Can the Fate of the Non-avian Dinosaurs Help us to Predict the Consequences of the Ongoing Biodiversity Crisis?

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Abstract. The ongoing biodiversity crisis has urged the scientific community to concentrate more research efforts on the mechanisms underlying the mass extinctions that have repeatedly affected our planet in deep time. This work implements a novel combination of palaeoecological and statistical routines to assess disruptions in the trophic architecture of non-avian dinosaur communities across the latest Cretaceous (83.6–66.0 Mya) of North America. Using these extinct beasts as model organisms, this work aims at increasing our ability to predict the susceptibility of ecological communities to extinction events under different levels of environmental disturbance. There was a trophic shift in the large, bulk-feeding herbivorous ornithischians and theropod carnivores during the Campanian–Maastrichtian transition that led to a simplification of North American terrestrial food webs several million years before the asteroid impact. Their disappearance during the Maastrichtian (72.0–66.0 Mya) made terrestrial communities more prone to extinction in the aftermath of the Chicxulub impact, which suggests that conservation schemes should pay special attention to keystone species in present-day food webs. In conclusion, palaeoecological transitions in the fossil record provide a valuable source of information for predicting the potential consequences of large-scale disturbances on contemporary biodiversity.

Keywords: Disturbance · Late cretaceous · Mass extinction

1 Introduction

The current biodiversity crisis (sensu [1]) has urged the scientific community to investigate the drivers of the mass extinctions that have affected our planet millions of years ago. The growing awareness of species conservation and the maintenance of the functioning of ecological systems leads us to address three fundamental questions: (i) how and (ii) why extinctions occur and (iii) what role do ecological dynamics (e.g., the trophic architecture) play in the survival and disappearance of species in the face of disturbing events.

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Since the beginning of this century, numerous studies have been executed to characterize the ecological role of some contemporary threatened species, such as large mammals (e.g., [2, 3]). The study of their food webs has shown that large predators play a key role in controlling top-down processes in present-day ecosystems [4], as well as that large herbivores contribute to the redistribution of nutrients in the ecosystem [3]. However, these analyses lack a reference scenario to compare their results with phenomena that occurred in the Earth's past. This aspect limits our view on the potential responses of ecosystems to disturbances that act as a factor of selection and extinction of species at large spatial and temporal scales, especially when it comes to the implications of the trophic architecture on the evolution of these events.

Paleontologists have strong background in studying and characterizing the causes of mass extinctions, their degree of impact and the resilience of different ecosystems, including the mechanisms underlying the survival or extinction of specific biotic groups following these geological events (e.g., [5–13]). However, bridging paleontological and modern ecological evidence could provide a new approach to study mass extinctions [14] and recent research seems to support the conceptual unification of these two disciplines [15–18]. Indeed, paleoecological dynamics associated with food webs of extinct biota can help us understand their resilience and recovery capacity in the face of large-scale disturbances across different spatiotemporal and paleobiogeographical contexts [19]. These conclusions might contribute to nuanced models on the potential responses of current ecosystems to human-induced impacts, thereby helping to prioritize key taxa that need special conservation status.

The last of the big five mass extinctions occurred 66 million years ago [20], marking the end of the age of the dinosaurs [9] and motivating the subsequent rise of the mammals during the Cenozoic [21–23]. Therefore, this event has been an important turning point for the ecological patterns and processes of our present-day world and the evolutionary legacies of the flora and fauna that we share the planet with today [24].

Various theories have been proposed to explain the causes underlying the disappearance of the non-avian dinosaurs, although there is a consensus in the paleontological community that suggests that it was the impact of an extraterrestrial bolide (over 10 km in diameter) that caused their dramatic extinction [5, 16, 25]. There is, however, empirical evidence that seems to suggest that the Chicxulub impact was not the only destabilizing factor during the transition between the Cretaceous and the Paleogene (K/Pg) [26, 27]. For instance, the Late Cretaceous experienced environmental changes resulting from intense volcanic activity on the Deccan Plateau [23], global temperature oscillations [28] and sea level fluctuations [29]. Some studies [30–32] also suggest that several groups and families of ornithischian dinosaurs were already in ecological decline before the impact of the extraterrestrial bolide. Nevertheless, modern re-evaluations of these hypotheses using novel statistical models seem to contradict these previous findings [15, 18].

