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Late Permian (Lopingian) terrestrial ecosystems: A global comparison with new data from the low-latitude Bletterbach Biota

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ABSTRACT

The late Palaeozoic is a pivotal period for the evolution of terrestrial ecosystems. Generalised warming and aridification trends resulted in profound floral and faunal turnover as well as increased levels of endemism. The patchiness of well-preserved, late Permian terrestrial ecosystems, however, complicates attempts to reconstruct a coherent, global scenario. In this paper, we provide a new reconstruction of the Bletterbach Biota (Southern Alps, NE Italy), which constitutes a unique, low-latitude record of Lopingian life on land. We also integrate floral, faunal (from skeletal and footprint studies), and plant–insect interaction data, as well as global climatic interpretations, to compare the composition of the 14 best-known late Permian ecosystems. The results of this ecosystem-scale analysis provide evidence for a strong correlation between the distribution of the principal clades of tetrapod herbivores (dicynodonts, pareiasaurs, captorhinids), phytoprovinces and climatic latitudinal zonation. We show that terrestrial ecosystems were structured and provincialised at high taxonomic levels by climate regions, and that latitudinal distribution is a key predictor of ecosystem compositional affinity. A latitudinal diversity gradient characterised by decreasing richness towards higher latitudes is apparent: mid- to low-latitude ecosystems had the greatest amount of high-level taxonomic diversity, whereas those from high latitudes were dominated by small numbers of higher taxa. The high diversities of tropical ecosystems stem from their inclusion of a mixture of late-occurring holdovers from the early Permian, early members of clades that come to prominence in the Triassic, and contemporary taxa that are also represented in higher latitude assemblages. A variety of evidence suggests that the Permian tropics acted as both a cradle (an area with high origination rates) and museum (an area with low extinction rates) for biodiversity.

1. Introduction

The late Palaeozoic is a pivotal time interval for the evolution of terrestrial ecosystems. A generalised aridification trend, best documented in Europe and North America (Chumakov and Zharkov, 2002; Roscher and Schneider, 2006), shows a transition from hygrophytic,

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everwet communities to xerophytic, seasonally dry ones (e.g., DiMichele et al., 2001; Looy et al., 2014). For plants, this transition triggered a replacement of older Palaeozoic lineages by more modern Mesozoic groups (e.g., DiMichele et al., 2001; Looy et al., 2014), and the development of the four phytogeographic provinces of Gondwana, Cathaysia, Euramerica and Angara (Meyen, 1982; Archangelsky, 1990; Ziegler, 1990; Wagner, 1993). Tetrapod faunas experienced a major changeover, most famously with the gross compositional change from those dominated by basal synapsids ('pelycosaurs') to those dominated by non-mammalian therapsids, such as Anomodontia, Gorgonopsia, and Cynodontia (e.g., Brocklehurst et al., 2017; Angielczyk and Kammerer, in press and ref. therein). Moreover, this period saw the diversification of parareptiles (Tsuji and Müller, 2008; Ruta et al., 2011; Benton, 2016), and the radiation of diapsid reptiles (Müller and Reisz, 2006; Reisz et al., 2011), including the emergence of archosauriforms (Ezcurra et al., 2014; Bernardi et al., 2015).

Late Permian ecosystems generally are considered to be more ecologically integrated than those of the early Permian, at least in terms of the number of trophic levels (Olson, 1966; Benton, 2012). However, the dynamics of both floral and faunal turnover are still poorly understood. The transition from Palaeozoic to Mesozoic plant groups, for example, seems to be globally diachronous (Knoll, 1984; DiMichele et al., 2001; Looy et al., 2014), and late Permian vertebrate communities have been described as highly homogeneous across the whole of Pangaea (Sues and Boy, 1988; Rage, 1988; Milner, 1993; Dilkes and Reisz, 1996; Sues and Munk, 1996) to moderately endemic (Modesto et al., 1999; Modesto and Rybczynski, 2000; Angielczyk and Kurkin, 2003; Sidor et al., 2005; Angielczyk, 2007). Although new discoveries (e.g., Angielczyk and Sullivan, 2008; Smith et al., 2015; Huttenlocker et al., 2015; Benton, 2016; Huttenlocker and Sidor, 2016) and macroevolutionary studies (e.g., Fröbisch, 2009; Sidor et al., 2013) are contributing to a new and more comprehensive picture of late Permian terrestrial life, the geographic patchiness of well-preserved Lopingian ecosystems complicates attempts to outline a coherent, global scenario. Furthermore, a deep understanding of Permian terrestrial ecosystems is especially relevant because this time interval precedes the most severe biotic crisis of Earth history, the end-Permian mass extinction (Benton and Twitchett, 2003).

