RESEARCH ARTICLE

Geological control on dinosaurs' rise to dominance: Late Triassic ecosystem stress by relative sea level change

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Abstract

The Late Triassic is enigmatic in terms of how terrestrial life evolved: it was the time when new groups arose, such as dinosaurs, lizards, crocodiles and mammals. Also, it witnessed a prolonged period of extinctions, distinguishing it from other great mass extinction events, while the gradual rise of the dinosaurs during the Carnian to Norian remains unexplained. Here we show that key extinctions during the early Norian might have been triggered by major sea-level changes across the largest delta plain in Earth's history situated in the Triassic Boreal Ocean, northern Pangea. Fossil and rock records display extensive marine inundations with floral turnover, demonstrating how susceptible widespread low-gradient delta plains were to transgressions. Landward shoreline translocation implies decrease in important coastal regions and ecological stress on the dominant Archosauria, thriving in these habitats, and we argue that these unique geological factors played an important role in dinosaurs gradual rise to dominance.

1 | INTRODUCTION

The Late Triassic was a time of significant biotic upheaval, with the origination of new groups such as dinosaurs, lizards, crocodiles and mammals, but also characterized by a prolonged period of extinctions, distinguishing it from other great mass extinction events, while the gradual rise of the dinosaurs during the late Carnian to Norian remain unexplained (Benton, Forth, & Langer, 2014; Brusatte, Nesbitt, et al., 2010; Sereno, 1999). This stepwise, important shift in terrestrial life occurred over a prolonged period with complex patterns of mass extinctions (Bernardi, Gianolla, Petti, Mietto, & Benton, 2018; Lucas & Tanner, 2018; Tanner, Lucas, & Chapman, 2004). Each extinction event was characterized by distinct turnovers in flora and fauna, but these events have all been attributed to different forcing factors, including the Carnian Pluvial Event (CPE), triggered by Wrangellian volcanism (Dal Corso et al., 2012). Putative extinction events through the Norian have been explained by bolide impacts (Clutson, Brown, & Tanner, 2018). Importantly though, other

distinct extinction events during the Late Triassic (Brusatte, Nesbitt, et al., 2010) are not associated with any known external forcing factors. Because of this complexity, the very premise of a singular end-Triassic mass extinction event has been questioned (Hallam & Wignall, 1999; Lucas & Tanner, 2018; Rigo et al., 2020).

Low-gradient delta plains are key habitats that have been instrumental in the evolution of life throughout Earth history by acting as shelters for surviving species following environmental crises and providing an arena for interaction between the marine and terrestrial realm (Greb, DiMichele, & Gastaldo, 2006). Lethally hot equatorial temperatures at the onset (Sun et al., 2012) of, and periodically through (Whiteside et al., 2015), the Triassic placed extra emphasis on these important deltaic refugia, but also meant that parts of the world normally not crucial in the evolution of life (Jablonski, Roy, & Valentine, 2006) became more important (Spalletti, Artabe, & Morel, 2003)—as demonstrated by prolific tetrapod faunas north of 30°N and south of 40°S during the Triassic (Lucas, 2018). At such northern latitudes, vast delta systems developed within the

Triassic Boreal Ocean (TBO) and have been mapped across areas unmatched by any analogue in Earth's history (Klausen, Nyberg, & Helland-Hansen, 2019).

Terrestrial palynomorph records document the change in dominant plants in a given geographical area and are routinely used as a relative age proxy in addition to being considered indicators of climate and depositional environment. Extensively documented miospore assemblages from the western Barents Sea region record the first occurrence of several new taxa at the Carnian–Norian transition. These include *Cingulizonates rhaeticus*, *Kyrtomisporis gracilis*, *K. laevigatus*, *K. speciosus*, *Limbosporites lundbladiae* and *Retitriletes austroclavatidites* (Paterson & Mangerud, 2015, 2019). The botanical affinity of *Kyrtomisporis* is enigmatic but it is generally interpreted as a fern spore, whereas *Cingulizonates*, *Limbosporites* and *Retitriletes* are considered to represent lycopsid spores (Bonis & Kürschner, 2012) Collectively, these species reflect a parent plant flora, which grew in a warm temperate climatic belt along the northern Pangaean coast (Boucot, Chen, & Scotese, 2013; Sellwood & Valdes, 2006). Palynological investigations (Hochuli & Vigran, 2010; Paterson & Mangerud, 2015; Paterson et al., 2016; Vigran, Mangerud, Mørk, Worsley, & Hochuli, 2014) have revealed that significant compositional differences exist between the composition Late Triassic palynofloras of the TBO and those of the 'classic' Germanic and Alpine areas (Table S1). This includes both differences in the relative abundances of various palynomorph groups (Vigran et al., 2014) and in the stratigraphical ranges of key species and events (Mueller, Hounslow, & Kürschner, 2016). The former has been related to palaeoclimatic control, whereas the latter has been tentatively linked (Paterson et al., 2019) to the earlier origination of several plant genera in the TBO during the late Carnian–early Norian.