The main aim of this work is to assess spatiotemporal disruptions in the trophic architecture of Late Cretaceous non-avian dinosaur communities. More precisely, by using a detailed database of the fossil record for the stratigraphic formations of Laramidia and applying state-of-the-art ecological models [33–35], this work hopes to contribute to the theoretical and empirical unification of the ecological science and paleontology.

More specifically, we aim to (i) evaluate the ecogeographical mechanisms underlying the distributional patterns of non-avian dinosaurs and the changes experienced in the relative importance of these factors between the Campanian (83.6–72.0 Mya) and the Maastrichtian (72.0–66.0 Mya), and (ii) identify the central nodes in the trophic interaction networks. Overall, using dinosaurs as model organisms and the changes that these animals experienced before their dramatic disappearance, this work hopes to contribute to assess the susceptibility of modern ecological communities to disturbances in the current context of biodiversity loss.

2 Materials and Methods

2.1 Fossil Database

Fossil occurrences and the geologic and paleogeographic context for the latest Cretaceous were downloaded for a total of 25 North American formations using the Paleobiology Database (https://paleobiodb.org/). Curation and data harmonization are explained in detailed in [36]. Overall, the final database included all fossil material available for the Late Cretaceous of North America, totaling 107 genera from 13 different families of ornithischian and theropod dinosaurs.

2.2 General Circulation Models (GCMs), Land Surfaces and Digital Elevation Models (Paleo-DEMs)

Paleoclimatic models and land surfaces used in this study are from the AOGCM HadCM3L ver. 4.5 of the BRIDGE Group (http://www.bridge.bris.ac.uk/resources/simulations). The variables included in this study (2.75° × 3.25° spatial resolution) were: near-surface (1.5 m) mean annual temperature (°C), near surface (1.5 m) annual temperature standard deviation (°C), annual average precipitation (mm), annual precipitation standard deviation (mm), net primary productivity (NPP, g C m^{-2} yr^{-1}), and plant functional types (i.e., from broadleaf and needleleaf trees to C3-type and C4-type groundcover). The simulations and settings of the terminal Cretaceous models used here are described in full by [37–39], and their applicability in paleobiogeographic studies has been discussed previously in [15–17, 40–42].

The paleogeographies used for this study are those of [43], originally created as a paleo-digital elevation model (DEM) on a 1° × 1° grid, and upscaled to the HadCM3L Earth System model resolution (2.75° × 3.25°). This means that topographic and bathymetric information was broadly conserved as it was resolved at a lower spatial resolution [16–18]. The 117 maps created by [43] have provided a global atlas for paleogeographic interpretations at different spatial scales over the last 540 million years of Earth history, including the changing distribution of the world's oceans and continents.

Sediment flux (cm kyr^{-1}) is a parameter that influences the quality of the fossil record, controlling the preservation of skeletons, and is dependent on geography, geomorphology, tectonics and climate. Here, the sedimentary flow values are those from [15], who applied the predictive model BQART98 [44] in Campanian and Maastrichtian paleofluvial landscapes.

2.3 Statistical Analysis

Distributional patterns of non-avian dinosaurs were analyzed for each time interval (Campanian versus Maastrichtian) using a special type of joint species distribution models, hierarchical modelling of species communities (HMSC hereafter, [33]). In brief, by simultaneously analysing information from multiple taxa, the HMSC routine incorporates aspects of traditional species distribution models to quantify patterns of cooccurrence among taxa and, at the same time, accounts for variation attributed to environmental filtering (here, paleogeographies, paleoclimatic and land surfaces) and random effects (here, the number of collections and sediment flux). For this work, distribution patterns of non-avian dinosaurs were modelled using the *probit* option for presence-absence data with the R *Hmsc* package [45].

All explanatory variables were logarithmically transformed before running the models. Following the criteria established by [35], all models were fitted with 10,000 Markov chain Monte Carlo (MCMC). The first 2000 steps were discarded as *burn in* and the remaining samples were reduced by a factor of 10. The predictive performance of the models was based on Tjur R^2 coefficients [46].

Finally, potential species associations (sensu [33]) were examined by calculating the residual correlations in the HMSC models (see [33] for a similar approach). Note, however, that these potential associations should not be interpreted as proven biotic interactions [47]; rather, residual correlations indicate that biotic interactions might be the primary cause underlying these empirical associations [48].