Lopingian tetrapod faunas, yielding skeletal and/or footprint remains, are known from Scotland (Benton and Walker, 1985), Great Britain and Germany (Benton and Walker, 1985; Sues and Boy, 1988), Poland (Ptaszyński and Niedźwiedzki, 2004; though its age is controversial, see Bachman and Kozur, 2004; Nawrocki et al., 2005; Racki, 2005), Italy (Conti et al., 1977), Morocco (Jalil and Dutuit, 1996; Voigt et al., 2010; Hminna et al., 2012), Tunisia (Newell et al., 1976), Malawi (Haughton, 1926; Jacobs et al., 2005; Kruger et al., 2015), Mozambique (Latimer et al., 1995; Castanhinha et al., 2013), Tanzania (Gay and Cruickshank, 1999; Sidor et al., 2010; Angielczyk et al., 2014a), Zimbabwe (Bond, 1973; Gaffney and Mc Kenna, 1979), Zambia (Drysdall and Kitching, 1963; Kemp, 1976; Lee et al., 1997; Angielczyk et al., 2014b), Niger (Sidor et al., 2005; Smith et al., 2015), South Africa (MacRae, 1990; Smith, 1993a, 1993b; De Klerk, 2002; Ward et al., 2005; Rubidge, 2005; Smith et al., 2012; Rubidge et al., 2016), Madagascar (Mazin and King, 1991; Schoch and Milner, 2000), Brazil (Battail, 2000; Langer, 2000; Dias-da-Silva, 2012; Costa da Silva et al., 2012; Boos et al., 2013), India (Kutty, 1972; Ray, 1999, 2000; Ray and Bandyopadhyay, 2003; Kammerer et al., 2016), China (Li and Cheng, 1995a, 1995b; Lucas, 2001; Metcalfe et al., 2009; Liu, 2013; Liu et al., 2014), Laos (Battail, 2000, 2009) and Russia (Ivakhnenko et al., 1997; Gubin et al., 2003; Benton et al., 2004; Surkov et al., 2007). Plant fossil assemblages have been described from the Germanic Basin (mostly Germany and England; e.g., Stoneley, 1958; Haubold and Schaumberg, 1985; Schweitzer, 1986; Uhl and Kerp, 2002 and ref. therein), Italy (e.g., Visscher et al., 2001; Kustatscher et al., 2012, 2014); Oman and Jordan (Berthelin et al., 2003; Kerp, 2006; Hamad et al., 2008), China (Sun, 2006; Deng et al., 2009), Brazil (Archangelsky, 1986; Rohn and Rösler, 1989, 2000; Langer et al., 2008), Antarctica (McLoughlin et al., 1997; Manus et al., 2002), South Africa (Anderson and Anderson, 1985; Prevec et al., 2009, 2010), Laos (Bercovici et al., 2012), and Australia (Beattie, 2007). Notably, the lack of plant and animal fossil co-occurrence, or alternatively their extremely low diversity, prevents the full reconstruction of terrestrial ecosystems for most of these sites. Complex and structured terrestrial ecosystems have been reconstructed so far only from South Africa (Karoo Basin; e.g., Gastaldo et al., 2005; Prevec et al., 2009, 2010; Nicolas and Rubidge, 2010; Smith et al., 2012), Russia (Southern Urals; e.g., Benton et al., 2004; Sahney and Benton, 2008) and China (Ordos and Yunggur Basins; Lucas, 2001), although co-occurring plant and animal remains are available also from other sites (see below).

Even when floral and faunal data are available for ecosystem reconstruction, vertebrates have generally received considerably more attention and more integrated studies have seldom been performed. For example, an approach developed by Roopnarine and colleagues (Angielczyk et al., 2005; Roopnarine et al., 2007; Roopnarine, 2009; Roopnarine and Angielczyk, 2012, 2015, 2016) focuses on trophic interactions between animals while reducing primary producers to units of productivity necessary to support the system. Perhaps the most direct research on Permian plant–animal interactions comes from studies of the trophic relationships between herbivorous terrestrial arthropods and vascular plants. These studies span the early Permian of Texas (Schachat et al., 2014, 2015; Schachat and Labandeira, 2015); the early and middle Permian of southeastern Brazil (Adami-Rodrigues et al., 2004a, 2004b); the late Permian to late Triassic of the Karoo Basin of South Africa (Prevec et al., 2009, 2010; Labandeira et al., 2017) and the early Permian to Middle Triassic of the Dolomites, northeastern Italy (Wappler et al., 2015; Labandeira et al., 2016). The patterns emerging from this research provide an important baseline for understanding changes in plant-animal interactions across the Permo-Triassic transition.

The palaeogeographic configuration of the late Permian identifies three great continental masses that are principally distributed at the mid-latitudes (Gondwana, Laurussia and Siberia), joined together into a quasi-continuous supercontinent (Pangaea), bordered to the east by a series of islands (Cathaysia) and the Tethys Ocean (Scotese, 2003; Stampfli and Borel, 2004; Blakey, 2008). Climate has been suggested as the main controlling factor of biogeographic and phytogeographic distributions under this continental configuration (Ziegler, 1990; Rees et al., 2002; Sidor et al., 2005), and long- and short-term climate changes have been investigated for this interval using fossil floras, climate-sensitive rocks, and modelling (Cuneo, 1996; Fluteau et al., 2001; Rees, 2002; Rees et al., 2002; Roscher et al., 2008, 2011; Wopfner and Jin, 2009; Schneebeli-Hermann, 2012).

In this paper we provide a new, comprehensive reconstruction of the Bletterbach Biota (Lopingian of Southern Alps, NE Italy), and we review and discuss the other 13 best-known Lopingian terrestrial associations containing both vertebrate (documented by skeletal and footprint data) and plant remains, with the ultimate goal of providing the most complete analysis of late Permian ecosystems worldwide. Given the limited amount of data available on Lopingian low latitude terrestrial ecosystems (cf. Sidor et al., 2005), we suggest that the Bletterbach ecosystem constitutes a unique record that is a key reference for global studies. By integrating floral, faunal and climatic global interpretations, we discuss the composition of late Permian ecosystems and provide evidence for a strong correlation between the distribution of the main herbivorous tetrapod groups (dicynodonts, pareiasaurs, captorhinids), phytoprovinces and climatic latitudinal zonation.

2. Late Permian climates and terrestrial ecosystems

The progressive trend towards drier climates during the late Palaeozoic had its most dramatic effect in the continental interior and