatic reduction of taxon richness, and a significant increase of paleocommunity stability ($\overline{\Delta Se} > 0$). The increase of stability is a result of both the May-Wigner theorem, in which less taxonomically rich food webs are expected to be more stable, and of the biased extinction of small amniotes and large carnivores (noted previously by Roopnarine and Angielczyk, 2015 and Roopnarine et al., 2018). Stability continued to increase during the second phase of the extinction (Ph1→Ph2), but the third phase, Ph3 in the earliest Triassic, is marked by both an increase of richness and a significant reduction in relative stability. Thus, this early "recovery" community, comprising survivors and presumed immigrant taxa, still represented a loss of the stable dynamics that characterized the Permian communities. The succeeding LAZ paleocommunity, in which 25 of 38 vertebrate taxa are new to the Karoo Basin, is less stable than Ph3, and therefore also all the Permian communities. The steadily increasing richness of the Early Triassic is thus not accompanied by increases of stability or species persistence. The lack of persistence or incumbency of the LAZ is highlighted by the turnover between it and the CAZ subzone B, in which only one of the 38 CAZ vertebrate taxa was present in the Early Triassic. The LAZ to CAZ transition, however, is marked by a significant increase of stability.

4. Discussion

The hypothesis proposed here as an explanation of biotic incumbency on geological timescales claims that particular community-level patterns of biotic interactions promote increased levels of species persistence and coexistence (global stability) in the absence of external environmental disturbance. The patterns, which develop