All analyses were performed in R (R Development Core Team, 2018) for CentOS Linux 7.7 (The CentOS Project, https://www.centos.org/) using supercomputing resources managed by SCAYLE (Supercomputing Centre of Castilla y León, https://www.scayle.es/).

3 Results

3.1 Performance of HMSC Models

The HMSC models applied in our study showed a moderate predictive performance (Fig. 1). More specifically, the average values of Tjur R^2 coefficients for Campanian and Maastrichtian dinosaurs ranged between 0.29 and 0.39, which is consistent with modern assessments of present-day ecological communities (e.g., [49, 50]).

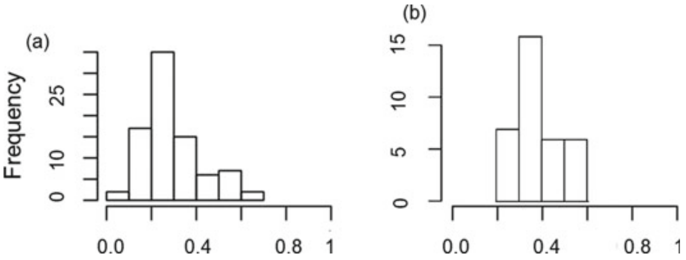
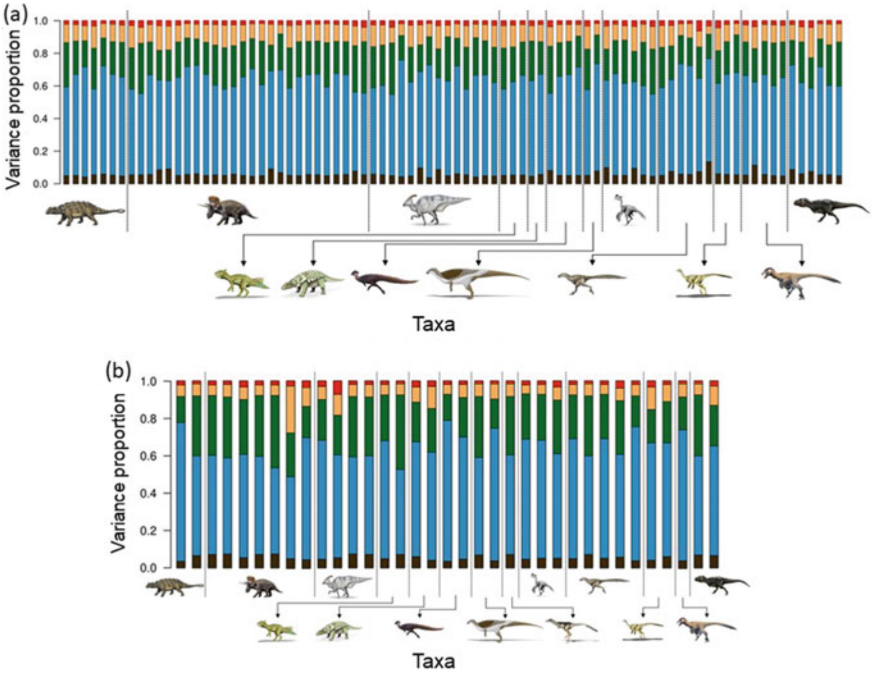


Fig. 1 Values of Tjur's R^2 coefficients for **a** Campanian and **b** Maastrichtian non-avian dinosaur communities

3.2 Variation Partitioning

Paleoclimatic correlates (i.e., mean annual surface temperature, standard deviation of annual surface temperature, mean annual precipitation and standard deviation of annual precipitation) were the most important explanatory variables underlying non-avian dinosaur distributions in the latest Cretaceous of North America (Fig. 2). The structuring role of climatic mechanisms was consistent across taxa for both Campanian and Maastrichtian time intervals, suggesting that paleoclimates were the main ecological gradient for these tetrapods, regardless of their ecologies, such as body size or diet.



