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## Land-sea ecological connectivity during a Jurassic warming event

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## ABSTRACT

Knowledge on how climate change affects land-sea ecological connectivity in deep time is scarce. To fill this knowledge gap we have assembled a unique dataset through a Jurassic (early Toarcian) warming event that includes quantitative abundance data from pollen and spores, organic-walled marine plankton and benthic macro-invertebrates, in association with geochemical data derived from the same sampled horizons, from the Cleveland Basin, UK. Using this dataset we: (i) reconstruct the timing of degradation and recovery of land-plants, marine primary producers and benthic fauna in response to this event, and (ii) test for connectivity between changes in land and marine ecosystems. We find a discrepancy between the timing of the response of land-plant and marine ecosystems to the event. Land-plants were the first to be affected by initial warming, but also recovered relatively quickly after the peak of warmth to return to pre-event levels of richness and diversity. Plankton and benthic fauna instead experienced a delayed response to initial warming, but as warming peaked, they suffered a rapid and extreme turnover. Recovery in the shelf sea was also delayed (particularly for the benthos) compared to the vegetation. Ecological connectivity analyses show a strong link between changes in terrestrial and marine ecosystems. The loss of large trees on land contributed to changes in marine plankton, from dinoflagellate- to prasinophyte algal-dominated communities, by enhancing erosion, runoff and nutrient-supply into shallow seas. Eutrophication and changes in primary productivity contributed to the decrease of dissolved oxygen in the water column and in bottom waters, which in turn affected benthic communities. Such cause-effect mechanisms observed in the Cleveland Basin are likely to have occurred in other basins of the Boreal Realm, and in part also in basins of the Sub-Boreal and Tethyan realms. Although palaeolatitudinal and palaeoceanographic gradients may have controlled local and regional changes in land-plants and marine ecosystems during the Early Jurassic, the main climatic and environmental changes linked to rapid global warming, enhanced weathering and high primary productivity, are shared among all the examined realms.

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## 1. Introduction

In the near future, species are likely to experience climates for which no current analogue exists, with future projections indicating a potentially catastrophic loss of biodiversity (Trisos et al., 2020). Climate change, and specifically temperature rise, has a critical impact on both terrestrial and marine ecosystems, which are closely linked by physical, chemical and biological processes (Fang et al., 2018). Understanding how land and marine environments respond differently to climate change in the long-term, and how climate change influences links between these environments

is critical for developing whole-ecosystem response models for the long-term impacts of climate change (Häder and Barnes, 2019). The deep-time fossil record provides valuable insight into understanding the response and recovery of plant and animal communities to environmental change and habitat degradation, increasing our ability to predict the behaviour of systems outside of modern observations (Williams and Jackson, 2007).

Here we utilise the early Toarcian event (eTe; Early Jurassic, ~183 million years ago, Ma) as a model system for exploring how land-sea connectivity responds to climate change. Intense and rapid global warming (e.g., Dera et al., 2011), oceanic anoxia (Them et al., 2018), and widespread extinction in the oceans (Bucefalo Palliani et al., 2002; Danise et al., 2019; Little and Benton, 1995) characterise this event. Global warming was likely driven by the release of greenhouse gases into the atmosphere through volcanism of the Karoo-Ferrar Large Igneous Province (LIP), which oc-

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curred in two major phases between 184.2 and 182.7 Ma (Ruebsam and Al-Husseini, 2020 and references therein). Data from the NW Tethyan epicontinental seas indicate that temperatures rose by around 5–10°C (Bailey et al., 2003; Ruebsam et al., 2020), which in turn accelerated the global hydrological cycle, and increased the rate of continental weathering and riverine run-off (Kemp et al., 2020). These processes are hypothesised to have increased nutrient supply to the oceans, boosting primary productivity and organic matter fluxes, in turn elevating oxygen demand in subsurface water and ultimately triggering anoxic (no oxygen; dissolved oxygen 0.0 ml/l) and euxinic (no oxygen and high levels of hydrogen sulphide) conditions in more restricted settings (Jenkyns, 2010). Widespread and prolonged deposition of organic-rich, laminated, black shales occurred in many epicontinental seas of the NW Tethys and in the Panthalassa Ocean (Fig. 1) (Dickson et al., 2017; Jenkyns, 2010). The eTe is recognised globally in the rock record by a major negative carbon isotope excursion (CIE), which lasted ~300 kyr (Kemp et al., 2005), and has been identified in marine and terrestrial reservoirs (Hesselbo et al., 2007). A smaller negative CIE has been recorded preceding the eTe, at the Pliensbachian/Toarcian boundary (Pl-To; ~184 Ma) in the NW Tethys (Littler et al., 2010). This smaller event, is associated with several environmental and ecological disturbances (Bodin et al., 2016; Them et al., 2018), and likely corresponds to the initial pulse of volcanism of the Karoo-Ferrar LIP (Percival et al., 2015), see also (Greber et al., 2020) for a different interpretation.

Here we employ a high-resolution dataset and integrative approach to quantitatively assess changes in the fossil records of land-plants, represented by spores and pollen, marine plankton and benthic invertebrates from various trophic levels, derived from the Cleveland Basin, North Yorkshire, UK. In addition, we integrate these records with an array of geochemical data to determine: (i) the sequence and timing of biotic responses, and (ii) the possible causal links between changes in terrestrial and marine ecosystems during the eTe. Crucially, the terrestrial and marine fossil data originate from the same samples enabling us to precisely determine the relative timing of changes in these two environments and to examine the connectivity between terrestrial and marine ecosystems. To our knowledge, our study is unique in that it represents the only dataset from a past warming event that includes high-resolution quantitative species abundance counts from land-plants (pollen and spores), marine plankton and benthic fauna, in association with geochemical data derived from the same sampled horizons. With this integrated approach, we aim to provide a whole-ecosystem analysis of a past episode of extreme global warming, to further understand, in particular, ecological connectivity between terrestrial and marine environments and to uncover how environmental and ecosystem changes on land may impact those in the ocean.

## 2. Material and methods

### 2.1. Study site: palaeogeography and stratigraphy

The samples analysed in this study derive from the Cleveland Basin, North Yorkshire, UK (Fig. 1, S1), which is one of the most studied localities for the eTe, due to the excellent rock exposure and abundant marker beds that permit correlation of different outcrops, and the exquisite preservation and abundance of fossils. The Cleveland Basin, located at a palaeolatitude of 30–40°N during the Jurassic, was a sub-basin of the epicontinental Laurasian Seaway in the NW Tethys (Powell, 2010; Fig. 1) under warm-temperate climatic conditions (Dera et al., 2009). It was a semi-restricted basin, with a positive water balance (Bailey et al., 2003), which experienced fluctuations in the rate of exchange with Tethyan open

ocean waters during the Early Jurassic (Dickson et al., 2017). Together with central European basins in Germany, northern France, Hungary, and other northern European localities, the Cleveland Basin was biogeographically part of the Boreal Realm. Further south, the Tethyan Realm encompassed Italy and southern Europe (Fig. 1B). These two major biogeographic provinces are separated by the Sub-Boreal Realm, which includes southern France, Spain and Portugal, and has intermediate faunal and floral compositions between the Boreal and the Tethyan realms (Palliani and Riding, 2003).

The base of the studied succession comprises an alternation of silty mudstones and ooidal ironstones of the Pliensbachian Cleveland Ironstone Formation, deposited in shallow littoral seas (Powell, 2010). In the lower Toarcian portion of the section, facies and lithological changes record a progressive deepening of the succession (Hesselbo, 2008), which fines up from fine sandstones to silty mudstones and shales of the Whitby Mudstone Formation. The Grey Shale Member of the Whitby Mudstone Formation records an increase in sediment influx, and was deposited under predominantly oxic conditions, with the exception of four distinct stratigraphic levels, called *sulphur bands*. These represent brief intervals of low oxygen conditions (with peaks in TOC of 2.1 to 3.7%; McArthur et al., 2008). Increasing amounts of organic carbon within laminated black shales (peaking at 18.2% TOC; (McArthur et al., 2008), record anoxic/euxinic and dysoxic (dissolved oxygen < 2.0 ml/l) conditions in the Mulgrave Shale Member (Dickson et al., 2017; Hesselbo, 2008). The Alum Shale Member records a renewed flux of fine-grained terrigenous siliciclastics and a gradual return to more oxygenated conditions (Powell, 2010).

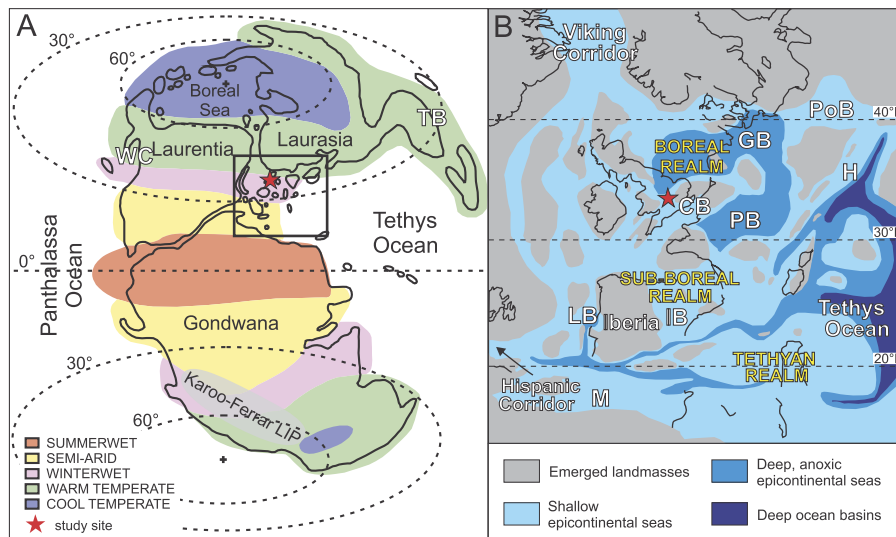
### 2.2. Data collection and analysis

Fifty-four bulk rock samples were collected from coastal sections along the North Yorkshire coast, UK (Figs. S1, S2). Analysis of their fossil content (Supplementary Methods) resulted in three, distinct, datasets with quantitative abundance data: one for the benthic macro-invertebrates (Danise et al., 2013), one for the terrestrial pollen and spores (Slater et al., 2019), and one for the marine plankton (this study). A fourth dataset comprises environmental variables derived from published literature [ $\delta^{13}\text{C}_{\text{org}}$ ,  $\delta^{18}\text{O}$ ,  $\delta^{34}\text{S}$ ,  $^{87}\text{Sr}/^{86}\text{Sr}$ ,  $\delta^{98/95}\text{Mo}$ , Total Organic Carbon – TOC (Danise et al., 2015; Supplementary Dataset).