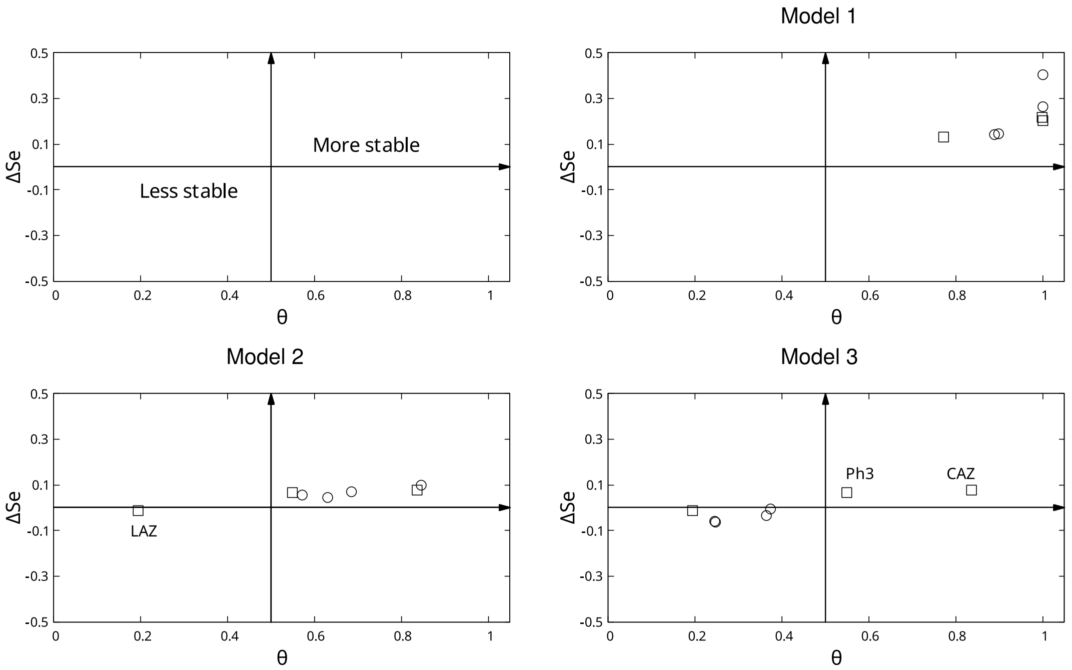


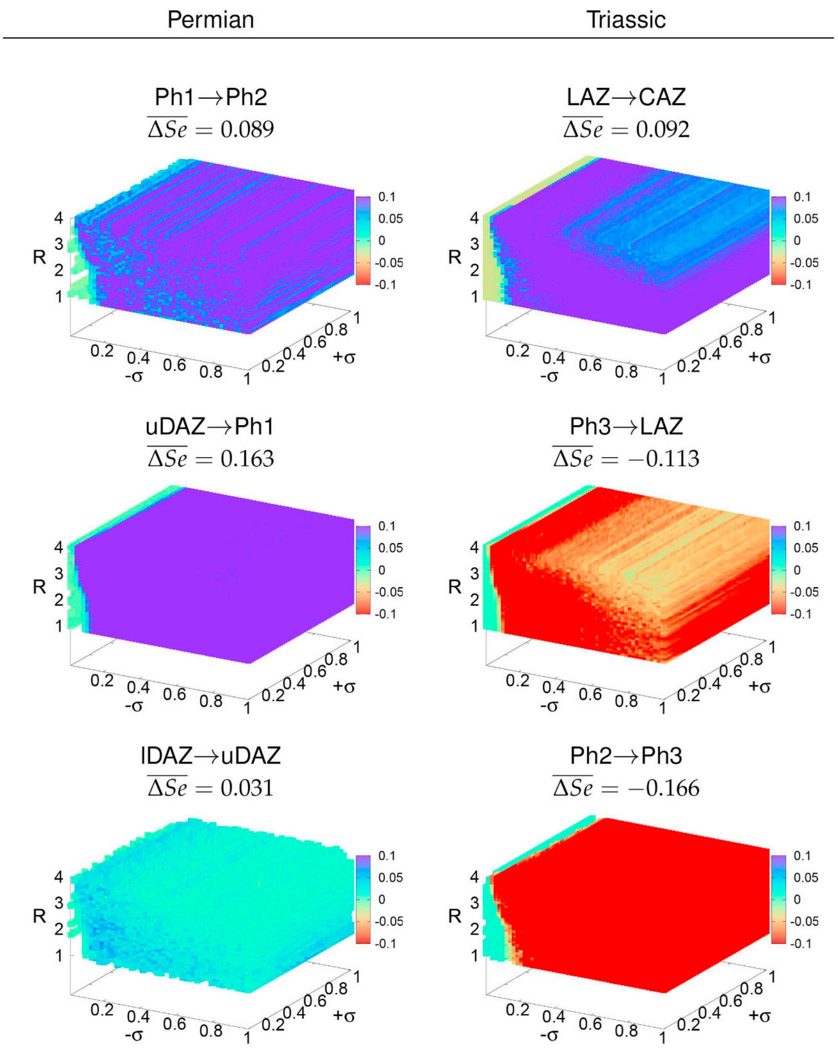
Fig. 9. Summary of overall simulation statistics, θ and $\overline{\Delta Se}$. Paleocommunity stability is increasingly differentiated from model stability along increasing values of both statistics. Plot regions can be divided into a region where $\theta > 0.5$ and $\overline{\Delta Se} > 0$, and paleocommunities are therefore most stable relative to model communities; and a region where $\theta < 0.5$ and $\overline{\Delta Se} < 0$, and paleocommunities are therefore least stable relative to model communities (upper left plot). In comparisons to Model 1 (upper right plot), all paleocommunities fall into the more stable region, whereas LAZ is in the less stable region compared to Model 2 (lower left plot). Compared to Model 3, only the Triassic Ph3 and CAZ paleocommunities are more stable than the model (lower right plot). Plot symbols: circles, Permian paleocommunities; squares, Triassic paleocommunities.

coevolutionarily on geological timescales, are stable on those timescales and give clades an appearance of ecological incumbency because they generate communities that are more globally stable than communities generated by alternative patterns of interaction, such as would be produced by alternative macroevolutionary histories. There are no prohibitions or constraints on the production of alternative macroevolutionary and hence ecological trajectories, but their lesser stabilities would render them geologically ephemeral relative to incumbent patterns, to an extent determined by their relative stabilities because of the higher extinction probabilities of their constituent species. Nevertheless, incumbent patterns may be undone by externally-driven disruptions of sufficient magnitude, for example, mass extinctions. The hypothesis further proposes that intervals of taxonomic diversification and ecological reorganization following mass extinctions cease when new, globally stable patterns of interaction emerge. Such emergences are true markers of biotic recovery.

We tested the hypothesis by examining the global stabilities of terrestrial paleocommunities from the Karoo Basin of South Africa, spanning the Permian-Triassic transition and mass extinction (PTME). Using a numeric model of population and interspecific dynamics to assess paleocommunity stability under a broad range of demographic and predator-prey parameters, we found results supportive of the incumbency-biotic interactions hypothesis, which we discuss in the following sections. Finally, we use the re-establishment of stability in the Middle Triassic to estimate a minimum time of recovery from the PTME in the Karoo Basin.

4.1. Functional compartmentalization increases stability

The May-Wigner Theorem (MWT), which in an ecological context states that the probability of a food web remaining in stable equilibrium after perturbation declines as the complexity of the food web increases (May, 1973), is viewed as paradoxical because it implies a negative relationship between community complexity and stability. Sinha and Sinha (2005) demonstrated that the MWT also holds true when applied to the global stability (*Se*) of non-equilibrium community models such as the one employed in this paper (see also Chen and Cohen, 2001). Complexity as defined in the MWT, however, refers to only three community properties, namely species richness, the density of interspecific interactions, and the average strength of those interactions. An additional key component of community complexity is the organization of species into sub-groups, and May (1973) suggested that such compartmentalization could resolve the complexity-stability paradox. This suggestion has been theoretically validated repeatedly, with emphasis placed on community modularity, or the division of communities into sub-communities, where members of a sub-community interact with each other significantly more frequently than they do with species of other sub-communities (Guimera et al., 2010). Modularity has been demonstrated in modern communities (Krause et al., 2003; Rezende et al., 2009; Roopnarine and Dineen, 2018; but see Wirta et al., 2015), although Roopnarine and Dineen (2018) suggest that, at least for marine communities, modularity may be enhanced artificially by the anthropogenic extirpation of high trophic level predators. Those predators tend to reduce modularity by preying on species within multiple sub-communities. Another, and somewhat overlooked form of community compartmentalization consistent with May's concept, is the organization of species into groups based on functional similarity. Such compartments (i.e., guilds in this study), comprise species that are expected to overlap significantly in their interspecific interactions, being subjected to many of the same predators, and sharing many of the same prey. Sharing prey also means that members of guilds compete with each other. Guilds are an expected feature of biodiversity and community organization, both because ecological opportunity and evolutionary innovation combine to produce lineages of species that share similarities of competition, predation, and mutualisms, and because species are expected to self-organize over evolutionary time into groups of trophically similar species (Scheffer and van Nes, 2006; Scheffer, 2009; Roopnarine and Angielczyk, 2016).