In this study, we show how the palynological record of the TBO compares to other basins around the world and explain the terrestrial turnover by significant shifts in major deltaic systems. This terrestrial turnover reinvigorates old ideas about extinctions in the Late Triassic and we hypothesize that cyclic turnovers in terrestrial environments could explain the punctuated rise to dominance of Dinosauria.

2 | RESULTS

The first appearance of the spore taxa *C. rhaeticus*, *K. gracilis*, *K. laevigatus*, *K. speciosus*, *L. lundbladiae* and *R. austroclavatidites* in the western Barents Sea region is recorded in the uppermost parts of the De Geerdalen Formation and correlative Snadd Formation (Paterson & Mangerud, 2015, 2019). This interval is assigned to the late Carnian (Tuvalian) by magnetostratigraphy (Lord et al., 2014), which is calibrated to the global time-scale by an early Norian ammonite fauna from the overlying Flatsalen Formation (Korčinskaya, 1980). Elsewhere in the TBO, such as in the Sverdrup Basin of Arctic Canada, comparable palynomorph assemblages are recorded from lower Norian deposits (e.g. Fisher & Bujak, 1975; Suneby & Hills, 1988). *Kyrtomisporis gracilis* is endemic to the TBO.

While the other spore species listed are commonly represented in Late Triassic assemblages from other basins in the northern Pangaea, their first occurrence elsewhere is significantly delayed. For instance in the more arid continental interior regions, such as the UK and Germany, these taxa do not appear in the fossil record until the late Rhaetian (Morbey, 1975; Lund, 1979; Kürschner & Herngreen, 2010) (Figure 1a), coinciding with an apparent humid phase (Ahlberg, Arndorff, & Guy-Ohlson, 2002; Götz, Ruckwied, & Barbacka, 2011; Hesselbo, McRoberts, & Pálfy, 2007). The origination of these species in the TBO region (Figure 1b) therefore predates their earliest consistent occurrences within the Germanic Realm by up to 20 million years (Figure 2a). Although the distribution of these palynomorphs is facies-controlled to some degree, it seems probable that their parent plants first evolved in the TBO during the late Carnian, before spreading southwards into the interior of Pangaea in the Rhaetian.

The appearance of these species in the TBO coincides with a major floral turnover and paleoenvironmental change in the region. At the maximum regressive stage, slightly prior to their appearance, the deltaic flora over this vast area was dominated by the 'tree like' fern *Asterotheca meriani* (Pott, 2014), as reflected by an acme of its spore *Leschikisporis aduncus* (Hochuli & Vigran, 2010; Paterson & Mangerud, 2015; Paterson et al., 2016, 2019). The abrupt regional extinction of this species in the western Barents Sea during the latest Carnian coincides with marine inundation of the delta, an increased abundance of palynomorphs derived from putative halophytic plants, brackish water algae, agglutinated foraminifera and, in the latter stages, marine microphytoplankton (Mangerud, Paterson, & Riding, 2019; Paterson et al., 2016). The recorded turnover implies significant environmental stress and loss of terrestrial habitats were potential drivers for the evolution of these forms, suggesting they were produced by opportunistic plant species that were able to colonize the new niches created by the widespread flooding of the delta.