◀**Fig. 2** Results of variance partitioning from our HMSC models explaining the distributional patterns of non-avian dinosaurs during the **a** Campanian and **b** Maastrichtian of North America. Colors represent different groups of explanatory variables. Altitude: dark brown; palaeoclimatic conditions: blue; land surfaces: green; number of palaeontological collections: orange; and sediment flux: red. Taxa are ordered (from left to right) using the following criteria: [**Campanian**; *Akainacephalus, Dyoplosaurus, Euoplocephalus, Oohkotokia, Platypelta, Scolosaurus, Zuul* (Ankylosauridae), *Achelousaurus, Agujaceratops, Albertaceratops, Anchiceratops, Arrhinoceratops, Avaceratops, Centrosaurus, Chasmosaurus, Coronosaurus, Diabloceratops Einiosaurus, Machairoceratops, Medusaceratops, Mercuriceratops, Nasutoceratops, Pachyrhinosaurus, Pentaceratops, Rubeosaurus, Spiclypeus, Spinops, Styracosaurus, Utahceratops, Vagaceratops, Wendiceratops, Xenoceratops, Yehuecauhceratops* (Ceratopsidae), *Acristavus, Adelolophus, Angulomastacator, Brachylophosaurus, Corythosaurus, Edmontosaurus, Gryposaurus, Hypacrosaurus, Kritosaurus, Lambeosaurus, Maiasaura, Parasaurolophus, Probrachylophosaurus, Prosaurolophus* (Hadrosauridae), *Cerasinops, Prenoceratops, Unescoceratops* (Leptoceratopsidae), *Edmontonia, Panoplosaurus* (Nodosauridae), *Colepiocephale, Gravitholus, Sphaerotholus, Stegoceras* (Pachycephalosauridae), *Orodromeus, Thescelosaurus* (Thescelosauridae), *Apatoraptor, Caenagnathus, Chirostenotes, Epichirostenotes, Hagryphus, Leptorhynchos* (Caenagnathidae), *Bambiraptor, Boreonykus, Dromaeosaurus, Hesperonychus, Saurornitholestes, Richardoestesia* (Dromaeosauridae), *Ornithomimus, Rativates, Struthiomimus* (Ornithomimidae), *Latenivenatrix, Paronychodon, Stenonychosaurus, Talos, Troodon* (Troodontidae), *Albertosaurus, Bistahieversor, Daspletosaurus, Gorgosaurus, Lythronax and Teratophoneus* (Tyrannosauridae). **Maastrichtian**; *Ankylosaurus, Anodontosauru* (Ankylosauridae), *Anchiceratops, Eotriceratops, Ojoceratops, Pachyrhinosaurus, Regaliceratops, Torosaurus, Triceratops* (Ceratopsidae), *Edmontosaurus, Gryposaurus, Hypacrosaurus, Saurolophus* (Hadroauridae), *Leptoceratops, Montanoceratops* (Leptoceratopsidae), *Denversaurus, Edmontonia* (Nodosauridae), *Pachycephalosaurus, Sphaerotholus* (Pachycephalosauridae), *Parksosaurus, Thescelosaurus* (Thescelosauridae), *Albertonykus* (Alvarezsauridae), *Anzu, Chirostenotes, Ojoraptorsaurus* (Caenagnathidae), *Acheroraptor, Atrociraptor, Dakotaraptor, Dineobellator, Richardoestesia* (Dromaeosauridae), *Ornithomimus, Struthiomimus* (Ornithomimidae), *Pectinodon* (Troodontidae), *Albertosaurus, Bistahieversor, Daspletosaurus, Gorgosaurus, Lythronax* and *Teratophoneus* (Tyrannosauridae)]

Land surfaces were the second most important group of predictor variables for the spatial ecology of non-avian dinosaurs. However, these predictors (i.e., plant functional types and NPP) were more relevant for the megaherbivores (ankylosaurids, ceratopsids and hadrosauroids) than for the remaining species groups (Fig. 1). By contrast, the predictive role of palaeotopographic features was relatively weak (5–10%), especially compared to the importance detected for paleoclimates and land surfaces. Similarly, proxies associated with the quality and potential preservation of the fossil record played a minor role ($\leq$ 15%) in our HMSC models, supporting the reliability of our modelling exercises when it comes to reconstructing the spatial distributions and ecologies of North American non-avian dinosaurs before their demise.