Permian

Triassic

Ph1→Ph2
$\overline{\Delta Se} = 0.089$

LAZ→CAZ
$\overline{\Delta Se} = 0.092$

uDAZ→Ph1
$\overline{\Delta Se} = 0.163$

Ph3→LAZ
$\overline{\Delta Se} = -0.113$

lDAZ→uDAZ
$\overline{\Delta Se} = 0.031$

Ph2→Ph3
$\overline{\Delta Se} = -0.166$

Fig. 10. Comparisons of mean global stability ($\overline{\Delta Se}$) between successive paleocommunities. Paleocommunity transitions are organized stratigraphically, with oldest at the bottom of a column. Stability increases through the late Permian (left column), declines in the Early Triassic (Ph3 and LAZ), before increasing in the Middle Triassic (CAZ).

The importance of guild-level organization to the dynamics of the Karoo Basin paleocommunities has been demonstrated previously with several different modeling approaches (Roopnarine et al., 2007; Roopnarine, 2012; Roopnarine and Angielczyk, 2012; Roopnarine, 2018; Roopnarine and Angielczyk, 2015, 2016). Roopnarine and Angielczyk (2015) showed that the guild-structured paleocommunities would have been more stable than randomly structured food webs of equal richness, link density, and average interaction strength, as predicted by MWT. The framework of alternative evolutionary histories presented here shows additionally that, in general, any guild-structured community, observed or hypothetical, is expected to be more stable than randomly structured ones (Figs. 7 and 8). Thus, the expected development or evolution of guilds because of ecological differentiation confers “stability for free” on communities, regardless of the nature of the guilds, although certain guild-level organizations may be more effective at conferring stability than others. Compartmentalized communities would sustain significantly more species than random communities ($\overline{\Delta Se} > 0$) of equal richness because of their greater structural complexity. Guilds promote species coexistence relative to random food webs because the negative impacts of species on each other are dampened when there are no direct interactions between species, and because pathways between those species through the food web are longer (Roopnarine, 2012). During the PTME, when taxonomic richness was lowest, the presence of guilds would have permitted greater species coexistence under all values of R and ± σ, relative to random communities (Fig. 7). Therefore the preservation of some guild structure during the extinction promoted greater species coexistence and survival than would be expected of a causal disturbance of equal magnitude but where guild structure had been eliminated altogether. Consequently, even as a community is reduced by externally driven extinctions, the ecological pressures stemming from species coexistence are eased. We suggest that this accounts for the observed biases of extinction during Ph1, and might be a common feature during mass extinctions. The mechanism is not expected to operate, however, in modern anthropogenically-driven extinctions, where biases are based on human intention, and not a sorting among species based on their roles in system stability.

4.2. *Alternative macroevolutionary histories*

We considered two models of macroevolutionary histories alternative to those represented by the actual paleocommunities. The first, Model 2, comprises communities with structural complexities equal to those of the Karoo paleocommunities, but with contrasting richnesses within guilds and interactions between guilds. In general, Permian communities (lDAZ, uDAZ, Ph1 and Ph2) would have been more stable ($\overline{\Delta Se} > 0$) than Model 2 alternatives along a gradient of decreasing net reproductive rates (R) and negative interactions strengths ($-\sigma$) (Fig. 7).

Prior to the PTME (i.e., lDAZ and uDAZ in this study), Model 2 communities could have been more stable at higher values of R and $-\sigma$, whereas during the PTME (Ph1 and Ph2) the observed paleocommunities were essentially always more stable. Thus Permian communities consisting of the observed species and their histories would promote greater species persistence and stable coexistence than a majority of the 9.3 million model communities to which each was compared ($\theta > 0.5$). It is possible that some of the randomly generated model communities were ecologically unfeasible structures, but we consider it highly unlikely that this would be true for a majority, and additionally unlikely that unfeasible structures would be confined to such cohesive and contiguous regions of the Model 2 parameter space, rather than being distributed randomly (Fig. 7). The stability, or incumbency of the late Permian communities therefore would have been maintained by a low likelihood that eco-evolutionary innovations that altered the functional structure of the community could persist; such innovations would more often than not have reduced community stability.

The second model, Model 3, comprises communities with guild structures identical to those of the observed paleocommunities, but in which total species richness is partitioned differently among the guilds. Such model communities represent alternative macroevolutionary histories in which lineages and their ecological properties are consistent with the observed paleocommunities, but in which diversification rates and species longevities are different, leading to lineages being represented by different numbers of species. During the Permian, including the PTME, a majority of simulated Model 3 communities are more stable than the observed paleocommunities ($\theta < 0.5$, $\overline{\Delta Se} < 0$; Fig. 7), although the differences decline as the PTME proceeds. This means that guild richnesses could have varied without having negative impacts on community stability, and in fact could frequently have resulted in more stable communities. It is therefore unlikely that lineage diversity dynamics (unaccompanied by major ecological innovations) were constrained by biotic interactions during this time interval. The incumbency of the Permian ecosystem was instead maintained by the comparatively greater global stability generated by the large-scale pattern of biotic interactions which remained unchanged during that time. Neither the pattern nor the interactions were so constraining, however, that species could not evolve, nor lineages diversify, beyond the richnesses observed in the fossil record. This is contrary to other hypotheses seeking to explain paleocommunity persistence on the basis of biotic or environmental constraints, such as coordinated stasis, or hierarchical ecosystem theory (Morris et al., 1995; Brett et al., 1996; Zambito et al., 2012) (but see Tang and Bottjer, 1996; Dimichele et al., 2004). Indeed, the fact that many alternative partitionings of richness produce more stable arrangements implies that factors other than biotic interactions and community stability also affected diversification patterns.