Richness (number of taxa, S) and diversity (Shannon index, SH) were calculated for each of the three separate fossil groups, in each sample. Each dataset was analysed through nonmetric multidimensional scaling (nMDS) to reconstruct and visualize changes in community structure through time. Nonparametric multivariate regression, using the DISTLM routine was used to investigate relationships between datasets. First, we analysed the relationships of each explanatory variable with the response dataset (marginal test), and secondly, selected explanatory variables were subjected to a step-wise selection procedure (sequential test) to develop a best-fit model using the sample-size corrected Akaike's information criterion (AICc). Distance-based redundancy analysis (dbRDA) was then applied to explicitly visualize the relationship between response and explanatory variables (additional details in Supplementary Methods).

## 3. Results and discussion

We start with identifying the response of land-plants, organic-walled marine plankton and marine benthos through time across the eTe in the Cleveland Basin. We then use this framework to describe, interpret and discuss the results of nonparametric multivariate regression analysis, in which we: (i) test for ecological connectivity between land-plants and marine plankton ecosystems,



**Fig. 1.** (A) Global palaeogeographic map of the Early Jurassic with palaeoclimatic belts inferred from sedimentological and palaeophytogeographic data, modified from Dera et al. (2009). Red star indicates the location of the study site. (B) Palaeogeographic map of the NW Tethys, modified from Danise et al. (2019), highlighting the location of the Boreal, Sub-Boreal and Tethyan realms, and the localities discussed in the text. WC, Western Canada; TB, Tabe Basin, Japan; CB, Cleveland Basin, UK; GB, German Basin; PB, Paris Basin; PoB, Polish Basin; H, Hungary; LB, Lusitanian Basin; IB, Iberian Basin; M, Morocco. (For interpretation of the colours in the figure(s), the reader is referred to the web version of this article.)

(ii) test which specific environmental factors controlled changes in marine primary productivity, and (iii) test for ecological connectivity between primary productivity and changes in benthic communities, in the Cleveland Basin. Following our interpretations for the Cleveland Basin, we then discuss the implications of our results for global trends.

### 3.1. The sequence and timing of biotic responses to the early Toarcian event in the Cleveland Basin

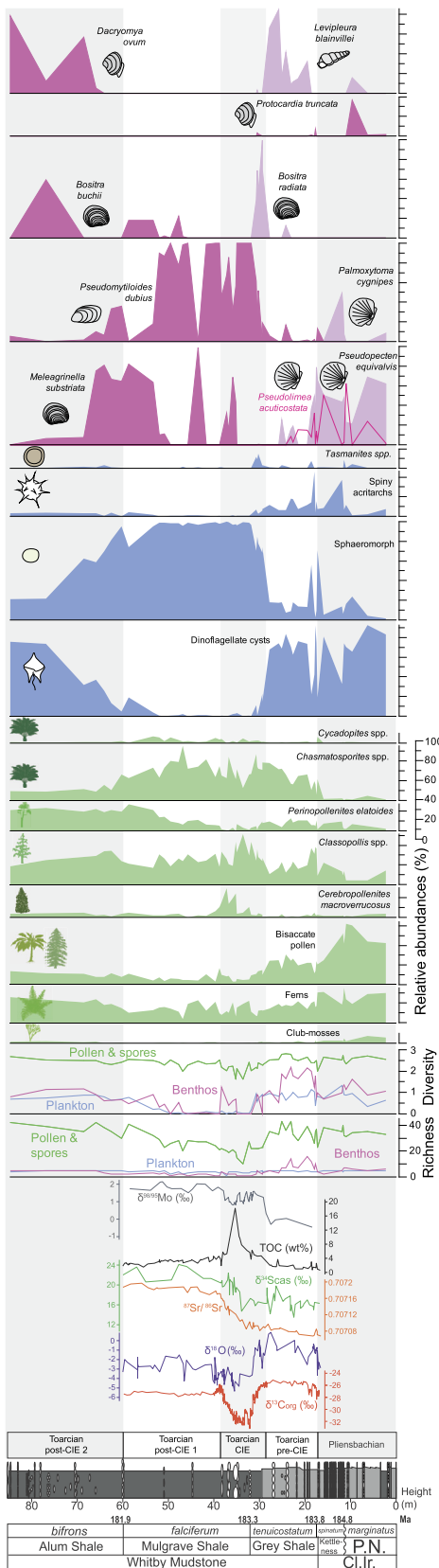
The complete dataset comprises benthic macro-invertebrate species abundance data of Danise et al. (2013), terrestrial pollen and spore data of Slater et al. (2019), geochemical proxy data of Danise et al. (2015), and new quantitative species abundance data of marine organic-walled plankton derived from the same samples. Combined analyses of relative abundances, richness and diversity (Fig. 2), with multivariate ordinations (Fig. 3), enable the comparison between land-plants, marine plankton and benthic fauna through the eTe to be examined at the species- and community-level for the Cleveland Basin composite section (Fig. 4). To ease discussion of the changes through the studied succession, we have divided the section into five main intervals (Pliensbachian, Toarcian pre-CIE, Toarcian CIE, Toarcian post-CIE 1 and Toarcian post-CIE 2). These are defined primarily by the main lithological and carbon isotope changes (Fig. 2). In addition, we have subdivided the Toarcian CIE into two parts: the lower part which encompasses the negative trend in isotope values from the onset of the CIE through the decline to the minimum carbon-isotope values; the upper part which encompasses the subsequent positive trend in isotope values from peak minimum values to the end of the CIE. When referring to palaeotemperature change, we follow the work by Ruebsam et al. (2020), which, using TEX<sub>86</sub> palaeothermometry proxies, estimated a warming of 5°C at the Pliensbachian-Toarcian boundary and a peak of 10°C warming concomitant to the Toarcian CIE, for the NW Tethys.

During the Pliensbachian, prior to the onset of the warming phase, the vegetation comprised high-diversity forests (richness of pollen and spores up to 40 taxa, diversity up to 2.5), dominated by a mixture of bisaccate pollen-producing conifers and seed ferns (Fig. 2). Higher proportions of spore-producing mosses (bryophytes) and club-mosses (lycophytes) in this part of

the studied succession are suggestive of relatively wetter conditions on land at this time (Slater et al., 2019). In the sea, organic-walled marine plankton communities were dominated by dinoflagellates (represented by cysts), with minor abundances of spiny acritarchs (of unknown biological affinities) and *Tasmanites* spp. (prasinophyte algae) (Fig. 2, 3B, S4), indicating overall mesotrophic conditions in the water column (Head, 1996). Epifaunal suspension feeders (e.g., the abundant pectinid bivalve *Pseudopecten equivalvis*; Fig. 2, S5B, Supplementary Data) dominated the macro-invertebrate benthic communities inhabiting the sea floor in proximal shelf settings, and co-occurred with deep- and shallow-infaunal species (Supplementary Data). The presence of these infauna is indicative of oxygenated conditions within the sediment (see also Danise et al., 2013).

At the PI-To transition, land-plants declined in richness and diversity (Fig. 2, 3). A drop in abundance of bisaccate pollen-producing conifers and seed ferns is mirrored by an increase in cycads, represented by *Chasmatosporites* spp. (Fig. 2, S3E; Slater et al., 2019), suggestive of warm and dry conditions (Balme, 1995). Marine plankton communities, instead, experienced a more muted turnover at the PI-To boundary compared to the land-plants, and remain dominated by dinoflagellates throughout the Toarcian pre-CIE interval (Fig. 2, 3B, 4, S4). A rise in sea level and shift to deeper and lower energy marine environments during the pre-CIE interval at this location (Powell, 2010) correspond to an increase in the diversity of benthic communities (Fig. 2), with a greater variety of benthic modes of life recorded amongst the macro-invertebrates (i.e., deep-, shallow-, semi-infaunal suspension feeders; grazers; carnivores; Supplementary Data). Towards the end of the pre-CIE interval an increase in deposit- and detritus-feeders (e.g., the gastropod *Leviplera blainvillei*, and the bivalve *Palaeonucula navis*) suggests that organic matter content was increasing in the still well-bioturbated and oxygenated sediments, with the arrival of significant levels of terrigenous input (Bucefalo Palliani et al., 2002).