3.3 Trophic Architecture

Residual correlations from our HMSC models suggest a relatively high degree of trophic connectivity across the Campanian communities of North America (Fig. 3a). In this regard, key taxa for Campanian food webs were (i) the megaherbivores, including ankylosaurids (e.g., *Euoplocephalus* and *Oohkotokia*), ceratopsids (e.g., *Achelousaurus*) and hadrosauroids (e.g., *Acristavus*, *Coryristavus*); (ii) some small herbivores (< 100 kg), such as *Prenoceratops*; (iii) the omnivorous caenagnathids (e.g., *Leptorhynchos*); and (iv) the medium-sized (e.g., *Bambiraptor*, *Saurornitholestes*) and large-sized (e.g., *Daspletosaurus*) carnivorous theropods.

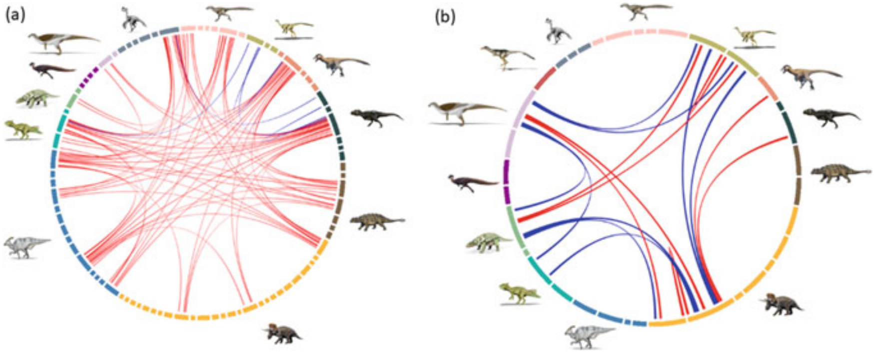


Fig. 3 Chord diagram illustrating positive (red) and negative (blue) dinosaurian associations with at least 95% posterior probability in the **a** Campanian and **b** Maastrichtian ecosystems of North America. Dinosaurian taxa are ordered (clockwise) Fig. 2

On the other hand, we found a strong decline in trophic connectivity of dinosaurian communities during the Maastrichtian, potentially contributing to their demise. For instance, most associations for Maastrichtian food webs were constrained to those registered for few ceratopsids (e.g., *Torosaurus* and *Triceratops*), the armored nodosaurid *Edmontonia* and some ornithomimids (e.g., *Ornithomimus* and *Struthiomimus*).

4 Discussion

The analysis of trophic architecture has gained importance in recent decades because it plays a key role for our understanding of the complexity of ecological systems [24]. From a paleontological perspective, it is hardly difficult to delineate food webs based exclusively on empirical fossil data. This means that paleontologists and ecologists need to join forces in order to reconstruct potential species associations in ancient ecosystems. These representations of trophic structure are a reliable proxy of extent food webs (sensu [19]), not least because they overcome the limitations arising from the difficulty of collecting and interpreting all the anatomical information needed to extrapolate biotic interactions from fossil remains [24].

HMSC models have been used successfully in modern ecology and the recent implementation of joint species distribution modelling in paleontology represents an opportunity to increase our understanding of mass extinctions by overcoming the limitations associated to fossil data [51].

The relative importance of paleoenvironmental correlates for the spatial distribution of non-avian dinosaurs is consistent with recent works (e.g., [17, 18]). Paleoclimatic features have found to be one of the main mechanisms underlying non-avian dinosaur communities in North America. Interestingly, climatic control appears to be a universal mechanism for biodiversity throughout Earth's history [52], even in times when climate variability was much lower than today, as it was the case in North America during the latest Cretaceous. The destabilization of food webs and the concomitant loss of species at different spatial scales is an issue that is still under evaluation, although the fossil record in our study seems to indicate that, even in times of minor changes in climatic conditions (such as the transition from the Campanian to the Maastrichtian), environmental changes can lead to strong ecological constraints on vertebrate trophic dynamics (Fig. 3).

The second mechanism controlling the distribution of non-avian dinosaurs in North American Late Cretaceous was a combination of plant functional types and NPP. Land surfaces were particularly important for large herbivores, which depended on a stable and continuous production of plant biomass [53]. The disappearance of forests after the bolide impact by the end of the Maastrichtian significantly altered net primary production in terrestrial ecosystems on a global scale [54–56]. The few large herbivores that survived to the thermal radiation (sensu [57]) died of prolonged starvation within a few weeks [9], a signal that cascaded through the food web [51, 56, 58]. However, a long-lasting turnover in the composition of these tetrapods, associated with changes in terrestrial vegetation, was already discernible in the transition from the Campanian to the Maastrichtian [59], 6 My before the bolide impact.