The earliest community of the Triassic, Ph3, comprising survivors from the Permian ecosystem and new (likely immigrant) taxa, witnessed a rebound of richness from the end Permian Ph2 (Fig. 1). New taxa consisted primarily of herbivorous tetrapods of various body sizes, compared to a continued decline of faunivores. Ph3 also represents the end of Permian incumbency in the Karoo ecosystem. In contrast to the Permian communities, the magnitude of difference between more stable Model 2 communities and the Ph3 community increases. Thus, structural re-organizations or replacement of the Ph3 community by communities like those generated by Model 2, could have resulted in more stable and persistent communities. At the same time, both the proportion of paleocommunity simulations that are more stable than Model 3 communities (θ), and the overall magnitude of the paleocommunity's stability relative to Model 3 ($\overline{\Delta Se}$), increase (Fig. 8), again in contrast to the Permian communities. Therefore, although the Ph3 community comprised species capable of surviving the PTME, options for subsequent variation of clade richnesses within the observed guild structure were very narrow. Changes via origination and extinction within existing lineages likely would have yielded less stable communities, producing macroevolutionary dead-ends.

This prediction is supported by the faunal differences between Ph3 and the *Lystrosaurus* Assemblage Zone (LAZ). Only 13 of 38 vertebrates in the LAZ are survivors from Ph3 (Roopnarine et al., 2018) (Fig. 1). Nine Ph3 tetrapods persist into the LAZ, whereas five do not. Of the remaining Ph3 survivors, three are higher fish taxa that cannot be identified at a low taxonomic level (indeterminate chondrichthyan, indeterminate actinopterygian, indeterminate actinopterygian in Supplementary Table S1 in Roopnarine et al., 2018) and one is the fish genus *Elonichthys*; this lack of taxonomic resolution might mask additional differences between the assemblages. The LAZ has been noted for its unusually rich amphibian fauna (Roopnarine et al., 2007; Smith et al., 2012), numerical dominance of the herbivorous therapsid *Lystrosaurus* (Smith et al., 2012), accelerated ontogenetic development of some tetrapods (Huttenlocker, 2014; Botha-Brink et al., 2016), high beta diversity (Brocklehurst et al., 2017), and unusual ecological dynamics (Roopnarine and Angielczyk, 2012; Irmis and Whiteside, 2012). Our results show that both variation of guild richnesses (Model 3), and re-organizations of guild structure (Model 2) would have been overwhelmingly likely to result in more persistent species and stable communities than those observed ($\theta < 0.2$, $\overline{\Delta Se} < 0$). The LAZ community itself could have persisted unchanged, with lineages therefore apparently incumbent, only if negative species interactions ($-\sigma$) (i.e., the impacts of predators on prey) were exceedingly weak. Alternative macroevolutionary trajectories would have generated more persistent communities over much of the parameter space, thus rendering LAZ an easily replaced and expectedly ephemeral community. The modeling prediction is again consistent with observation, as the transition of the LAZ to the succeeding Middle Triassic *Cynognathus* Assemblage subzone B (CAZ) was accompanied by an almost complete turnover of tetrapod taxa (1 of 38 LAZ tetrapods persist into the CAZ) (Fig. 1). Unlike the Early Triassic communities, however, variations of the CAZ paleocommunity structure (Model2) were not likely to yield more persistent or stable communities. This condition is similar to those of the Permian communities. Furthermore, changes to guild richnesses (Model 3) were also unlikely to yield greater persistence, and in this regard the CAZ exhibits the greatest differentiation from Model 3 of all the paleocommunities. The CAZ community therefore signaled the emergence of a strong incumbency in the Karoo ecosystem by the Middle Triassic.

4.3. Recovery after the PTME

Determination of the time taken for the Karoo Basin ecosystem to recover from the PTME first requires a definition of recovery. Multiple measures of recovery from mass extinction have been proposed, most of which focus on rebounds of taxonomic diversity. Expectations are often based on richness prior to an extinction, but there are no theoretically-based expectations of how rich any system should, or can be. How rich must a post-extinction system be in order to be considered recovered? In a review of studies of post-PTME recovery in marine systems, Dineen et al. (2014) noted that 96% considered the presence of high taxonomic diversity to signify a recovered paleocommunity. Other, less used, measures of recovery have focused instead on ecological features, such as numerical abundance, body size distributions, or presumed indicators of ecosystem function, for example evenness or guild diversity. Recovery is considered complete when normal ecosystem functioning has resumed (Krassilov, 1996; Erwin, 2001), but again, there are no expectations of what constitutes “normal”. Here we offer an alternative measure of ecosystem recovery: recovery is complete when system global stability, that is the stability of species persistence and coexistence, has attained or exceeded levels of stability that were present prior to the extinction. Recovery, therefore, is complete when ecosystems are once again geologically persistent and have the semblance of incumbency. This definition of recovery encompasses features often noted in the aftermaths of mass extinctions, including an absence of ecological turnover (e.g. the end Ordovician mass extinction), a decoupling of taxonomic and ecological rediversification, and ecological reorganization or restructuring (Dineen et al., 2014).