At the onset of the Toarcian CIE, ~600,000 years after the PI-To boundary, land-plants suffered a major drop in their richness and diversity (Fig. 2). Diverse bisaccate pollen-producing conifer, and seed fern, forests were replaced by low-diversity vegetation, dominated by cheirolepids (represented by *Classopollis* spp.) and



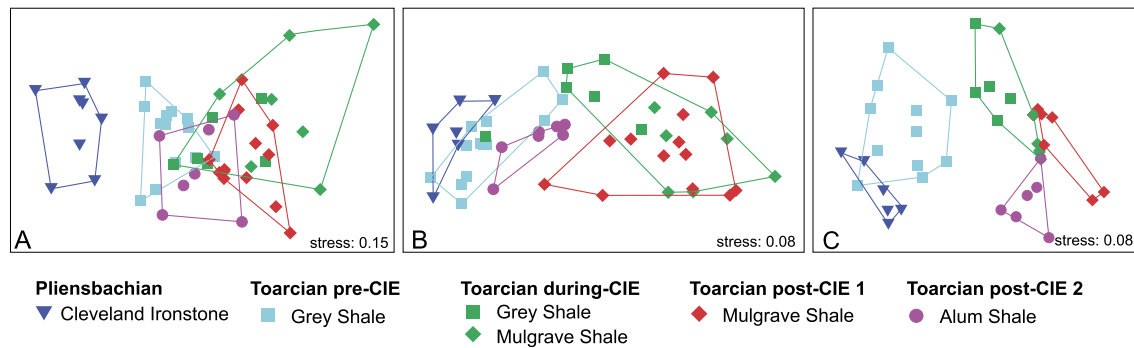
**Fig. 2.** Stratigraphic log, environmental proxies, changes in richness (S), diversity (SH), and relative abundances of the main taxa of pollen and spores, marine plankton and benthic macro-invertebrates spanning the early Toarcian event. The studied succession is subdivided into five discrete intervals (Pliensbachian, early Toarcian pre-CIE, early Toarcian CIE, early Toarcian post-CIE 1, early Toarcian post-CIE 2), which are defined by geological age, lithostratigraphy and the carbon isotope excursion (CIE). Age and duration of ammonite biozones from McArthur et al. (2000).

cycads (represented by *Chasmatosporites* spp.). At the same time, marine plankton also declined in richness and underwent a major compositional turnover (Fig. 2, 3, S4). A sharp decline in the abundances of dinoflagellate cysts and spiny acritarchs is mirrored by a massive increase in sphaeromorphs (Fig. 2, 4, S4), which are the fossil remains of prasinophyte green algae, similar to *Tasmanites* (Bucefalo Palliani et al., 2002; van de Schootbrugge et al., 2013, 2005). The long-term bloom of sphaeromorphs coincides with the onset of bottom water anoxia, recorded in the sedimentary record by the disappearance of bioturbation and the onset of laminated black shales. This major change in the marine environment is associated with the main loss of marine diversity and turnover of benthic communities (Fig. 2, 3C). With the onset of the CIE and the development of bottom water anoxia (see, Them et al., 2018), infaunal species disappeared, and only mono- and bi-specific assemblages of epifaunal, suspension-feeding bivalves persisted (Fig. 2, S5). The appearance and short-term dominance of the posidoniid *Bositra radiata* marks the lower part of the CIE (Fig. 2, S5D). Subsequently, the inoceramid *Pseudomytiloides dubius* dominates the second part of the CIE (Fig. 2, S5E), sometimes together with *Meleagrinnella substriata* (Fig. 2, S5G). These three species were small, opportunistic bivalves, characterized by a relatively large surface area, and colonized the sea-bottom intermittently, during brief periods of the year when oxygen levels were slightly elevated and conditions were dysoxic rather than anoxic and/or euxinic (Danise et al., 2013; Little and Benton, 1995).

On land, the upper half of the CIE is characterized by an abundance peak of *Cerebropollenites macroverrucosus* (Fig. 2, S3D), which was probably produced by an extinct relative of the extant conifers hemlock (*Tsuga*) or Japanese umbrella-pine (*Sciadopitys*), and was likely adapted to hot, arid climates and/or disturbed settings (Slater et al., 2019). Based on the abundance and diversity records throughout the studied interval (Fig. 2), both terrestrial and marine records reveal notably different communities during the first and second stages of the warming event.

After the CIE, land-plant communities gradually return to their pre-CIE diversity and richness levels (Fig. 2), but they differ in taxonomic composition compared to pre-event Pliensbachian communities and, to a lesser extent, pre-CIE Toarcian communities (Fig. 3A). Bisaccate pollen-producing conifers and seed ferns remain in low abundance; their niche was likely filled by Cheirolepidiaceae conifers (represented by *Classopollis* spp.) and Cupressaceae (represented by *Perinopollenites elatoides*), which indicate a return to more temperate conditions following the peak of warmth (Slater et al., 2019). Following the CIE, the abundance of *Cerebropollenites macroverrucosus* returned to pre-CIE levels, suggesting that its parent plant was pre-adapted to the hot and seasonal climate of the CIE interval and less well-suited to more temperate conditions, post-CIE. In the marine environment, no major changes are recorded in the structure of marine communities during the post-CIE interval 1 (Fig. 2, 3, S4, S5). Marine plankton assemblages remain dominated by sphaeromorphs, although, towards the end of post-CIE interval 1, dinoflagellate cysts and spiny acritarchs begin to increase in abundance (Fig. 2, Supplementary Data). In benthic assemblages only the epifaunal suspension feeders *Pseudomytiloides*, *Bositra* and *Meleagrinnella* occur (Fig. 2, Supplementary Data). Indeed, post-CIE interval 1 appears to be a period of relative ecological stasis in the marine environment, with marine plankton in the photic zone adapted to eutrophic conditions and benthic animals at the sea floor adapted to extremely low oxygen levels.

At the onset of post-CIE interval 2, a second phase of recovery in land-plant communities is recorded, as diversity and richness return to levels recorded in the Pliensbachian. Notably, the abundance of cycads (represented mainly by *Chasmatosporites* spp.), which proliferated throughout the peak of warmth, declines again to Pliensbachian, pre-event levels. The marine plankton also



**Fig. 3.** nMDS multivariate ordination showing temporal changes in (A) land-plants (pollen and spores), (B) marine plankton, and (C) benthic communities through the late Pliensbachian and early Toarcian.

returns to its pre-CIE composition and diversity. This represents the first phase of recovery for marine communities after the CIE, and lags behind the first phase of recovery of land-plant communities by  $\sim 300,000$  years, according to the age estimates of McArthur et al. (2000) (Fig. 2, S4B, S4E). Initial signs of recovery are also recorded in benthic ecosystems. Better-oxygenated conditions, marked by the return of bioturbated sediments, enabled recolonization of the sea floor by infaunal species, including the fossil remains of the deposit-feeding bivalve *Dacryomya ovum* (Fig. 1, S5F) and the suspension-feeding brachiopod *Lingularia longovicensis* (Supplementary Data). Benthic communities within post-CIE interval 2 record increases in both richness and diversity, but neither reach pre-CIE values (Fig. 2). This indicates that recovery was more protracted for the benthos compared to the marine plankton and land-plants.

### 3.2. Connectivity between land-plants and marine primary productivity in the Cleveland Basin

Vegetation turnover, and in particular, the loss of plant biomass, which is a common consequence of warming events, may result in an array of environmental changes including: changes in the hydrological cycle, reduced landscape stability, changes in river morphology, and increased soil erosion and run-off on land (Vajda et al., 2020; van de Schootbrugge et al., 2009). Such processes have been hypothesised to be central in degrading shelf sea environments during past extinction events, through increased nutrient supply, stimulating algal blooms and eutrophication (e.g., Algeo et al., 2011). Here we quantitatively tested this hypothesis by examining if changes in land-plant communities through the eTe controlled changes in marine plankton communities. In our analyses, pollen and spore taxa were used as predictor variables for changes in marine plankton, choosing the best-fitting model of nonparametric multivariate regression with the AICc model selection criterion (Fig. 5A-D, Table 1).

#### 3.2.1. Results of the statistical test

The marginal test shows that eight of the twelve variables of the pollen and spore dataset, taken alone, significantly explain variation in marine plankton communities (Table S1). The highest variation is explained by bisaccate pollen (37.7%), club-mosses (32.0%) and *Chasmatosporites* spp. (31.8%). In the sequential test, according to the best AICc fitted model, five variables in the pollen and spore dataset best explain variation of marine plankton through time (62.5% of cumulative proportion of explained variation; Table 1). The length and direction of the vectors in the constrained ordination help to visualize the influence of each explanatory variable on changes in marine plankton (Fig. 5A). These analyses indicate that the decrease of bisaccate pollen during the event, mirrored by the increase in *Chasmatosporites* spp., signifying

**Table 1**

Sequential test, using the step-wise model selection criterion, modelling which combination of variables of the pollen and spores dataset explains changes in marine plankton communities.

Predictor variables	AICc	Pseudo-F	P value	Prop.	Cumul.
+Bisaccate pollen	316.55	31.457	0.0001	37.7%	37.7%
+ <i>Cerebropollenites macroverrucosus</i>	309.17	9.9506	0.0003	10.2%	47.9%
+ <i>Cycadopsites</i> spp.	303.69	7.7847	0.0024	7.0%	54.9%
+ <i>Chasmatosporites</i> spp.	299.43	6.4609	0.0046	5.3%	60.1%
+Other conifers	298.63	3.0643	0.0576	2.4%	62.5%

AICc, Akaike Information Criterion corrected for sample size. The lowest AICc, the best the model. Pseudo-F, pseudo-F statistic. The larger the Pseudo-F, the likelihood the null hypothesis of no relationship between response and predictor variables being true diminishes. Prop., proportion of explained variation. Cumul., cumulative proportion of explained variation.

