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The overlooked role of landscape dynamics in steering biodiversity

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[Strapline] Evolution

[Title] Landscape's overlooked role steering biodiversity

[Longer title] *The overlooked role of landscape dynamics in steering biodiversity*

Alexandre Pohl

[Standfirst: a short item that precedes the main text, intended to provide a general introduction to entice readers to read on]

Scientists have long sought to understand what drives biodiversity changes. A study unifies ideas about marine and terrestrial biodiversity in one explanatory framework pointing to physical geography as dictating life's trajectory.

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Writing in *Nature*, Salles *et al.*¹ present numerical simulations of changing continental landscapes during the last 540 million years, and these simulations represent the high-resolution surface elevation changes (topography) on land and the associated sedimentary fluxes resulting from the interaction of climate and plate tectonics. In the model, the flux of sediments generated by the erosion of the continents and then delivered to the oceans mimics the pattern of long-term changes in marine biodiversity reconstructed based on fossil data, and simulated sediment cover on the continents strongly correlates with land plant biodiversity. These results suggest that landscape dynamics modulated Earth's ability to support numerous biological species (carrying capacity) and ultimately dictated the evolution of biodiversity in the oceans and on the continents over geological ages – reconciling for the first time the histories of marine and terrestrial biodiversity within a single theory.

Reconstructions of the evolution of marine biodiversity on Earth, based on the compilation of paleontological data, date back to a key publication² in the early 1980s. Biases have been reduced and trends refined over time, but some patterns seem robust (Fig. 1a). This includes the strong increase in marine biodiversity during the Cambrian and Ordovician Periods (539 to 444 million years ago, Ma), stabilization during the second part of the Paleozoic Era (444–252 Ma), a large drop in biodiversity at the Permian-Triassic boundary – corresponding to the largest mass extinction ever – and a subsequent rise to unprecedentedly high levels during the Mesozoic and Cenozoic Periods (252 Ma to today).

Plants on land showcase a completely different story, roughly showing a monotonic increase that started almost 100 million years later than biodiversity in the ocean, during the Devonian (around 420 Ma) (Fig. 1b). Many hypotheses have been put forward to explain these temporal trends but there is no consensus and previous work mostly considered marine and terrestrial biodiversity separately.

Salles and colleagues' model represents the interplay between tectonics and climate, which together drive the evolution of landscape —valleys, mountains and rivers — on our planet (Fig. 2). Their model is driven by palaeogeographical reconstructions describing changes in shorelines, large-scale topography and the position of the landmasses over the last 540 million years, and climatic simulations showing the concomitant changes in the water cycle. The model simulates elevation on land at high resolution (5 kilometres) using a source-to-sink approach which means that sediments eroded on land are tracked while they travel in river networks until they reach the ocean. By doing so, the model also represents the location and magnitude of deposition of sediments on the continents. The model has been calibrated and validated in the present day before being used to analyse the deep geological past. This approach forms part of the current efforts to build a virtual planet, in which a variety of processes are integrated to generate a digital twin of the Earth permitting researchers to gain mechanistic understanding of the coupling between Earth's surface and interior.

The simulations demonstrate a striking, positive correlation between marine biodiversity and the flux of sediments delivered to the ocean (Fig. 1a). Nutrients constitute the fundamental building blocks required by organisms to build their tissues. In the ocean, nutrients mainly come from the river-provided input of dissolved chemical species generated by the alteration of rocks on land. Postulating that the quantity of nutrients delivered to the ocean scales with the sedimentary flux, the authors interpret the correlation between the simulated sedimentary flux and marine biodiversity as reflecting the nutrient-driven variation in the carrying capacity of the oceans.

On land, the authors designed an index representing the landscape's capacity to host diverse species. This index combines the area of the sediment cover on land and the landscape variations (heterogeneity). The former represents the spatial extent available for land plants to develop their rooting networks, whereas the latter is a way to represent the number of different ecological niches, thus the potential number of species. The biodiversity of land plants strongly correlates over time with this index, suggesting that landscape dynamics have also set the agenda for the evolution of land plants during the last 540 million years (Fig. 1b).