For the Karoo Basin, although the increase of taxonomic diversity began in the Early Triassic, system persistence was not attained in our dataset until the Middle Triassic CAZ (Fig. 10). We can therefore use the development of the CAZ as a minimum estimate of the time required for post-PTME recovery of the Karoo ecosystem. If our estimates of the ages of the CAZ subzones discussed earlier are correct, and assuming that the loss of incumbency occurred at the PTB (251.902 Ma; revision 2017/2 of the International Chronostratigraphic Chart; see Cohen et al., 2013), then the ages imply that incumbency could have been re-established in as little as 4–5 Ma, or to have taken as long as 9–17 Ma after the PTB. These estimates assume that the *Cynognathus* subzone B assemblage was the first stable tetrapod community in the Triassic of the Karoo. A shorter time to recovery might be possible if the upper Katberg Formation assemblage documented by Neveling (2004; "*Procolophon* Abundance Zone" of that paper) or the *Cynognathus* subzone A assemblage were stable communities. Both of these communities have comparatively limited fossil records (Neveling, 2004; Smith et al., 2012), however, which makes them difficult to analyze in the modeling framework developed here. Nevertheless, our range of estimated recovery times provides a useful benchmark that can be further tested by additional research in the Karoo and in other fossiliferous sequences.

Irmis and Whiteside (2012) performed an extensive specimen-based analysis within the then current stratigraphic framework, noting the low evenness of the LAZ, and also supporting a Middle Triassic recovery of the Karoo system. The high relative abundance of *Lystrosaurus* in the LAZ has lead to its frequent description as a "disaster taxon", i.e., a taxon able to take advantage of the presumably unusual environmental conditions of the Early Triassic. The current study, however, raises the possibility that the low relative abundances of other taxa in the LAZ (Irmis and Whiteside, 2012) was driven by the structure of the community and consequent difficulties with stable coexistence, independent of the Early Triassic environment. What then were the relative contributions of coevolutionary factors and environmental parameters to the delayed recovery? We propose that the modeling framework presented here could address this question in the future with the incorporation of increasingly detailed sampling analyses (Irmis and Whiteside, 2012; Fröbisch, 2013; Roopnarine et al., 2018) and stratigraphic refinements (Fröbisch, 2013, 2014; Smith and Botha-Brink, 2014; Viglietti et al., 2018a; Roopnarine et al., 2018).

4.4. *Extinction, recovery, and incumbency*

Discussions of the interplay between mass extinctions and incumbency typically focus on the role of extinction itself in breaking preexisting patterns of incumbency (e.g., see reviews in Jablonski, 2001, 2005, 2008). This relationship is intuitively appealing: extinction literally removes incumbents, freeing ecological space or generating new ecological opportunities that other taxa can occupy, potentially establishing themselves as new incumbents. However, our results suggest that even in an event as severe as the PTME, extinction alone may not alter community structure sufficiently to undermine the compositional stability that promotes incumbency. Instead, addition of new taxa to the community through immigration and origination may be required. If we assume that the lDAZ represents a pre-extinction background community, and use it as a starting point, it is clear that the community was strongly affected by extinction during the PTME and that origination was trivial. Based on the compilation underlying our analyses (also see Roopnarine et al., 2018), 53 of the 68 vertebrate taxa present in the lDAZ were extinct by Ph2 (78% extinction), whereas only two taxa (*Lystrosaurus maccaigi* and *L. curvatus*) had their first appearances in the same interval. However, despite these losses of richness, stability steadily increased (Fig. 10). In contrast, while the transition from Ph2 to Ph3 also involved extinction (12 of the 16 vertebrate taxa present in Ph2 do not persist into Ph3), this was much more closely balanced by origination (14 of the 18 vertebrate taxa present in Ph3 are new), and stability is significantly lower in Ph3 than in Ph2. The transition between Ph3 and the LAZ is even more strongly dominated by origination (five of the 18 vertebrates in Ph3 do not persist into the LAZ; 25 of 38 vertebrates in the LAZ are new), and stability further declines. These decreases in stability likely stem in part from the increased species richness of Ph3 relative to Ph2, and the LAZ relative to Ph3 because, according to the MWT, richer communities are expected to be less stable. Richness alone cannot explain the low stability of Ph3 and the LAZ, though, because the lDAZ, uDAZ, and CAZ are of equal or greater richness as LAZ but all are more stable. Instead, it is the distribution of the new taxa among the guilds of the community that causes the loss of stability and incumbency, and our alternative histories demonstrate that there are many ways the same number of new taxa could have been added that would not have result in reduced stability. As the recovery proceeded (represented in our example by the transition to CAZ), stability eventually recovered, but with new sets of taxa in incumbent roles.

An implication of these results is that even if members of formerly incumbent groups survive an extinction event, changing ecological circumstances that accompany the addition of many new taxa could prevent them from participating in the new post-extinction communities in the same fashion as they did in pre-extinction communities. A natural question, then, is why is this the case? Is it because of fundamental changes in community structure and the nature of interactions that are possible, or does it stem from the loss of specific interactors even if the same general type of interactions are possible (e.g., the loss of a particular prey species even if predator-prey relationships are still "allowed")? Other explanations, including those focusing on aspects of ecology other than trophic interactions, are possible as well. Answering these questions will be important for understanding whether top-down effects of community structure on species evolution, or species level-properties and the idiosyncracies of individual species' evolutionary histories, play a preeminent role in the establishment of particular taxa as incumbents (our results only address the role of community structure in the maintenance of incumbency).