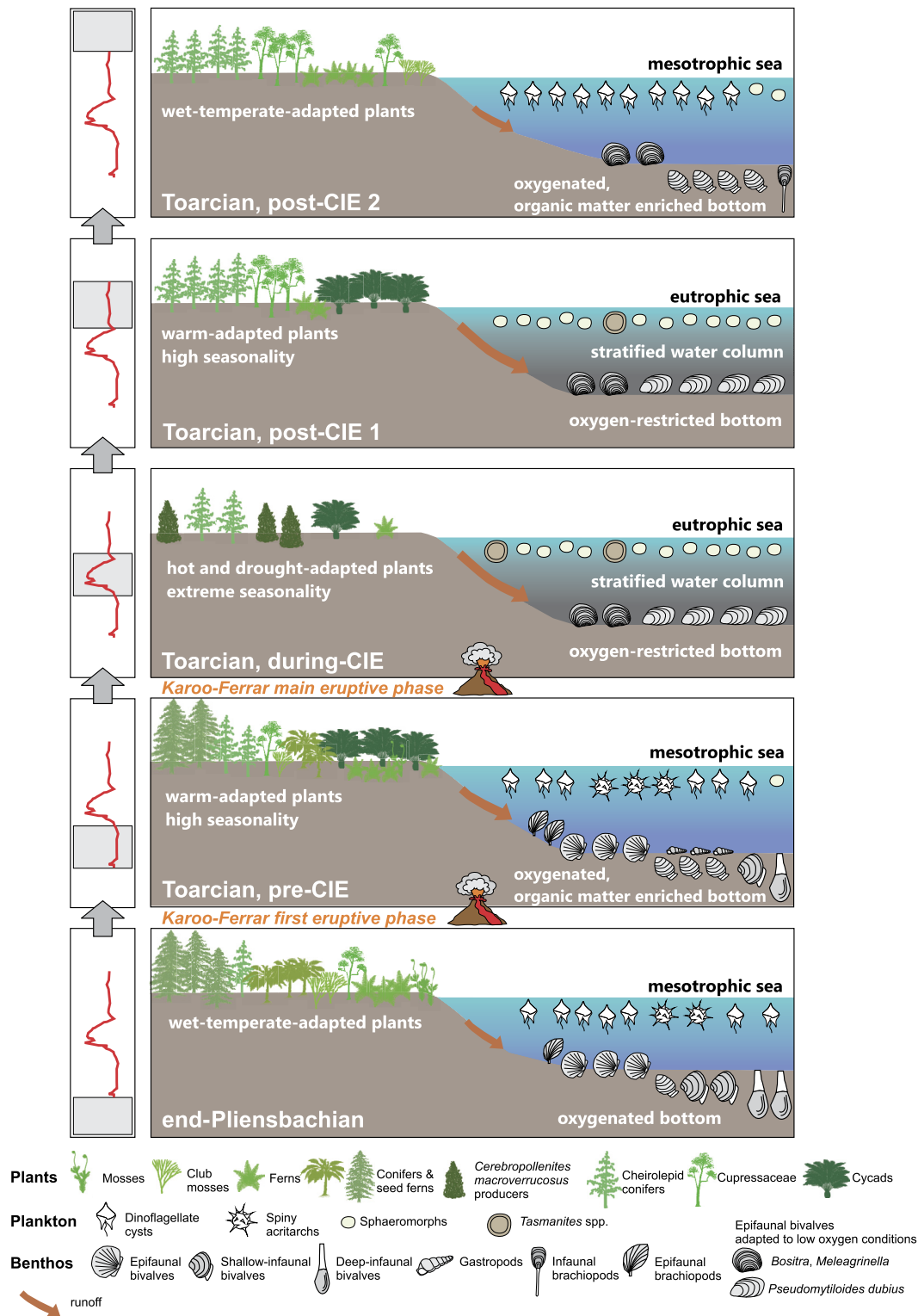
a loss of large trees and plant biomass, strongly influenced changes in marine plankton. A further test shows that changes in the richness and diversity of land-plants explain, respectively, 42% and 32% of the variation in marine plankton communities (Table S2).

#### 3.2.2. Interpretation of the statistical test

These results imply significant connectivity between land-plants living in coastal habitats and the marine plankton in the adjacent shelf seas during the eTe. We infer that the loss of land-plant richness at the Pl-To boundary and again during the CIE, together with the demise of forest-forming conifers and their replacement by drought-adapted plants, had a profound effect on hydrological and erosional processes on land, which in turn influenced marine plankton communities. These results strongly support the hypothesis that the loss of large trees on land led to increased erosion and run-off during the eTe, which boosted nutrient fluxes to adjacent shelf seas, resulting in dramatic increases in primary productivity and the development of eutrophic conditions.

### 3.3. Environmental factors influencing primary productivity in the Cleveland Basin

Besides testing for changes in land-plant cover, we also tested what other environmental variables may have driven changes in marine plankton communities, these include: changes in weathering rates [ $^{87}\text{Sr}/^{86}\text{Sr}$ ; (McArthur et al., 2000)]; the carbon cycle [ $\delta^{13}\text{C}_{\text{org}}$ ; (Cohen et al., 2004; Kemp et al., 2005; Littler et al., 2010)]; seawater temperature and salinity [ $\delta^{18}\text{O}$ ; (Korte and Hesselbo, 2011; McArthur et al., 2000; Saelen et al., 1996)]; euxinia [ $\delta^{34}\text{S}$ ; (Gill et al., 2011; Newton et al., 2011)]; anoxia [ $\delta^{98/95}\text{Mo}$ ; (Pearce et al., 2008)]; and the content of total organic carbon [TOC; (McArthur et al., 2008)] (Fig. 2). Richness (S) and diversity (SH) of pollen and spores were also included in the dataset as explanatory variables, to test their possible combined effects on marine plankton communities.



**Fig. 4.** Reconstruction of temporal changes in terrestrial and marine planktonic and benthic environments through the early Toarcian warming event. Timing of the Karoo-Ferrar volcanism from Ruesam and Al-Husseini (2020).

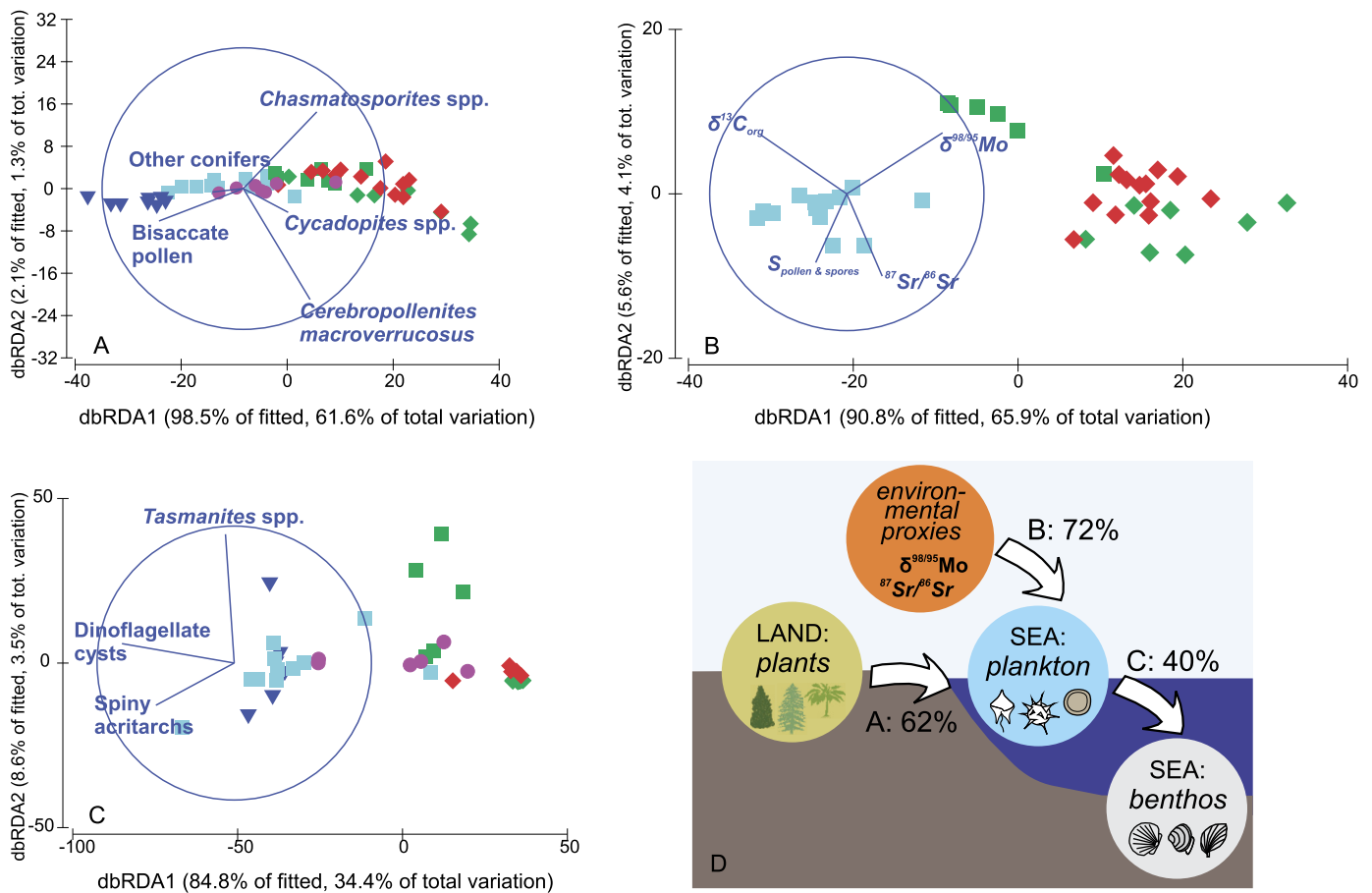
### 3.3.1. Results of the statistical test

According to the marginal test, each of the selected variables, taken alone, significantly explains variation in the marine plankton data (Table S3), with  $\delta^{18}\text{O}$  (46.9%) and  $\delta^{98/95}\text{Mo}$  (45.8%) explaining the highest proportion. In the sequential test, the best AICc model selects four variables ( $\delta^{98/95}\text{Mo}$ ,  $^{87}\text{Sr}/^{86}\text{Sr}$ ,  $\delta^{13}\text{C}_{\text{org}}$ ,  $S_{\text{pollen \& spores}}$ ), which together explain 72.5% of the variation of marine plankton

through time (Table 2, Fig. 5B). The high similarity between the PCO unconstrained ordination of marine plankton (Fig. S6B), and the dBRDA constrained ordination (Fig. 5B), supports the validity of the fitted model.