These results are novel in many different aspects. They explain the evolution of terrestrial and marine biodiversity together and notably suggest that the limited sediment cover and small landscape heterogeneity delayed the development of land plants before the Devonian, explaining the previously mysterious temporal lag observed between marine and terrestrial biodiversity curves (Fig. 1). This study offers a new reading of biodiversity on geological time scales that involves the existence of a carrying capacity of the environment, but does not need to explicitly account for ecological innovations and evolution, raising questions about existing models that do account for such factors^{3,4}. In this new framework, several of the major mass extinctions correspond to times in the aftermath of large drops in the sediment flux to the ocean. This is notably the case of the largest such mass extinction, at the Permian–Triassic boundary, that post-dates the largest decrease in sediment flux simulated over the last 540 million years. The vision that nutrient shortage could constitute an important precondition to extinctions contrasts with the widely admitted notion that

nutrient increase would drive these extinctions⁵ (by fostering the production of organic matter by photosynthetic algae in the shallow ocean and its degradation by bacteria consuming dissolved oxygen deeper down in the water column, ultimately leading to ocean deoxygenation).

There is still some room for improvement regarding this type of simulations. They could be refined by adding additional information on both the type of rocks eroded on land (lithology) and the location and elevation of ancient mountains. In addition, the conclusions are based on temporal correlations and alternative interpretations are possible. The correlation between marine biodiversity and the simulated sediment flux might imply that biodiversity curves mostly reflect preservation biases with a more completely preserved fossil record, thus higher documented biodiversity, during periods of high marine sedimentation rates. To go beyond temporal correlations and to assess causality, it would now be beneficial to quantify the effect of landscape dynamics on biodiversity using macroecological models⁶ based on the high-resolution, open-access layers of environmental data produced in this study⁷ (topography and climate). Such an additional step would help to confirm or revise the interpretations and might also help to explain some model-data mismatches, such as the lack of signs of the Great Ordovician Biodiversification Event⁸ in the simulations (Fig. 1a).

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[Thanks for your suggested figures. I'll discuss them with the art editor and get back to you in due course.]