4.5. *Caveat lector*

The validity of the analyses and findings presented in this paper depends on the reliability of the stratigraphic and chronologic frameworks, the paleocommunity data, and the ecological model. The sequence of paleocommunities, their reconstructions, and their relationship to both the PTB and PTME, all influence tests of the incumbency-biotic interactions hypothesis. Reliability of the community reconstructions has recently been established with extensive compilation, revision, and validation (e.g. rarefaction analyses) of the data (Roopnarine et al., 2018), and the assemblage zone-based subdivision of the Karoo ecosystem is based on the most recent considerations of relevant data (e.g., see review in Rubidge et al., 2016; recent detailed work near the PTB by Viglietti et al., 2016, 2018b). Problems remain with establishing a precise relationship between the Karoo sequence and the PTB, and this generates uncertainty about whether the dramatic faunal turnovers reported here and elsewhere are contemporaneous with the better-established PTME in the marine realm. However, such synchrony does not affect our analyses, nor the eco-evolutionary reasoning in our hypothesis. Moreover, synchrony perhaps should not be expected given our changing understanding of both the driving mechanisms of the PTME and their timing. Although Siberian volcanism is now widely accepted as the ultimate driver of the PTME, diachrony in the marine realm would be expected based on geographic proximity, which in turn is important because of regional effects of early eruptive volcanism, followed later by climate-driven global effects resulting from the broad intrusion of sub-surface lava sills (Burgess et al., 2017). Those temporal and geographic heterogeneities would also affect the PTME on land, and the relationship of various regional terrestrial and marine records to the PTB.

Similarly, even if the extinction phases first proposed by Smith and Botha-Brink (2014) are not real, the basic DAZ-LAZ-CAZ sequence documents major changes in tetrapod community composition and structure, with similarly significant changes in predicted community stability. The magnitude of these changes, and the associated disruption and recovery of incumbency, are consistent with those expected for a mass extinction-level event. Therefore, we assert that a record of a mass extinction near the end of the Permian is recorded in the sedimentary record of the Karoo Basin, and that the associated loss and recovery of incumbency that we document here is correct in at least its broad outline, regardless if the details of the hypothesized stepped extinction and the exact relationship to the event in the marine record of south China are eventually shown to be incorrect.

The mathematical model used here simplifies the complexities of ecological interactions and systems in a manner that makes them tractable for the analysis of large systems, while retaining features necessary for comparative analyses of paleocommunities. Complex systems, and complex phenomena such as ecosystem responses to significant environmental perturbations, lead naturally to a multitude of explanatory hypotheses, e.g. Erwin's “Murder on the Orient Express” explanation of the PTME (Erwin, 2015). Simple models bear the advantages of yielding insight into the workings of the models, which then provide insight into which details of a system may be important or unimportant to the explanation of a particular dynamic, and provide frameworks for controlled and methodical hypothesis testing. In this regard, models are superior to simulations that seek to recreate reality. Attention must always be paid, however, to simplifying assumptions and those details omitted by a model, and whether inclusion could potentially alter results in any significant way. The present model makes a large simplifying assumption, that is, that species in a community all have equal net reproductive rates (R). R is difficult to measure empirically in modern species, but typically ranges between $\approx$one and four, with values concentrated toward the lower end of the range. These empirical measures were used to determine the range over which we conducted our analyses, but species within a community will realistically have a diversity of values, in contrast to our model. The difficulty we encounter is in determining R for fossil taxa, as there are currently no such data for taxa in our analyses. However, reasonable approximations could be forthcoming from uniformitarian examinations of distributions of R values in modern terrestrial communities (e.g., see Sæther and Engen, 2002; Delean et al., 2012), and features of fossil taxa, including: relative abundances, the dynamics of relative abundances (Irmis and Whiteside, 2012; Codron et al., 2017), and growth trajectories and life history traits reconstructed from observations of bone histology.

Our model also does not attempt to recreate the actual food webs of the paleocommunities. Two general approaches, which we refer to as the precision and accuracy approaches (Roopnarine, 2018) have dominated the reconstruction of paleontological food webs. The precision approach relies on exquisite fossil preservation, i.e. Konservat-Lagerstätten, and has been applied to Cambrian marine communities from the Burgess Shale and Chengjiang (Dunne et al., 2008), and more recently the terrestrial Messel Shale (Dunne et al., 2014). This approach, however, is limited by the occurrences of Konservat-Lagerstätten, which do not necessarily coincide with intervals of particular paleontological interest. The accuracy approach, employed here, relies on accurate reconstructions of the general functional relationships among groups of ecologically similar fossil taxa, that are then used to constrain the simulated food webs to those plausibly consistent with a particular paleocommunity. The uncertainty inherent in this approach is dealt with by the generation and statistical examination of large ensembles of model food webs. The accuracy approach can be applied to any fossil assemblage, with an understanding that uncertainty and the variability of results increase with declining preservation.

4.6. Future directions

Finally, there are several avenues of research that must be addressed to test the generality of the hypothesis presented here. First, our record of the Permian Karoo Basin ecosystem extends back to the Middle Permian *Eodicynodon* Assemblage Zone, and encompasses the Guadalupian epoch. Thus there is the opportunity to examine the emergence of incumbency in the Karoo Permian ecosystem over a longer time interval, and to observe the impact, if any, of the end-Guadalupian extinction event (see Day et al., 2015; Rey et al., 2016, 2018; Lucas, 2017 for recent discussions of this extinction in the Karoo). Second, additional terrestrial ecosystems roughly coeval to the Karoo Basin must be considered. For example, our analyses could be applied to other areas that preserve late Permian and Early-Middle Triassic paleocommunities, such as Russia and northwestern China (Benton et al., 2004; Ivakhnenko et al., 1997; Liu and Abdala, 2017; Lucas, 2001; Metcalfe et al., 2009; Sennikov, 1996; Sennikov and Golubev, 2017). Third, the hypothesis must be tested in the marine realm, where the geological persistence of paleocommunities and ecosystems is well established. This is particularly relevant here for the PTME, but both marine and terrestrial systems bounding other mass extinctions should eventually be considered.