### 3.3.2. Interpretation of the statistical test

The inclusion in the model of  $^{87}\text{Sr}/^{86}\text{Sr}$ , together with  $S_{\text{pollen \& spores}}$ , further supports the role that continental weath-



**Fig. 5.** Distance-based redundancy analysis (dbRDA) constrained ordinations of fitted models according to the best Akaike's information criterion (AICc) procedure. A, Pollen and spores explaining variations in marine plankton communities (entire study interval). B, Environmental variables, including richness of pollen and spores, explaining changes in marine plankton communities (only Grey Shale and Mulgrave Shale members). C, Marine plankton explaining variations of benthic communities. D, Scheme showing the direction of the three dbRDA analyses (A, B, C) and the total explained variation of each marginal test, as shown in Tables 1, 2, 3. Vectors in A, B, and C indicate strength and direction of influence of individual predictor variables in the fitted model.

ering and run-off had on primary productivity during the early Toarcian event. The recorded increase in  $^{87}Sr/^{86}Sr$  values during the early Toarcian, together with a positive excursion in Osmium isotopes, has been interpreted as reflecting enhanced continental weathering in the studied area (Cohen et al., 2004; McArthur et al., 2000), which most likely led to decreased salinity and stratification of the water column and anoxia (Bailey et al., 2003; French et al., 2014). The inclusion in the model of  $^{98/95}Mo$  is another indication of the significant role that changes in the oxygenation of shelf seas had on marine plankton: a positive excursion through the eTe indicates basinal restriction with the development of anoxic and euxinic conditions in the water column and on the sea floor (Dickson et al., 2017; Pearce et al., 2008). The development of anoxia has previously been hypothesised as causal for the sharp decline of dinoflagellate cysts during the CIE (Bucefalo Palliani et al., 2002; van de Schootbrugge et al., 2005). As dinoflagellates thrive in oxygenated water under mesotrophic conditions, the anoxic and low salinity surface waters of the Cleveland Basin during the early Toarcian event most likely led to unsuitable conditions. While bottom-water anoxia probably prevented cyst-forming dinoflagellates from successfully excysting (Bucefalo Palliani et al., 2002), prasinophyte algae thrived throughout the event. This may be linked to their evolution in low-oxygen Proterozoic and early Phanerozoic oceans, making prasinophytes more tolerant of anoxic and low-salinity conditions (van de Schootbrugge et al., 2013).

**Table 2**

Sequential test, using the step-wise model selection criterion, modelling which combination of environmental variables, including richness (S) and diversity (SH) of pollen and spores, explain changes in marine plankton communities (short dataset, including only Grey Shale and Alum Shale members).

Predictor variable	AICc	Pseudo-F	P value	Prop.	Cumul.
$\delta^{18}O$	225.47	32.699	0.0001	46.91%	46.91%
+ $\delta^{98/95}Mo$	217.46	10.951	0.0002	12.38%	59.30%
+ SH <sub>pollen &amp; spores</sub>	213.69	6.1029	0.0019	6.04%	65.34%
+ $^{87}Sr/^{86}Sr$	210.13	5.8523	0.0025	5.09%	70.43%
+ $\delta^{13}C_{org}$	209.26	3.262	0.0558	2.66%	73.09%
- $\delta^{18}O$	208.54	1.8066	0.2149	1.47%	71.62%
+ S <sub>pollen &amp; spores</sub>	208.46	2.5325	0.1077	2.02%	73.64%
- SH <sub>pollen &amp; spores</sub>	207.25	1.3804	0.3086	1.10%	72.54%

**Note.** The best, final solution includes:  $\delta^{98/95}Mo$ ,  $^{87}Sr/^{86}Sr$ ,  $\delta^{13}C_{org}$ , S<sub>pollen & spores</sub>. At each step, in the step-wise selection method, forward selection seeks for possible backward variable eliminations to improve the criterion. In this test the removal of  $\delta^{18}O$  and SH<sub>pollen & spores</sub> improves the model.

**Table 3**

Sequential test, using the step-wise model selection criterion, modelling which combination of marine plankton variables explains changes in benthic communities.

Predictor variable	AICc	Pseudo-F	p value	Prop.	Cumul.
+Dinoflagellate cysts	351.31	17.13	0.0001	28.49%	28.49%
+Spiny acritarchs	348.11	5.4591	0.0005	8.23%	36.71%
+Tasmanites spp.	347.71	2.6495	0.0235	3.84%	40.56%

**Note.** Even if in the marginal test *Tasmanites* spp. alone, had no significant relationship with the multivariate benthos dataset, this is not the case when its variation is combined with the other predictor variables.

### 3.4. Connectivity between primary productivity and benthic communities in the Cleveland Basin

Here we test the hypothesis that changes in marine plankton directly impacted benthic communities during the early Toarcian event. In modern coastal areas, marine plankton are the main source of nutrition for benthic macro-invertebrates, and variability in the production of phytoplankton can rapidly influence benthic community structure, including changes in abundance, richness and faunal composition (Gili and Coma, 1998). Although an increased supply of organic matter implies increased food supplies for marine benthos, during events such as algal blooms, the decay of this organic matter in excess may cause deoxygenation of the sediments, thereby negatively affecting the benthos (Quijón et al., 2008). Moreover, considering that many benthic organisms are able to select their food source, especially suspension feeders which dominate in our dataset (95% of total abundances), the prevalence of certain species of phytoplankton may also have had specific controls on the benthos.

#### 3.4.1. Results of the statistical test

Marine plankton taxa were used as predictor variables for explaining variations in benthic macrofaunal community composition. To avoid redundancy, due to the high negative correlation between sphaeromorphs and dinoflagellate cysts (Spearman's  $r_s$ ,  $-0.94$ ,  $p < 0.001$ ), only one of the two variables (dinoflagellate cysts) were included into the fitted model. The marginal test shows that changes in dinoflagellate cysts, alone, explain 28.5% of variation in the benthos, followed by spiny acritarchs (18.6%), other prasinophyte algae (i.e., excluding *Tasmanites* and sphaeromorphs; 11.9%) and *Tasmanites* spp. (3.3%; Table S4). In the sequential test, with the AICc model selection criterion, dinoflagellate cysts (28.5%), together with spiny acritarchs (8.2%) and *Tasmanites* spp. (3.8%) explain 40.5% of the variation of benthic macro-invertebrate assemblages (Table 3; Fig. 5C-D).

#### 3.4.2. Interpretation of the statistical test

This result suggests that the change from dinoflagellate- to sphaeromorph-dominated plankton communities at the onset of the CIE had a direct effect on benthic communities, which experience a sharp decrease in richness and diversity, and a marked turnover. In particular, the occurrence of the bivalve *Bositra radiata* coincides with the peak of *Tasmanites* spp. at the onset of the CIE, while peak abundances of the bivalve *Pseudomytiloides dubius* coincide with the long-term bloom of sphaeromorphs (Fig. 2). The dominance of *P. dubius*, *M. substriata* and *B. radiata* during and after the CIE suggests that these species may have been adapted to exploit food derived from abundant prasinophyte algae under fluctuating anoxia. Similar processes occur in modern oxygen-minimum zones, where phytodetritus from plankton is the primary source of organic matter for the benthic macrofauna (Hunter et al., 2012). Our findings strengthen the conclusions of a previous study on *Bositra* and *Pseudomytiloides* from the same locality, which hypothesised that size changes of these two genera were possibly driven by changes in primary productivity due to a correlation between size and selected geochemical data, which were interpreted as proxies for primary production (Caswell and Coe, 2013).

The lower explanatory power of this test (Table 3) compared to the previous analyses (Tables 1, 2), and the lower similarity between the constrained (Fig. 5C) and unconstrained ordinations (Fig. S6C), indicates that other variables, besides primary productivity, such as the intensity of anoxia (Danise et al., 2015), also played a role in controlling benthic community dynamics. As previously demonstrated for nektonic ecosystems during this event (Danise et al., 2015), the delayed recovery of benthic ecosystems compared to those living in the water column, indicates that the development of

anoxia produced a strong decoupling between benthic and pelagic systems, with important negative consequences on nutrient cycling and energy transfer between the two ecosystems.

### 3.5. Ecological connectivity between terrestrial and marine ecosystems: from the Cleveland Basin to global trends

Our quantitative analyses have demonstrated significant connectivity between land-plants and marine plankton and benthic invertebrates in the adjacent shelf seas through the eTe in the Cleveland Basin. We have also demonstrated which environmental changes exerted the most influence on the composition of the marine plankton through this event, extending the work of Danise et al. (2015), who showed which environmental factors controlled the benthic and nektonic marine invertebrate communities through this event. Our unique sampling design allowed us not only to analyse the timing of change among these three ecosystems, but for the first time, to directly analyse the drivers of change and to test the strength of connectivity between them. Comparisons with other sections/localities worldwide are constrained by the different quality of the available data. In particular, detailed comparisons of the relative timing of change in different taxa or ecosystems in other locations are not often possible, and so here our discussion focuses on general trends, hoping that this study will set the base for future analyses integrating terrestrial and marine ecosystems, from microfossils to macro-invertebrates.