Evidence for severe habitat loss is clearly seen in, and explained by, the geomorphological characteristics of the TBO: stratigraphic intervals constrained by palynological ranges comprise deltaic and shallow marine environments that can be traced from Northeast Russia to Svalbard and beyond (Figure 1b). Delta plains within TBO covered more than 1.65×10^6 km^2 by conservative estimates (Klausen et al., 2019) at stages of maximum regression—roughly equal to 1% of total land areas in the modern world (Figure 1b). These widespread delta plains facilitated vast low-gradient coastal habitats, but inherently also made them highly susceptible to marine inundation during periods with increased eustatic sea level or altered sediment supply.

Gradients are usually very low on the tops of large-scale deltas (Paola et al., 2011), and although these landforms respond dynamically to fluctuations in relative sea level (RSL), an increase in only 10 m RSL could potentially shift the shoreline many hundreds of kilometres landward. This is exemplified by the abrupt change from deltaic to shoreline and back to deltaic deposits in the mid-Carnian (Figures 3a–c). Each transgression within the Triassic interval is characterized by deposits of deeper
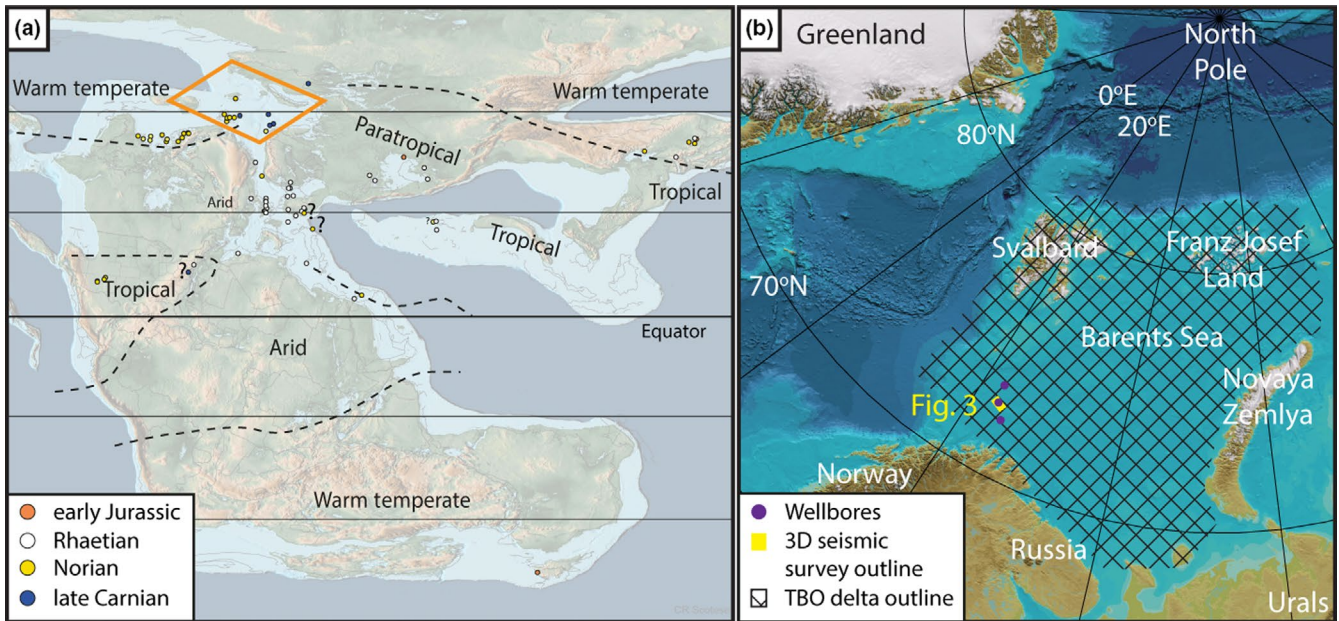
FIGURE 1 Global Late Triassic paleogeography and present day setting of study area. a Paleogeographic setting and climate belts of Triassic Pangaea (Boucot et al., 2013). Global record of palynological assemblages indicates a diachronous distribution of flora. The Triassic Boreal Ocean (orange box) are studied in the subsurface Barents Sea and outcrops on Svalbard b, located at higher latitudes than in the Triassic. Wells and seismic surveys used in the present study are indicated, and the hatched pattern indicates the minimum extent of the TBO delta system at maximum regression (Klausen et al., 2019) [Colour figure can be viewed at wileyonlinelibrary.com]
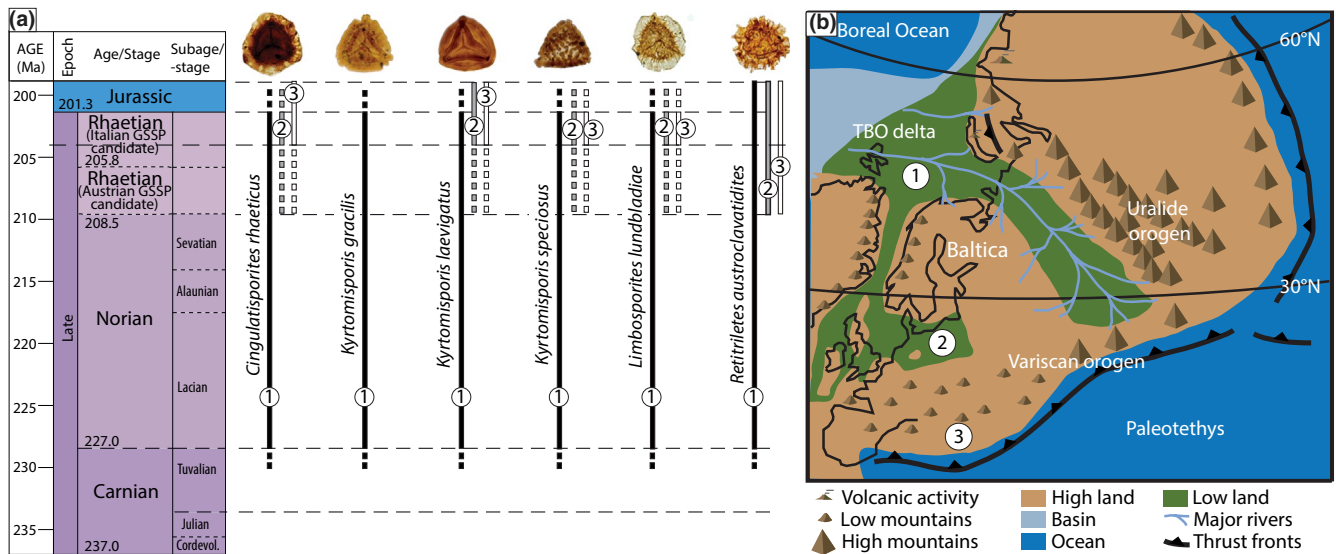