5. Conclusion

1. A hypothesis is presented stating that biotic incumbency on geological timescales is the result of the evolution of patterns of biotic interactions that promote and increase levels of species persistence and coexistence.
2. Any functional compartmentalization of species and diversification of functionality that emerge during the history of a community increases the global stability of the community, but some functional structures confer significantly greater stability than others.
3. Those patterns of functional structure and biotic interactions do not constrain or prohibit the generation of alternative macroevolutionary histories or community types, but their superior ecological stability render them more geologically persistent.
4. Incumbent patterns may be undone under conditions of extreme environmental perturbation, such as those prevailing during mass extinctions, but the addition of new (immigrant or newly evolved) taxa after mass extinctions might be of equal or greater importance in rendering formerly persistent patterns as macroevolutionary dead-ends.
5. When the hypothesis is applied to a Permian-Triassic sequence of paleocommunities from the Karoo Basin of South Africa, we observe that the patterns of biotic interactions that rendered incumbency on the late Permian system persisted through two phases of the PTME, but it was destroyed in the earliest Triassic by the addition of new taxa. The succeeding Early Triassic *Lystrosaurus* Assemblage Zone possessed relatively low global stability, and was geologically short-lived, as predicted by the hypothesis. Strong global stabililty and hence incumbency had recovered by the Middle Triassic development of the *Cynognathus* Assemblage Zone subzone B (CAZ), and we therefore claim that recovery from the PTME in the Karoo Basin was complete by 4–17 my after the PTME, based on current age estimates for the CAZ.

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Appendix A

Table A.1

Paleocommunity data model simulations and analyses. Numerical column headings correspond to paleocommunities. lDAZ, lower *Daptocephalus* Assemblage Zone; uDAZ, upper *Daptocephalus* Assemblage Zone; Ph1, first Changhsingian phase of the PTME in the Karoo Basin; Ph2, second Changhsingian phase of the PTME in the Karoo Basin; Ph3, third Induan phase of the PTME in the Karoo Basin; *Lystrosaurus* Assemblage Zone; *Cynognathus* Assemblage Zone; insect richnesses estimated or measured as outlined in Roopnarine et al. (2018).

Guild	lDAZ	uDAZ	Ph1	Ph2	Ph3	LAZ	CAZ
0 Plants accessible to tetrapods and arthropods	1	1	1	1	1	1	1
1 Aquatic macrophytes	1	1	1	1	1	1	1
2 Aquatic microphytes	1	1	1	1	1	1	1
3 Terrestrial plants accessible to arthropods only	1	1	1	1	1	1	1
4 Fish	8	8	8	4	4	13	11
5 Very small amphibians	0	0	0	0	1	3	0
6 Small amphibians	0	0	0	0	0	3	0
7 Medium amphibians	1	1	0	0	0	0	2
8 Large amphibians	0	0	0	0	0	1	1
9 Very large amphibians	2	2	2	1	0	3	2
10 Very small herbivores	4	4	0	0	4	4	10
11 Very small faunivores	1	8	1	1	1	12	4
12 Small herbivores	5	2	0	0	1	1	2
13 Small carnivores	12	9	2	1	3	4	0
14 Medium herbivores	4	6	5	4	2	1	0
15 Medium carnivores	9	5	1	1	2	2	0
16 Large herbivores	5	4	2	1	0	0	2
17 Large carnivores	3	5	0	0	0	0	0
18 Very large herbivores	3	3	3	0	0	0	0
19 Very large carnivores	2	3	1	0	0	0	2
20 Molluscs	2	2	1	0	0	1	1
21 Conchostracans	2	2	1	0	0	1	0
22 Myriapods	0	0	0	0	0	2	0
23 Carnivorous insects	8	8	2	1	1	8	7
24 Herbivorous insects	23	22	7	3	3	23	21
25 Omnivorous insects	30	29	20	9	9	29	27

Table A.2

Key to images used in Fig. 2. Guild numbers correspond to those outlined in Appendix ATable A.1. Communities with those guilds present are listed, followed by the representative taxon illustrated, attribution to the image's creator, and a link to the original image on the Phylopic database. To access images, prepend the following to each link: http://phylopic.org/. Note that the selected images are intended to approximate members of the various guilds but the use of a particular image does not imply the presence of the exact taxon listed in the phylopic database. For example, the Cisuralian temnospondyl *Edops* is used to represent the very large amphibian guild in the *Lystrosaurus* and *Cynognathus* zones because the silhouette roughly approximates the body plan of members of the guild such as *Jammerbergia*. However, *Edops* itself does not occur in the Karoo Basin and is not a member of any of the analyzes communities.