The first significant result of our analyses is the strong connectivity between terrestrial floral and marine plankton changes (Fig. 5A, D, Table 1). These results support the hypothesis that, in the Cleveland Basin, the loss of large trees on land led to increased erosion and run-off, which boosted nutrient fluxes to adjacent shelf seas, resulting in dramatic increases in primary productivity, during the eTe, as hypothesised for other past warming events (Algeo et al., 2011; Vajda et al., 2020). Similar changes in terrestrial and marine ecosystems have been observed in other marine basins of the Boreal Realm, such as in Germany, Hungary, and Poland, although with some differences in the timing and duration of ecological changes due to local depositional settings (see, Baranyi et al., 2016 and references therein). In the German Basin, bisaccate pollen-producing plants disappear at the onset of the CIE, and start to recover soon after its end (Galasso et al., 2021). Marine plankton shift from dinoflagellate cyst-dominated communities to prasinophyte- and sphaeromorph-dominated communities at the start of the CIE, but experience a slower recovery than terrestrial ecosystems (Galasso et al., 2021). The authors suggest an increased delivery of land-plant material by rivers during the CIE, and conclude that transportation of nutrients to the shelf seas would have stimulated marine primary productivity. Given the restriction of the basin, this resulted in fresh-water driven stratification, and oxygen-depleted water conditions (Galasso et al., 2021). A loss of conifers and other pollen-producing plants during the CIE is also observed in the Polish Basin, together with an increase in the activity of fungal wood decomposers during peak greenhouse conditions, due to high temperatures and humidity (Pieńkowski et al., 2016). These data support the hypothesis of a strong link between changes in terrestrial ecosystems and marine plankton, and suggest that results from the Cleveland Basin are applicable to other basins of the Boreal Realm.

Further south, in the western Tethys, the general climatic setting changed from winter-wet conditions in the Boreal Realm to semi-arid conditions and more open ocean conditions in the Sub-Boreal and Tethyan realms (Fig. 1; Dera et al., 2009). Even though these southerly bioprovinces and climatic belts contain different species compared to the northern areas, there is still evidence for changes in the terrestrial record that would have favoured soil erosion and run-off, affecting primary productivity. In the Lusitanian



Basin, increases in non-opaque, translucent, phytoclasts and terrestrial palynomorphs (including an increase in *Classopollis*, as is recorded in the Cleveland Basin) support the hypothesis of an enhanced hydrological cycle due to rising temperatures, and indicate increased export of terrestrial organic matter into marine environments during the eTe, especially during the CIE, in the western Iberian margin (Rodrigues et al., 2020). In the same basin, the CIE interval also records a complete loss of dinoflagellate cysts and a rise in prasinophytes, similar to the Cleveland Basin, which has been interpreted as reflecting significant environmental stress, caused by marine anoxia, elevated temperature and/or reduced salinity, with the former two controlling factors suggested as being the most important (Correia et al., 2017). In contrast to the Cleveland Basin, however, dinoflagellate cyst abundances did not rebound at the end of the anoxic episode in the Lusitanian Basin, but remained very low (Correia et al., 2017). Data from Morocco and northern Spain have been interpreted as indicating that the acceleration of the hydrological cycle during the eTe was less intense in northern Gondwana, and southern and western Iberian basins, than in northern Iberia and other northern areas of the West Tethys and Panthalassa shelf (Rodrigues et al., 2021). At the same time, enrichment in amorphous organic matter during both the Pl-To and early Toarcian events has been interpreted as reflecting an increase in primary productivity linked to increased continental weathering, fluvial run-off and riverine nutrient input into marine areas, which then led to water column stratification (Rodrigues et al., 2021). These data suggest that our model could be applicable to the Boreal Realm, and with caution, also to Sub-Boreal and Tethyan Realms. Specifically designed analyses are needed to test this, especially considering that the climatic and palaeoceanographic conditions differ between latitudes.

Results of our second statistical test confirm the connection between land-plant cover and marine plankton change, and strengthen the interpretation that increasing run-off and weathering rates are a key link between these ecosystems in the Cleveland Basin (Fig. 5B, D, Table 2). In particular, geochemical proxies, such as calcium (Brazier et al., 2015), osmium (Cohen et al., 2004), strontium isotopes (McArthur et al., 2000) and mercury (Them et al., 2019) indicate a dramatic increase of weathering rates in the early Toarcian worldwide from the Boreal and the Sub-Boreal realms, to the Panthalassa Ocean [e.g., Western Canada and Japan (Kemp et al., 2020; Them et al., 2017)], implying a massive discharge of terrigenous sediments into shelf seas during both intervals (e.g., Xu et al., 2018). Given the scale of these changes and their global extent, increased weathering and run-off likely impacted marine plankton communities worldwide.

We also found that intensity of anoxia was another controlling factor on marine plankton community change in the Cleveland Basin (Fig. 5B, D, Table 2). Although the development of anoxic conditions in the early Toarcian is considered a global event, from the Tethys to the Panthalassa (Jenkyns, 2010; Them et al., 2018), its intensity and duration varies between different marine basins, being mostly driven by differences in ocean circulation and water depth. For instance anoxia was more prolonged in the Boreal Realm compared to the Tethyan Realm (Wignall et al., 2005), with some Tethyan localities recording no anoxia and oxygenated conditions throughout (Nielsen et al., 2011; Ruvalcaba Baroni et al., 2018). Marine anoxia was also less pronounced in shallower shelf settings than in deeper shelf settings, both in the Boreal and Tethyan realms (e.g., Caswell and Coe, 2012; Danise et al., 2019). Given that dinoflagellates, the main primary producers before the onset of anoxic conditions, thrive in oxygenated water, the applicability of our model will depend on the local palaeoceanographic conditions.

Concerning marine benthos, based on the results of this study and our previous analyses of the Cleveland Basin (Danise et al.,

2015), marine anoxia was the most important environmental factor that controlled benthic diversity and structure. One likely cause of marine anoxia would have been excess consumption of oxygen in bottom waters driven by the decay of high quantities of organic matter caused by elevated primary productivity in plankton blooms (Quijón et al., 2008). Our Cleveland Basin results support this proposed link between marine plankton, anoxia and the loss of biodiversity in benthic macro-invertebrate communities. Similarly to the Cleveland Basin, other Boreal Realm locations, such as the German and the Paris basins, also experienced a dramatic loss of biodiversity at the onset of the CIE and the onset of anoxic/euxinic conditions, which has been linked to increased primary productivity (Galasso et al., 2021; van Breugel et al., 2006). In the German Basin, as in the Cleveland Basin, benthic communities return to high diversities in the post-CIE 2 interval (Galasso et al., 2021). Thus, we are confident that our model also applies to other basins in the Boreal Realm.

In basins from the Sub-Boreal and Tethyan Realm, however, other factors apart from anoxia and primary productivity seem to control changes in marine benthic communities through the early Toarcian (Danise et al., 2019; Piazza et al., 2020). It is worth noting, however, that none of these studies directly compare changes in primary productivity and changes in benthic communities from the same samples, so connectivity between these ecosystems has yet to be properly tested. In the Iberian Basin, a link between primary productivity and benthic richness has been hypothesised in one locality, owing to the correlation between TOC and benthic richness, strong changes in plankton primary producers (i.e. disappearance of dinoflagellates) at the onset of the CIE, and the subsequent dominance of terrestrially-derived palynomorphs (Danise et al., 2019). Otherwise, recorded declines in benthic diversity in relatively well-oxygenated facies have been commonly interpreted as being related to an increase in temperature (Danise et al., 2019; Piazza et al., 2020). In such settings, recovery to ecologically stable and diverse faunal assemblages also occurs rapidly at the end of the CIE, synchronously with decreasing water temperatures (Danise et al., 2019; Piazza et al., 2020). In comparison with the Boreal Realm basins such as the Cleveland Basin, these data show that recovery of benthic fauna after the eTe was faster in areas that were less impacted by bottom water anoxia.

#### 4. Conclusion

In this study we show how a detailed multi-proxy analysis of past ecosystem changes through time, across different realms (land-marine), and in different domains of the marine system (plankton-benthos), can enhance our understanding of the connectivity between these ecosystems through an interval of intense climate change.

First, our dataset reveals that the timing of terrestrial (land-plant) and marine ecosystem responses to the eTe was different in the Cleveland Basin (Fig. 4). Terrestrial ecosystems, which were more severely affected at the initial stages of warming, experienced a gradual compositional change from wet-temperate to hot and drought-adapted species during peak warming. However, land-plants recorded an initial phase of recovery earlier than marine communities, gradually returning to their pre-event diversities immediately following the CIE. Marine ecosystems instead experienced a delayed response to initial warming, but as warming peaked, plankton and benthic animals suffered a rapid and extreme turnover. Recovery in the shelf sea was delayed compared to recovery on land, especially for the benthos, which did not return to pre-warming diversities or structure, even when plankton communities had recovered.

Second, in testing for connectivity between changes in land and marine ecosystems in the Cleveland Basin, we found evidence that:

(i) the loss of large trees directly affected marine plankton communities; (ii) this change was directly linked to increased runoff and nutrient supply to coastal seas during peak temperatures; (iii) this contributed to the decrease of dissolved oxygen in the water column and in bottom waters; (iv) which in turn affected benthic communities.