FIGURE 2 Range chart and location map of palynological taxa. (a) Age range of different palynological taxa data with first occurrence in TBO and later arrival in the Germanic and Tethyan basins. Dashed lines indicate sporadic occurrences. (b) Schematic paleogeographic map of Triassic Europe showing the relative position of the sampling sites compared in A and possible migration paths southward, either along the Uralian foreland basin or the rifted remains of the Caledonides. *Kyrtomisporis gracilis* is endemic, reflecting geographically restricted evolution attesting to a prolific habitat in northern Pangea [Colour figure can be viewed at wileyonlinelibrary.com]

marine environments unconformably overlying deltaic deposits (Figure 3d). Interstratification of such different depositional environments attest to several discrete stages of significant RSL changes within TBO, observable in every well that penetrates the interval. Considering the Norwegian sector of the Barents Sea, there are landward shifts of the shoreline over more than 1,000 km occurring approximately every 3 million years.

In the prevailing Greenhouse setting of the Triassic (Retallack, 2013; Sellwood & Valdes, 2006), RSL was primarily controlled by tectonics, climate and sediment supply changing over longer time-scales than modern glacially driven RSL. These controls likely had a global impact on coastal regions around the globe, as reflected in the eustatic signal in basins from different parts of Pangea (Haq, Hardenbol, & Vail, 1988). Flooding of the low-gradient TBO
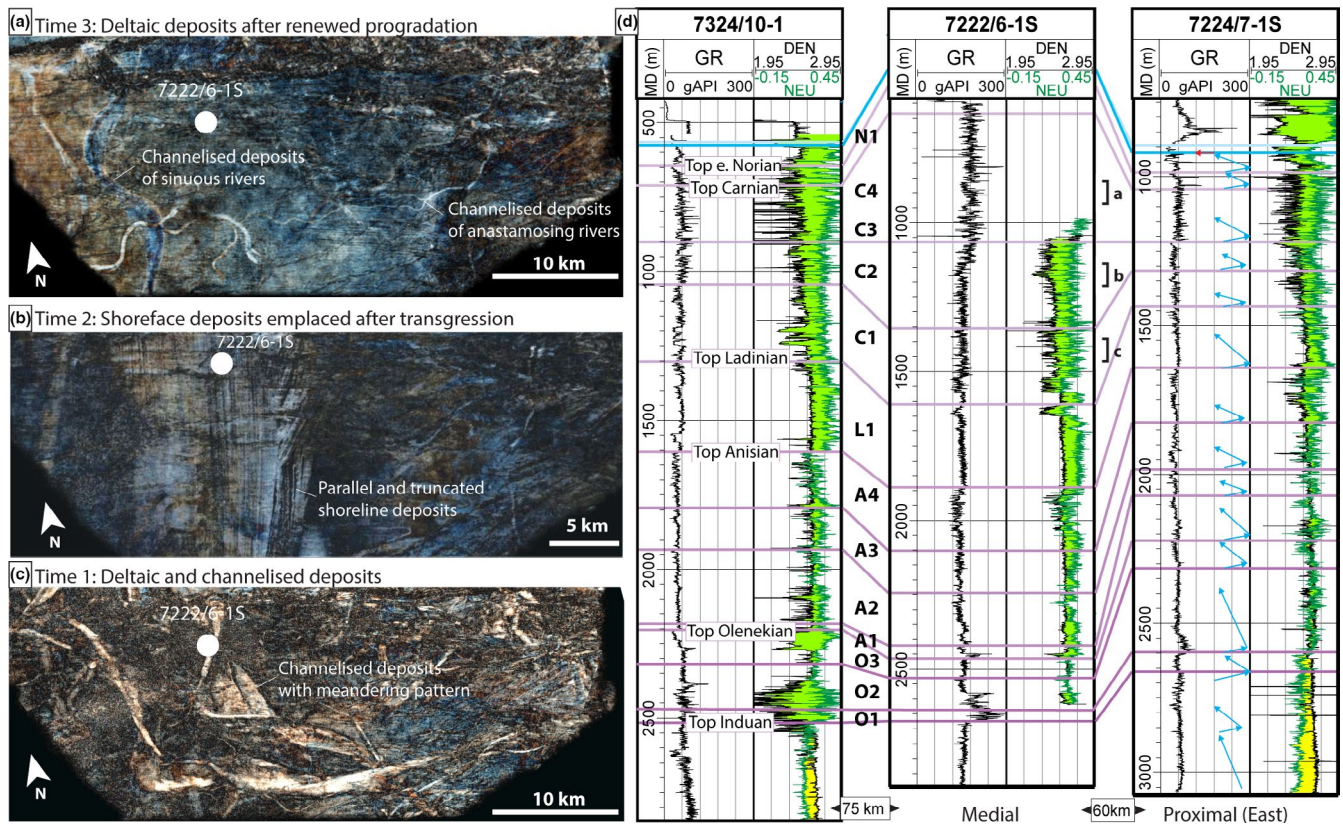
FIGURE 3 Seismic and well log evidence for marine incursion on TBO delta systems. 3D seismic attribute maps showing (a) deltaic deposits above (b) shoreface deposits overlying (c) older deltaic deposits characterized by meandering and anastomosing channel deposits. (d) Well log correlation panel showing a Triassic succession typically found throughout the subsurface Barents Sea. Low GR (gamma ray) indicate shallow marine or fluvial sandstone deposits. Intervals shown in attribute maps (a–c) are indicated. Blue arrows in (d) indicate relative sea-level trends observable in every borehole that penetrates the interval across the basin [Colour figure can be viewed at wileyonlinelibrary.com]

delta plain was therefore less frequent than modern, but, because of its size, much more extensive. Cyclic or episodic changes in sediment supply add to the potential of major RSL change in TBO.