Guild	Community	Taxon	Phylopic creator	Phylopic link
0	lDAZ, Ph1	*Pteridium*	Olegiwit	f2d82e69-89b2-4164-9dfe-e9e623cbd848/
	LAZ, CAZ	*Equisetum*	A. Schmidt-Lebuhn	3115ffd6-3ccc-423c-a4af-affca7fd0eca/
1	lDAZ, Ph1, LAZ, CAZ	Bryopsidales	S. A. Muñoz-Gómez	6295da8f-98b2-429a-8588-0e3e48012656/
2	lDAZ, Ph1, LAZ, CAZ	*Volvox*	Matt Crook	0ec3fcd6-6072-425a-8089-8c36b7d42a1d/
3	lDAZ, Ph1	*Zamites*		a2e8854f-7f6e-4604-a0be-59f903cf2e7b/
	LAZ	*Glossopteris*	P. Roopnarine	N/A
	CAZ	*Gingko*	J. Schneid	098b93a4-b9aa-4a80-9698-4528466fdb61/
4	lDAZ, Ph1, LAZ	*Perleidus*	Ghedo	c527d63a-32dc-428a-8a1f-ed2022c111be/
	CAZ	*Ceratodus*	N/A	de33e9bd-643d-4a68-a3c4-c3206f9b508e/
5	LAZ	*Balanerpeton*		44d75550-e908-48b7-9089-a377f7bb52ee/
6	LAZ	*Lydekkerina*		02568c97-85e7-4b78-9a2b-40efc8390f1d/
7	lDAZ	*Iberospondylus*	D. Bogdanov	8b2bfb80-0952-4679-aa9e-5bd2f7d5888e/
	CAZ	*Batrachosuchus*	D. Bogdanov	1c913df8-10d4-4f68-8b88-ed454a139695/
8	LAZ, CAZ	*Iberospondylus*	D. Bogdanov	8b2bfb80-0952-4679-aa9e-5bd2f7d5888e/
9	lDAZ	*Iberospondylus*	D. Bogdanov	8b2bfb80-0952-4679-aa9e-5bd2f7d5888e/
	LAZ,CAZ	*Edops*	D. Bogdanov	4e30477a-f64c-4d2f-9a5e-92cb24fe528f/
10	lDAZ	*Diictodon*	Smokeybib	00b96cf3-1802-4bda-a6cc-76aea0f6f05e/
	LAZ,CAZ	*Procolophon*	Nobu Tamura	7a7e93a2-00d4-41f2-aded-8483ad38c7f1/
11	lDAZ, Ph1	*Milleretta*	Nobu Tamura	00b96cf3-1802-4bda-a6cc-76aea0f6f05e/
	LAZ	*Prolacerta*	N/A	dec8dce0-d6f0-41a7-a9de-992fc558c341/
	CAZ	*Procynosuchus*	Nobu Tamura	c466a71f-90b9-4ea7-b6ba-56cb37d47f22/
12	lDAZ	*Diictodon*	Smokeybib	00b96cf3-1802-4bda-a6cc-76aea0f6f05e/
	LAZ	*Lystrosaurus*	N/A	b02c8c23-4263-436a-9a3a-068fc851dbb7/
	CAZ	*Cynognathus*		6cbe14b2-022a-4982-82c0-53c0e0fb5cb8/
13	lDAZ, Ph1, LAZ	*Procynosuchus*	Nobu Tamura	c466a71f-90b9-4ea7-b6ba-56cb37d47f22/
14	lDAZ, Ph1, LAZ	*Lystrosaurus*	N/A	b02c8c23-4263-436a-9a3a-068fc851dbb7/
15	lDAZ, Ph1	*Scylacosaurus*	N/A	6ecdac12-8832-401b-b6e2-8474dbc41b6a/
	LAZ	*Proterosuchus*	N/A	50514508-25e9-4f5b-9fc8-17994dff3edb/

(*continued on next page*)

Table A.2 (*continued*)

Guild	Community	Taxon	Phylopic creator	Phylopic link
16	lDAZ, Ph1	*Aulacephalodon*	D. Bogdanov	79b83f80-67f6-44ce-b372-28fe99e9c920/
	CAZ	*Vivaxosaurus*	D. Bogdanov	ca37ddd6-e5e6-4404-b9b2-fcea425aaccd/
17	lDAZ	*Gorgonops*	D. BOgdanov	27ae0ae2-5bfb-4ae5-b8c1-b18c6c5fc11f/
18	lDAZ, Ph1	*Bradysaurus*	Karkemish	993f5179-fff4-4c90-bbd1-deca577e562f/
19	lDAZ, Ph1	*Dinogorgon*	N/A	ddbd5048-3148-4088-9ab1-97becdcb7ae3/
	CAZ	*Vjushkovia*	Smokeybib	e6c1771a-f514-433a-be0e-5fd8607f8374/
20	lDAZ, Ph1, LAZ, CAZ	Protobranchia	N/A	d92d2313-359a-4649-9cb8-5c4d84474f4b/
21	lDAZ, Ph1, LAZ	Conchostraca	P. Roopnarine	N/A
22	LAZ	*Scutigerella*	R. Janssen	fbb34126-2757-4201-9717-c5a0df3fdfb7/
23	lDAZ, Ph1, LAZ, CAZ	*Calopteryx*	M. Dahirel	8af9c80d-92f9-4ba8-87c0-8ffa026c770c/
24	lDAZ, Ph1, LAZ, CAZ	*Miomoptera*	N/A	3010e744-6b06-4022-9ce6-354db93e99fe/
25	lDAZ, Ph1, LAZ, CAZ	*Epicharmeropsis*	E. Willoughby	19c45126-9daf-48c8-b241-fbfa0be7025f/

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