Although no comparable datasets exist currently, published data suggest that our models for connectivity from the Cleveland Basin are likely to be applicable to other basins of the Boreal Realm, belonging to the winter-wet climatic belt, and in part also to basins of the Sub-Boreal and Tethyan realms, belonging to the semi-arid climatic belt. Although palaeolatitudinal and palaeoceanographic gradients may have controlled local and regional changes in land-plants and marine ecosystems in the Early Jurassic, the main climatic and environmental changes during the eTe, linked to rapid global warming, enhanced weathering and high primary productivity, are shared among all the examined realms.

Our novel methodology and findings demonstrate the possibility, given adequate sampling and analytical design, of reconstructing biogeochemical cycles between the land and sea in deep time, especially in coastal zones, where terrestrial organic matter and nutrients enter the sea and are exchanged with the open ocean. In this study, we highlight how warming-induced vegetation changes may dramatically impact coastal marine ecosystems, with a cascade effect from land to marine plankton to sea floor faunas. Changes in land-plant ecosystems, such as variations in vegetation cover and shifts towards communities with more drought-tolerant traits, as has been observed in modern forests (Trugman et al., 2020), should therefore be considered as a hint to the possible disruption of current biogeochemical cycles.

#### CRediT authorship contribution statement

**Silvia Danise:** Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Sam M. Slater:** Conceptualization, Funding acquisition, Investigation, Visualization, Writing – review & editing. **Vivi Vajda:** Conceptualization, Funding acquisition, Writing – review & editing. **Richard J. Twitchett:** Conceptualization, Funding acquisition, Methodology, Writing – review & editing.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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#### Appendix A. Supplementary material

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#### References

Algeo, T.J., Chen, Z.Q., Fraiser, M.L., Twitchett, R.J., 2011. Terrestrial-marine teleconnections in the collapse and rebuilding of Early Triassic marine ecosystems. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 308, 1–11.

- Bailey, T.R., Rosenthal, Y., McArthur, J.M., van de Schootbrugge, B., Thirlwall, M.F., 2003. Paleocceanographic changes of the Late Pliensbachian–Early Toarcian interval: a possible link to the genesis of an Oceanic Anoxic Event. *Earth Planet. Sci. Lett.* 212, 307–320.
- Balme, B.E., 1995. Fossil in situ spores and pollen grains: an annotated catalogue. *Rev. Palaeobot. Palynol.* 87, 81–323.
- Baranyi, V., Pálffy, J., Görög, Á., Riding, J.B., Raucsik, B., 2016. Multiphase response of palynomorphs to the Toarcian Oceanic Anoxic Event (Early Jurassic) in the Réka Valley section, Hungary. *Rev. Palaeobot. Palynol.* 235, 51–70.
- Bodin, S., Krencker, F.-N., Kothe, T., Hoffmann, R., Mattioli, E., Heimhofer, U., Kabiri, L., 2016. Perturbation of the carbon cycle during the late Pliensbachian – early Toarcian: new insight from high-resolution carbon isotope records in Morocco. *J. Afr. Earth Sci.* 116, 89–104.
- Brazier, J.-M., Suan, G., Tacail, T., Simon, L., Martin, J.E., Mattioli, E., Balter, V., 2015. Calcium isotope evidence for dramatic increase of continental weathering during the Toarcian oceanic anoxic event (Early Jurassic). *Earth Planet. Sci. Lett.* 411, 164–176.
- Bucefalo Palliani, R., Mattioli, E., Riding, J.B., 2002. The response of marine phytoplankton and sedimentary organic matter to the early Toarcian (Lower Jurassic) oceanic anoxic event in northern England. *Mar. Micropaleontol.* 46, 223–245.
- Caswell, B.A., Coe, A.L., 2012. A high-resolution shallow marine record of the Toarcian (Early Jurassic) Oceanic Anoxic Event from the East Midlands Shelf, UK. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 365–366, 124–135.
- Caswell, B.A., Coe, A.L., 2013. Primary productivity controls on opportunistic bivalves during Early Jurassic oceanic deoxygenation. *Geology* 41, 1163–1166.
- Cohen, A.S., Coe, A.L., Harding, S.M., Schwark, L., 2004. Osmium isotope evidence for the regulation of atmospheric CO<sub>2</sub> by continental weathering. *Geology* 32, 157–160.
- Correia, V.F., Riding, J.B., Duarte, L.V., Fernandes, P., Pereira, Z., 2017. The palynological response to the Toarcian Oceanic Anoxic Event (Early Jurassic) at Peniche, Lusitanian Basin, western Portugal. *Mar. Micropaleontol.* 137, 46–63.
- Danise, S., Clémence, M.-E., Price, G.D., Murphy, D.P., Gómez, J.J., Twitchett, R.J., 2019. Stratigraphic and environmental control on marine benthic community change through the early Toarcian extinction event (Iberian Range, Spain). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 524, 183–200.
- Danise, S., Twitchett, R.J., Little, C.T.S., 2015. Environmental controls on Jurassic marine ecosystems during global warming. *Geology* 43, 263–266.
- Danise, S., Twitchett, R.J., Little, C.T.S., Clémence, M.-E., 2013. The impact of global warming and anoxia on marine benthic community dynamics: an example from the Toarcian (Early Jurassic). *PLoS ONE* 8, e56255.
- Dera, G., Brigaud, B., Monna, F., Laffont, R., Pucéat, E., Deconinck, J.-F., Pellenard, P., Joachimski, M.M., Durllet, C., 2011. Climatic ups and downs in a disturbed Jurassic world. *Geology* 39, 215–218.
- Dera, G., Pellenard, P., Neige, P., Deconinck, J.-F., Pucéat, E., Dommergues, J.-L., 2009. Distribution of clay minerals in Early Jurassic Peritethyan seas: palaeoclimatic significance inferred from multiproxy comparisons. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 271, 39–51.
- Dickson, A.J., Gill, B.C., Ruhl, M., Jenkyns, H.C., Porcelli, D., Idiz, E., Lyons, T.W., van den Boorn, S.H.J.M., 2017. Molybdenum-isotope chemostratigraphy and paleoceanography of the Toarcian Oceanic Anoxic Event (Early Jurassic). *Paleoceanography* 32, 813–829.
- Fang, X., Hou, X., Li, X., Hou, W., Nakaoka, M., Yu, X., 2018. Ecological connectivity between land and sea: a review. *Ecol. Res.* 33, 51–61.
- French, K.L., Sepúlveda, J., Trabucho-Alexandre, J., Gröcke, D.R., Summons, R.E., 2014. Organic geochemistry of the early Toarcian oceanic anoxic event in Hawsker Bottoms, Yorkshire, England. *Earth Planet. Sci. Lett.* 390, 116–127.
- Galasso, F., Schmid-Röhl, A., Feist-Burkhardt, S., Bernasconi, S.M., Schneebeil-Hermann, E., 2021. Changes in organic matter composition during the Toarcian Oceanic Anoxic Event (T-OAE) in the Posidonia Shale Formation from Dormettingen (SW-Germany). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 569, 110327.
- Gili, J.-M., Coma, R., 1998. Benthic suspension feeders: their paramount role in littoral marine food webs. *Trends Ecol. Evol.* 13, 316–321.
- Gill, B.C., Lyons, T.W., Jenkyns, H.C., 2011. A global perturbation to the sulfur cycle during the Toarcian Oceanic Anoxic Event. *Earth Planet. Sci. Lett.* 312, 484–496.
- Greber, N.D., Davies, J.H.F.L., Gaynor, S.P., Jourdan, F., Bertrand, H., Schaltegger, U., 2020. New high precision U-Pb ages and Hf isotope data from the Karoo large igneous province; implications for pulsed magmatism and early Toarcian environmental perturbations. *Results Geochem.* 1, 100005.
- Häder, D.-P., Barnes, P.W., 2019. Comparing the impacts of climate change on the responses and linkages between terrestrial and aquatic ecosystems. *Sci. Total Environ.* 682, 239–246.
- Head, M., 1996. Modern dinoflagellate cysts and their biological affinities. In: Janzonius, J., McGregor, D.C. (Eds.), *Palynology: Principles and Applications*. American Association of Stratigraphic Palynologists Foundation. College Station, Texas, pp. 1197–1248.
- Hesselbo, S., 2008. Sequence stratigraphy and inferred relative sea-level change from the onshore British Jurassic. *Proc. Geol. Assoc.* 119, 19–34.
- Hesselbo, S.P., Jenkyns, H.C., Duarte, L.V., Oliveira, L.C.V., 2007. Carbon-isotope record of the Early Jurassic (Toarcian) Oceanic Anoxic Event from fossil wood and marine carbonate (Lusitanian Basin, Portugal). *Earth Planet. Sci. Lett.* 253, 455–470.