While it is certainly not anticipated that an exogenous factor will interfere dramatically with modern terrestrial ecosystems, our results provide evidence of the importance of primary production and the geographical distribution plant functional types to maintain the stability of ancient food webs. Hence, we speculate that changes in the ecological characteristics of plant functional types in biomes and the spatial variation of NPP can trigger trophic disruptions at the level of entire continents that may increase the susceptibility of entire ecological communities to extinction. It is therefore essential to study species associations in ancient ecosystems in order to anticipate extinction scenarios arising under the ongoing biodiversity crisis. For instance, understanding the relationship between trophic complexity and extinction scenarios of Earth's past should be useful when it comes to predicting how trophic ecology responds to disturbances.

Our results are in line with the original findings of [30], suggesting a trophic restructuring during the Campanian–Maastrichtian transition that was characterized by strong decline in the trophic role of large herbivorous ornithischians. Relationships between food web structure and the susceptibility of Late Cretaceous ecosystems to extinction are still subject to debate (e.g., [15] versus [32]). In this context, interest in understanding how ecosystems respond to large-scale human-induced disturbances under different biogeographical settings has been growing in recent years [60]. According to [61], trophic architecture is, indeed, one of the main features underlying the functioning of present-day ecosystems, a view that supports classical assertions from [62–64]. These authors argued that structurally and functionally complex ecosystems are more stable against disturbances. Hence, the trophic architecture of dinosaurian guilds during the Campanian would have been more stable than Maastrichtian food webs, which argues in favor of previous conclusions in the original paper of [30]. For instance, as in the case of dinosaur-dominated ecosystems in North American Late Cretaceous, the loss of the megaherbivore component likely resulted in a widespread destabilization of Maastrichtian food webs, with concomitant higher secondary extinction rates across most (if not all) trophic guilds. Hence, conservation strategies should focus on *keystone species* for the development of heterogeneous habitats [65] in the context of the ongoing climate change (e.g., [66, 67]), especially when it comes to the gradual simplification of trophic structures in current ecosystems [68–70].

However, only a handful of trophic studies have been explicitly considered to design ecological management strategies (e.g., [4]), and ignoring this facet of nature (sensu [71]) could compromise the effectiveness of management schemes aimed at conserving ecosystem functionality. For instance, studying the evolution of ancient food webs and their response to disturbances in deep time offers a novel perspective to guide predictions on the long-term effects of human-induced impacts on present-day biotas. Researchers now have the opportunity to make reliable predictions and test hypotheses under different working scenarios by using intensely sampled and stratigraphically constrained fossil databases. Their findings, including those available in this chapter, have the potential to support modern decision making and conservation strategies aimed at bending the curve of biodiversity loss [72, 73].

5 Conclusions

- Improving our understanding on the background of mass extinctions may help us to predict how present-day ecosystems may respond to human-induced disturbances at large spatial extents (e.g., an entire continent).
- Paleoclimatic conditions and spatial variation in NPP and plant functional types were the main mechanisms explaining the distributional patterns of non-avian dinosaurs in the latest Cretaceous of North America. It is therefore expected that changes in climatic conditions and land-use at the level of biomes will lead to trophic disruptions that may increase the susceptibility of entire ecological communities to extinction. Thus far, the dinosaurian fossil record suggests that the Campanian–Maastrichtian transition was characterized by a strong decline in the trophic role of large herbivorous ornithischians that made Late Cretaceous dinosaur communities more susceptible to extinction, at least in North America.
- Our results encourage the protection of key species of large herbivores and carnivores in their natural ranges, not least because many of them may act as central nodes of present-day food webs at different spatial levels of interest. The disappearance of these large faunas from ancient food webs made Maastrichtian ecosystems more prone to extinction following the bolide impact.
- Overall, this study emphasizes how palaeoecological disruptions in the fossil record provide a valuable source of information for predicting the effects of large-scale anthropogenic impacts on biodiversity.

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