3 | DISCUSSION

Because of generally high sedimentation rates and stressed marginal marine conditions, deltaic successions in TBO only comprise cm-scale coal beds, and bay deposits dominate over lacustrine (Klausen, Ryseth, Helland-Hansen, Gawthorpe, & Laursen, 2015), making the fossil preservation potential low. Except for a 3-m-long temnospondyl amphibian (Vigran et al., 2014), ichthyosaurs (Kear, Lindgren, Hurum, Milàn, & Vajda, 2016) and unspecified 'vertebrate' (Fefilova, 2005) fossils found in prodelta to shallow marine deposits, body fossils are rare, and few potential fossil sites exist—placing extra emphasis on the palynological record for understanding the evolution of terrestrial life in TBO. Since floral species are fundamental building blocks of the food chain, it is natural to assume that the importance TBO deltas had for terrestrial plants is transferrable to the fauna. Paleogeographic reconstructions also show large contemporaneous delta plains in western America, Australia and northeast Africa (Klausen et al., 2019), but these were located very close to or at the equator—implying their associated habitats suffered under periodically extreme climatic conditions (Sun et al., 2012), as reflected in the global distribution of plants with respect to climatic zones (Figure 1a) and spatiotemporal trends in taxa occurrence (Figure 2).

Floral turnover in TBO at the Carnian–Norian transition is significant in another context because it records devastation of terrestrial habitats important for the semi-aquatic crurotarsans (Klein & Lucas, 2015; Stubbs, Pierce, Rayfield, & Anderson, 2013). Certain crurotarsan species were, and still are, in the form of crocodiles, especially adapted to a semi-aquatic lifestyle both in terms of locomotion and reproduction (Klein & Lucas, 2015; Mannion et al., 2015; Stubbs et al., 2013). Modern descendants survived several extinction events due to their specialization for semi-aquatic habitats such as rivers and marshes, but before repeated inundations triggered this specialization crurotarsans dominated the terrestrial realm with the largest diversity. Non-crocodilian crurotarsans started to disappear in the Middle Triassic and were largely gone by the latest Triassic (Stubbs et al., 2013), arguably reflecting their biomechanical inability to cope with the ecological stress induced by repeated flooding. Given the shallow gradient and extent of Triassic delta plains, marine inundations would be far more dramatic in deltaic habitats than in
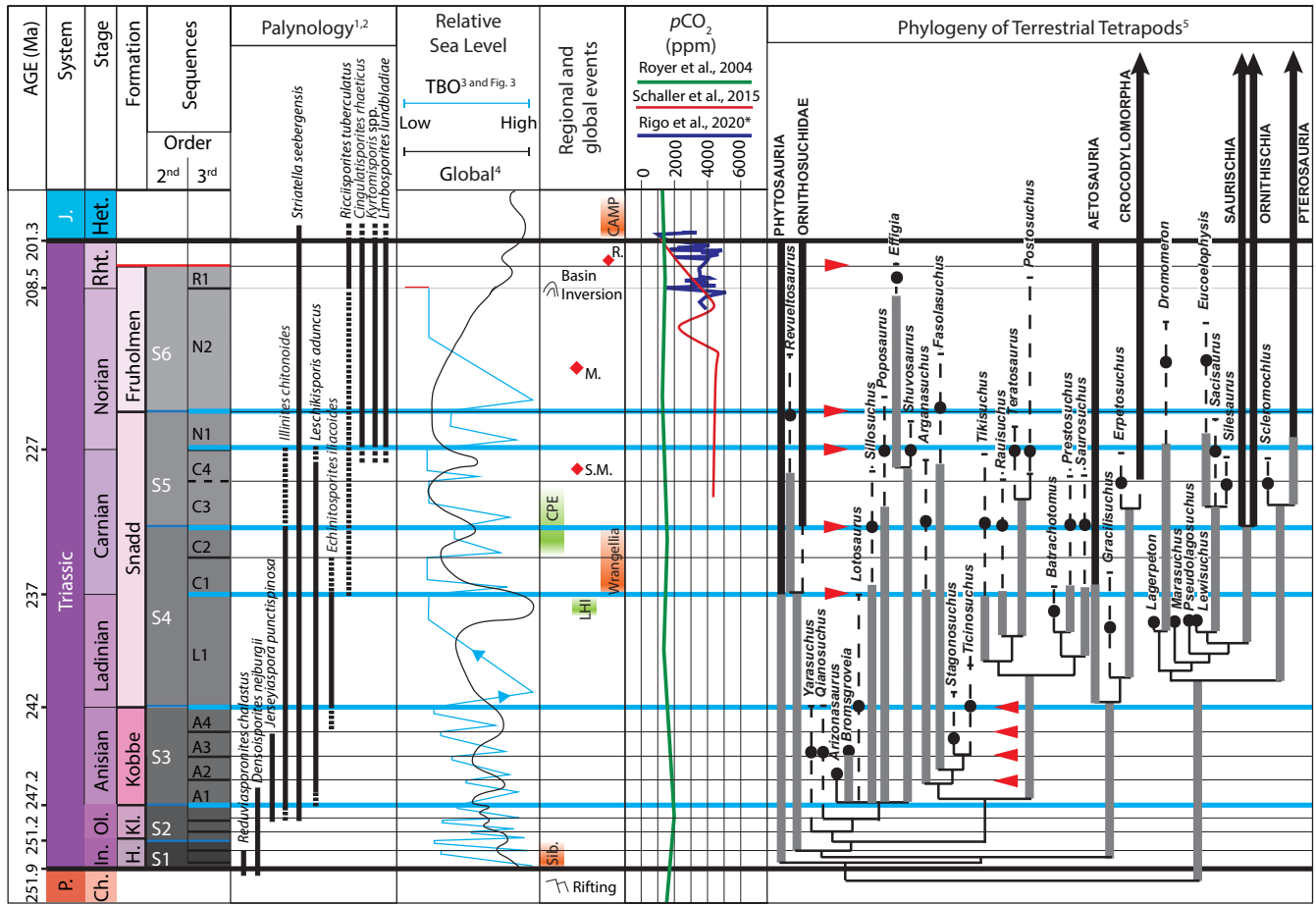