- Hunter, W.R., Levin, L.A., Kitazato, H., Witte, U., 2012. Macro-benthic assemblage structure and organismal stoichiometry control faunal processing of particulate organic carbon and nitrogen in oxygen minimum zone sediments. *Biogeo-science* 9, 993–1006.
- Jenkyns, H.C., 2010. Geochemistry of oceanic anoxic events. *Geochem. Geophys. Geosyst.* 11, Q03004.
- Kemp, D.B., Coe, A.L., Cohen, A.S., Schwark, L., 2005. Astronomical pacing of methane release in the Early Jurassic period. *Nature* 437, 396–399.
- Kemp, D.B., Selby, D., Izumi, K., 2020. Direct coupling between carbon release and weathering during the Toarcian oceanic anoxic event. *Geology* 48, 976–980.
- Korte, C., Hesselbo, S.P., 2011. Shallow marine carbon and oxygen isotope and elemental records indicate icehouse-greenhouse cycles during the Early Jurassic. *Paleoceanography* 26, PA4219.
- Little, C.T.S., Benton, M.J., 1995. Early Jurassic mass extinction: a global long-term event. *Geology* 23, 495–498.
- Littler, K., Hesselbo, S.P., Jenkyns, H.C., 2010. A carbon-isotope perturbation at the Pliensbachian–Toarcian boundary: evidence from the Lias Group, NE England. *Geol. Mag.* 147, 181–192. <https://doi.org/10.1038/s41467-021-25711-3>.
- McArthur, J.M., Algeo, T.J., van de Schootbrugge, B., Li, Q., Howarth, R.J., 2008. Basinal restriction, black shales, Re-Os dating, and the Early Toarcian (Jurassic) oceanic anoxic event. *Paleoceanography* 23, PA4217.
- McArthur, J.M., Donovan, D.T., Thirlwall, M.F., Fouke, B.W., Matthey, D., 2000. Strontium isotope profile of the early Toarcian (Jurassic) oceanic anoxic event, the duration of ammonite biozones, and belemnite palaeotemperatures. *Earth Planet. Sci. Lett.* 179, 269–285.
- Newton, R.J., Reeves, E.P., Kafousia, N., Wignall, P.B., Bottrell, S.H., Sha, J.-G., 2011. Low marine sulfate concentrations and the isolation of the European epicontinental sea during the Early Jurassic. *Geology* 39, 7–10.
- Nielsen, S.G., Goff, M., Hesselbo, S.P., Jenkyns, H.C., LaRowe, D.E., Lee, C.T.A., 2011. Thallium isotopes in early diagenetic pyrite—a paleoredox proxy? *Geochim. Cosmochim. Acta* 75 (21), 6690–6704.
- Palliani, R.B., Riding, J.B., 2003. Biostratigraphy, provincialism and evolution of European early Jurassic (Pliensbachian to early Toarcian) dinoflagellate cysts. *Paleontology* 27, 179–214.
- Pearce, C.R., Cohen, A.S., Coe, A.L., Burton, K.W., 2008. Molybdenum isotope evidence for global ocean anoxia coupled with perturbations to the carbon cycle during the Early Jurassic. *Geology* 36, 231–234.
- Percival, L.M.E., Witt, M.L.L., Mather, T.A., Hermoso, M., Jenkyns, H.C., Hesselbo, S.P., Al-Suwaidi, A.H., Storm, M.S., Xu, W., Ruhl, M., 2015. Globally enhanced Mercury deposition during the end-Pliensbachian extinction and Toarcian OAE: a link to the Karoo–Ferrar Large Igneous Province. *Earth Planet. Sci. Lett.* 428, 267–280.
- Piazza, V., Ullmann, C.V., Aberhan, M., 2020. Ocean warming affected faunal dynamics of benthic invertebrate assemblages across the Toarcian Oceanic Anoxic Event in the Iberian Basin (Spain). *PLoS ONE* 15, e0242331.
- Pieńkowski, G., Hodbod, M., Ullmann, C.V., 2016. Fungal decomposition of terrestrial organic matter accelerated Early Jurassic climate warming. *Sci. Rep.* 6, 31930.
- Powell, J.H., 2010. Jurassic sedimentation in the Cleveland Basin: a review. *Proc. Yorks. Geol. Soc.* 58, 21–72.
- Quijón, P.A., Kelly, M.C., Snelgrove, P.V.R., 2008. The role of sinking phytodetritus in structuring shallow-water benthic communities. *J. Exp. Mar. Biol. Ecol.* 366, 134–145.
- Rodrigues, B., Duarte, L.V., Silva, R.L., Mendonça Filho, J.G., 2020. Sedimentary organic matter and early Toarcian environmental changes in the Lusitanian Basin (Portugal). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 554, 109781.
- Rodrigues, B., Silva, R.L., Mendonça Filho, J.G., Reolid, M., Sadki, D., Comas-Rengifo, M.J., Goy, A., Duarte, L.V., 2021. The Phytoclast Group as a Tracer of Palaeoenvironmental Changes in the Early Toarcian. *Special Publications*, vol. 514. Geological Society, London. SP514-2020-2271.
- Ruebsam, W., Al-Husseini, M., 2020. Calibrating the Early Toarcian (Early Jurassic) with stratigraphic black holes (SBH). *Gondwana Res.* 82, 317–336.
- Ruebsam, W., Reolid, M., Sabatino, N., Masetti, D., Schwark, L., 2020. Molecular paleothermometry of the early Toarcian climate perturbation. *Glob. Planet. Change* 195, 103351.
- Ruvalcaba Baroni, I., Pohl, A., van Helmond, N.A.G.M., Papadomanolaki, N.M., Coe, A.L., Cohen, A.S., van de Schootbrugge, B., Donnadieu, Y., Slomp, C.P., 2018. Ocean circulation in the Toarcian (Early Jurassic): a key control on deoxygenation and carbon burial on the European Shelf. *Paleoceanogr. Paleoclimatol.* 33, 994–1012.
- Saelen, G., Doyle, P., Talbot, M.R., 1996. Stable-isotope analyses of belemnite rostra from the Whitby Mudstone Formation, England; surface water conditions during deposition of a marine black shale. *Palaios* 11, 97–117.
- Slater, S.M., Twitcheit, R.J., Danise, S., Vajda, V., 2019. Substantial vegetation response to Early Jurassic global warming with impacts on oceanic anoxia. *Nat. Geosci.* 12, 462–467.
- Them, T.R., Gill, B.C., Caruthers, A.H., Gerhardt, A.M., Gröcke, D.R., Lyons, T.W., Marroquín, S.M., Nielsen, S.G., Trabucho Alexandre, J.P., Owens, J.D., 2018. Thallium isotopes reveal protracted anoxia during the Toarcian (Early Jurassic) associated with volcanism, carbon burial, and mass extinction. *Proc. Natl. Acad. Sci.* 115, 6596–6601.
- Them, T.R., Gill, B.C., Selby, D., Gröcke, D.R., Friedman, R.M., Owens, J.D., 2017. Evidence for rapid weathering response to climatic warming during the Toarcian Oceanic Anoxic Event. *Sci. Rep.* 7, 5003.
- Them II, T.R., Jagoe, C.H., Caruthers, A.H., Gill, B.C., Grasby, S.E., Gröcke, D.R., Ying, R., Owens, J.D., 2019. Terrestrial sources as the primary delivery mechanism of Mercury to the oceans across the Toarcian Oceanic Anoxic Event (Early Jurassic). *Earth Planet. Sci. Lett.* 507, 62–72.
- Trisos, C.H., Merow, C., Pigot, A.L., 2020. The projected timing of abrupt ecological disruption from climate change. *Nature* 580, 496–501.
- Trugman, A.T., Anderegg, L.D.L., Shaw, J.D., Anderegg, W.R.L., 2020. Trait velocities reveal that mortality has driven widespread coordinated shifts in forest hydraulic trait composition. *Proc. Natl. Acad. Sci.* 117, 8532–8538.
- Vajda, V., McLoughlin, S., Mays, C., Frank, T.D., Fielding, C.R., Tevyaw, A., Lehsten, V., Bocking, M., Nicoll, R.S., 2020. End-Permian (252 Mya) deforestation, wildfires and flooding—An ancient biotic crisis with lessons for the present. *Earth Planet. Sci. Lett.* 529, 115875.
- van Breugel, Y., Baas, M., Schouten, S., Mattioli, E., Sinninghe Damsté, J.S., 2006. Isorenieratane record in black shales from the Paris Basin, France: constraints on recycling of respired CO<sub>2</sub> as a mechanism for negative carbon isotope shifts during the Toarcian oceanic anoxic event. *Paleoceanography* 21, PA4220. <https://doi.org/10.1029/2006PA001305>.
- van de Schootbrugge, B., Bachan, A., Suan, G., Richo, S., Payne, J.L., 2013. Microbes, mud and methane: cause and consequence of recurrent Early Jurassic anoxia following the end-Triassic mass extinction. *Palaeontology* 56, 685–709.
- van de Schootbrugge, B., McArthur, J.M., Bailey, T.R., Rosenthal, Y., Wright, J.D., Miller, K.G., 2005. Toarcian oceanic anoxic event: an assessment of global causes using belemnite C isotope records. *Paleoceanography* 20, PA3008.
- van de Schootbrugge, B., Quan, T.M., Lindström, S., Püttmann, W., Heunisch, C., Pross, J., Fiebig, J., Petschick, R., Röhlhng, H.G., Richo, S., Rosenthal, Y., Falkowski, P.G., 2009. Floral changes across the Triassic/Jurassic boundary linked to flood basalt volcanism. *Nat. Geosci.* 2, 589–594.
- Wignall, P.B., Newton, R.J., Little, C.T.S., 2005. The timing of paleoenvironmental change and cause-and-effect relationships during the early Jurassic mass extinction in Europe. *Am. J. Sci.* 305, 1014–1032.
- Williams, J.W., Jackson, S.T., 2007. Novel climates, no-analog communities, and ecological surprises. *Front. Ecol. Environ.* 5, 475–482.
- Xu, W., Ruhl, M., Jenkyns, H.C., Leng, M.J., Huggett, J.M., Minisini, D., Ullmann, C.V., Riding, J.B., Weijers, J.W., Storm, M.S., Percival, L.M., 2018. Evolution of the Toarcian (Early Jurassic) carbon-cycle and global climatic controls on local sedimentary processes (Cardigan Bay Basin, UK). *Earth Planet. Sci. Lett.* 484, 396–411.