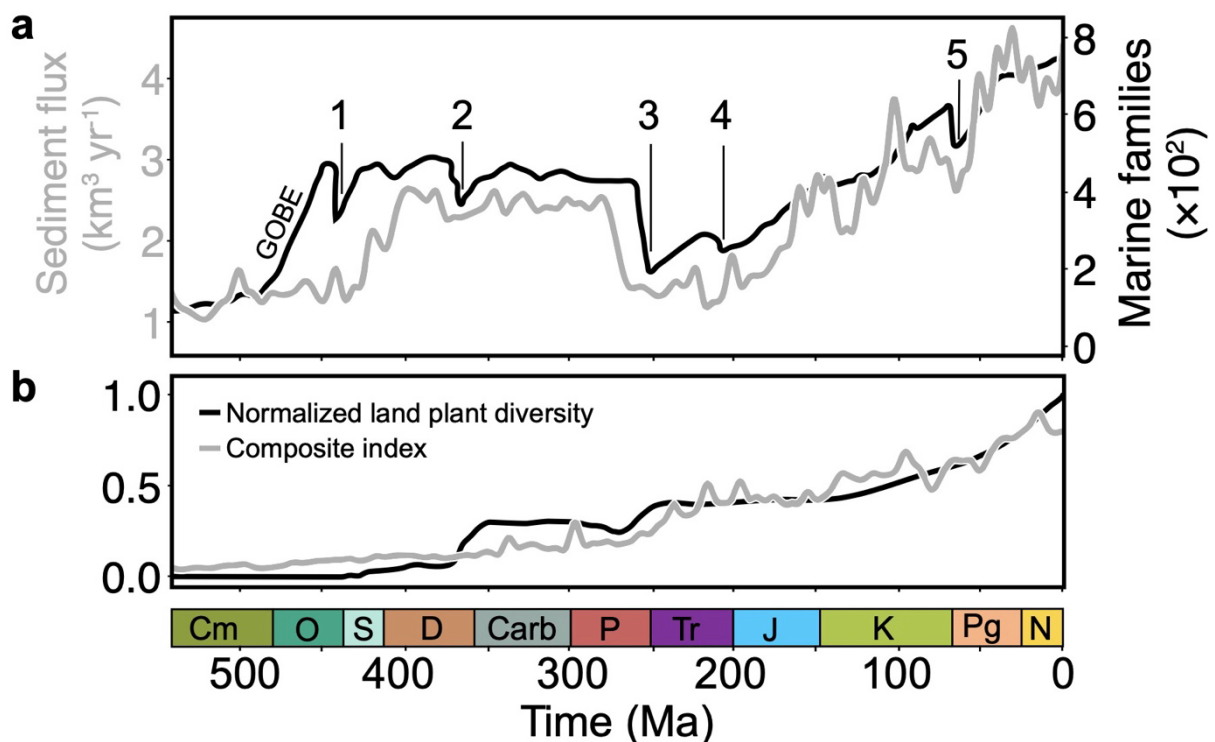


Figure 1: Simulation results vs. paleontological data. Salles et al.¹ simulated landscape dynamics over the last 540 million years and demonstrated that the latter, by modulating the carrying capacity of the Earth, may have driven the evolution of biodiversity in the ocean and on the continents. **a.** The simulated flux of sediments generated by alteration of the rocks on the continent and then delivered to the oceans (grey line) strongly correlates in time with the biodiversity of marine invertebrates reconstructed based on fossil data⁹ (black line). Numbers represent mass extinctions (1: Late Ordovician; 2: Late Devonian; 3: Permian-Triassic; 4: Triassic-Jurassic; 5: Cretaceous-Paleogene). GOBE: Great Ordovician Biodiversification Event. **b.** On land, the authors designed an index constituting a simple metrics for sediment cover and landscape heterogeneity (grey line) and showed that this index mimics the long-term trend in land-plant diversity¹⁰ (black line). Cm: Cambrian; O: Ordovician; S: Silurian; D: Devonian; Carb: Carboniferous; P: Permian; Tr: Triassic; J: Jurassic; K: Cretaceous; Pg: Paleogene; N: Neogene.

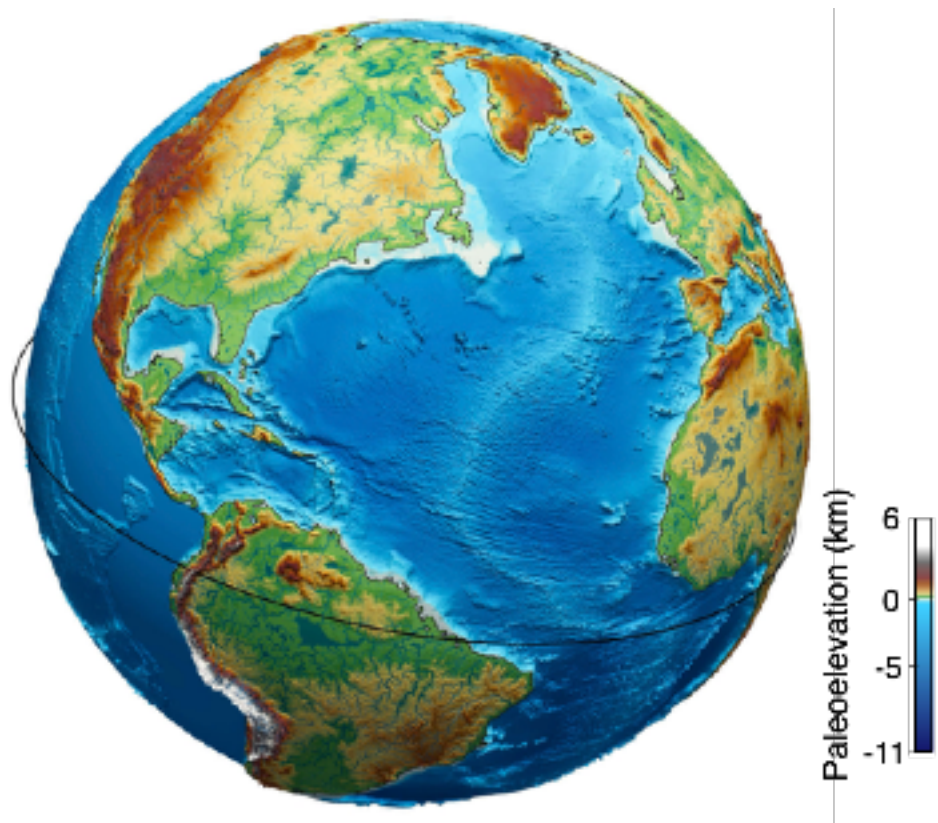


Figure 2: Simulation results for 15 million years ago. The authors simulated paleo-landscapes and drainage networks at a high resolution of around 5 kilometers.