FIGURE 4 Global climatic and evolutionary events plotted against observations from TBO. Relative sea level observed in wells from the Barents Sea (e.g. Figure 3d) with a complete record of the Triassic interval (Figure 3), regional and global events affecting sedimentation pattern and the evolution of life (Dal Corso et al., 2012; Whiteside et al., 2015), pCO_2 (Brusatte, Benton, et al., 2010; Royer, Berner, Montañez, Tabor, & Beerling, 2004), and terrestrial extinction events (Paterson & Mangerud, 2015). This record shows that although large volcanic events had important effects on the evolution of life, and climatic crises likely affected diversity (Bernardi et al., 2018), there are significant turnovers in the terrestrial realm at stages with no apparent change in pCO_2, volcanism, climatic events or any large bolide impact (Clutson et al., 2018). TBO RSL changes however tie directly to each major crurotarsan extinction, as indicated by red triangles. Note that extinctions of dinosaurs do not exhibit the same correlation to RSL as do crurotarsan species. CAMP = Central Atlantic Magmatic Province (Peters, 2005); CPE = Carnian Pluvial Event (Dal Corso et al., 2012); LHI = Ladinian Humid Interval (Bernardi et al., 2018); Sib. = Siberian Traps (Whiteside et al., 2015). Red diamonds marks large bolide impacts (Clutson et al., 2018): R. = Rochechouart (c. 201–206.9 Ma); M. = Manicouagan (c. 215.5 Ma); S.M. = Saint Martin (c. 228 Ma). Horizontal blue lines mark the onset of major marine flooding intervals (=decrease of land area). Eustatic sea level (Haq et al., 1988) approximates the overall trend of the RSL observed in TBO although with lower resolution and offset in time and relative magnitude concerning maximum regressive and flooding stages. 1 = (Paterson & Mangerud, 2015); 2 = Vigran et al. (2014); 3 = Klausen et al. (2015); 4 = Haq et al. (1988); 5 = Brusatte, Benton, et al. (2010). *The curve for atmospheric CO_2 in Rigo et al. (2020) is simplified and schematic and does not match the numeric ppm estimates in Royer et al. (2004) or Schaller et al. (2015), it is included only for comparison [Colour figure can be viewed at wileyonlinelibrary.com]

hinterlands less affected by fluctuations in RSL, and although significant overlap existed between different terrestrial habitats, exemplified by the co-occurrence of crurotarsan and dinosaur trace fossils in the Germanic basins, dinosaurs thrived in more marginal ecosystems in the continental interior (Brusatte, Niedźwiedzki, & Butler, 2011), whereas crurotarsans dominated vast, semi-aquatic coastal areas. The main difference was the fully bipedal posture of the former that was more advantageous in the terrestrial habitats that terrestrial species were confined to during sea level highstand. As RSL later dropped, vast deltaic habitats would be open for recolonization by species formerly confined to more marginal hinterlands.

The rise of Dinosauria as the dominant clade during the Late Triassic has been attributed to a corresponding decrease in the importance of crurotarsans, but explained by several factors: competitive advantage (Brusatte, Benton, Ruta, & Lloyd, 2008); changing environmental conditions (Brusatte et al., 2008); and altered atmospheric CO_2 (Schaller, Wright, & Kent, 2015; Whiteside et al., 2015). Competitive advantage as a causal mechanism has been refuted (Benton et al., 2014; Brusatte et al., 2008), and there are no direct links between pCO_2 and extinctions at the Carnian–Norian boundary (Figure 4). The most convincing indications of a link between abiotic stress and terrestrial life is the recent study linking Late Triassic

diversification of dinosaurs to the CPE (Bernardi et al., 2018), but this study fails to explain the numerous important extinctions and diversification stages after this climatic crisis (Lucas & Tanner, 2018). At the Carnian–Norian boundary, this study records a pronounced terrestrial turnover in TBO with no known corresponding volcanic (Dal Corso et al., 2012) or bolide events (Clutson et al., 2018).

The sole agent for extinction at this stage is ecological stress caused by marine inundation. Importantly, flooding seems to closely correspond to the last occurrence of several crurotarsan lineages also at other stages in the Triassic (Figure 4).Were the crurotarsans not able to migrate at pace with the receding shoreline and keeping up with the changing conditions? Although TBO transgressions likely span much shorter periods than regressions, implying they were relatively catastrophic events even within million-year cycles, decrease in habitat area must be regarded as more important than the pace at which it happen. As in the Anthropocene, land-loss could not have been a trivial matter for species depending on these habitats. However, the effect of sea-level change on Late Triassic extinctions has largely been considered to affect marine organisms and the discussion has been focused on the extinction at the Triassic–Jurassic boundary (Hallam & Wignall, 1999; Lucas & Tanner, 2018; Tanner et al., 2004). An additional major difference between our observations and previous studies is that we correlate last occurrence of terrestrial species to marine transgressions rather than the regressions proposed by previous studies.

Based on the terrestrial turnover in TBO at a time with no other external forcing factor, we propose that RSL played a much more important role for turnovers in the terrestrial realm than previously accepted. Correlation furthermore shows that cyclic RSL changes could also explain the disappearance of other crurotarsan lineages in the Triassic. Unlike other agents of extinction that seem to be unique to a given period and potentially coincidental (Bernardi et al., 2018; Clutson et al., 2018; Whiteside et al., 2015), RSL change re-occur at periods and with a timing that directly corresponds to important turnovers in the terrestrial realm (. 4). It is also a theory that can explain the gradual and stepwise disappearance of crurotarsans without a significant extinction event, but rather link the last occurrence of dinosaurs' main competitors to turnovers in the terrestrial habitat they were specialized for and dominated.

4 | CONCLUSIONS

Investigated palynological species have significantly earlier first occurrences within TBO, later dispersing to the Germanic and Tethyan realm—contrary to normal nucleation-dispersion trends. The largest delta system in Earth's history developed in the TBO at this time and its geomorphological character made it prone to widespread transgressions seen at multiple stratigraphic intervals, causing discrete turnovers in flora at maximum flooding. Inundations imply significant habitat loss and ecosystem stress impacting species adept to these areas, such as the crurotarsans. Distinct stepwise decrease in ecosystem importance suffered by the crurotarsans correlate directly to

discrete transgressions worldwide, and although some of these extinctions can also be correlated to other forcing factors, all of them can be linked to a distinct flooding event. The Carnian–Norian interval studied herein however is not associated with any other external factor but flooding, showing that environmental stress by relatively rapid marine inundation played a crucial role in the evolution and turnover of terrestrial habitats. We record cyclic devastation of vast delta plains in the Boreal Ocean, which represented large and important habitats for species such as crurotarsans that dominated the Triassic terrestrial realm, and suggest that this ecological stress facilitated the gradual and implicit rise to ecosystem dominance by Dinosauria.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Table S1 Dataset used in figures 1 and 2. First occurrence of palynological taxa listed by area/region and literature source