# INVITED REVIEW

# The Miocene wetland of western Amazonia and its role in Neotropical biogeography

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In the Miocene (23–5 Ma), a large wetland known as the Pebas System characterized western Amazonia. During the Middle Miocene Climatic Optimum (*c.* 17–15 Ma), this system reached its maximum extent and was episodically connected to the Caribbean Sea, while receiving sediment input from the Andes in the west, and the craton (continental core) in the east. Towards the late Miocene (*c.* 10 Ma) the wetland transitioned into a fluvial-dominated system. In biogeographic models, the Pebas System is often considered in two contexts: one describing the system as a cradle of speciation for aquatic or semi-aquatic taxa such as reptiles, molluscs and ostracods, and the other describing the system as a barrier for dispersal and gene flow for amphibians and terrestrial taxa such as plants, insects and mammals. Here we highlight a third scenario in which the Pebas System is a permeable biogeographical system. This model is inspired by the geological record of the mid-Miocene wetland, which indicates that sediment deposition was cyclic and controlled by orbital forcing and sea-level change, with environmental conditions repeatedly altered. This dynamic landscape favoured biotic exchange at the interface of (1) aquatic and terrestrial, (2) brackish and freshwater and (3) eutrophic to oligotrophic conditions. In addition, the intermittent connections between western Amazonia and the Caribbean Sea, the Andes and eastern Amazonia favoured two-way migrations. Therefore, biotic exchange and adaptation was probably the norm, not the exception, in the Pebas System. The myriad of environmental conditions contributed to the Miocene Amazonian wetland system being one of the most species-rich systems in geological history.

ADDITIONAL KEYWORDS:  Middle Miocene Climatic Optimum (MMCO) – Pebas System – wetlands.

## INTRODUCTION

The origin of Amazonian biodiversity has puzzled scientists for centuries. As the species richness of Amazonia gradually came to light from the initial accounts by de Carvajal (1541–42) to those of explorers in the 19th century such as von Humboldt, Bonpland (see Sandwith, 1925) and Bates (1863), the need to explain this biodiversity also emerged. Climate (e.g. Cowling, Maslin & Sykes, 2001; Cheng *et al.*, 2013; Rangel *et al.*, 2018), soils (e.g. Fine *et al.*, 2006; McClain & Naiman, 2008; Laurance *et al.*, 2010; Hoorn *et al.*, 2010a; Quesada *et al.*, 2011) and biological dispersal (e.g. Hoorn *et al.*, 2010a; Ledo & Colli, 2017; Antonelli *et al.*, 2018) have long been considered primary drivers of diversification, but the geological history of Amazonia has received less attention. However, geology can provide an insight into the deep time

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origins and history of modern species diversity (e.g. Hoorn, 1993; Latrubesse *et al.*, 1997; Monsch 1998; Antoine *et al.*, 2006, 2016, 2017; Wesselingh, 2006a; Hoorn *et al.*, 2010a, b, unpubl. data; Salas-Gismondi, 2015).

In this context, the sedimentary record of western Amazonia is of particular importance. This record, which captures a highly dynamic Cenozoic sedimentary system, can be observed along the rivers draining the lowlands where remarkable bright, turquoise-coloured clays, rich in molluscs (first reported by Gabb, 1869, but see Nutall, 1990, and Wesselingh, 2006a) and macrofossils of reptiles and fish are exposed (Monsch, 1998; Salas-Gismondi *et al.*, 2015; Pujos & Salas-Gismondi, 2020). Beyond these fossil-rich, riverside outcrops, drill cores such as those obtained in Brazilian Amazonia (Maia *et al.*, 1977) extend the spatial reach of our insight to Amazonia in deep time. In recent years, these cores have been the subject of intensive study, informing sediment age, depositional environments and past vegetation composition (Fig. 1A; Appendix 1) (Hoorn, 1993; da Silva-Caminha, Jaramillo & Absy, 2010; da Silva *et al.*, 2020; D'Apolito, 2016; Jaramillo *et al.*, 2017; Kachniasz & Silva-Caminha 2017; Leite *et al.*, 2017; Linhares, de Souza Gaia & Ramos, 2017; Leandro *et al.*, 2019; Linhares *et al.*, 2019; Gomes *et al.*, 2021; Kern *et al.*, 2020; Parra *et al.*, 2020; Sá *et al.*, 2020; Leite, da Silva-Caminha & D'Apolito, 2021).

The Neogene Amazonian sediments are known as Pebas, Solimões and Curaray Formations in Peru, Brazil and Ecuador, respectively, whereas in Colombia they are documented as Terciario Inferior Amazonico. These sediments were mainly deposited in a vast wetland that is also known as the 'Pebas System', the name we will use from here onwards (Fig. 1B; 15 Ma), which existed between *c*. 20 and 10 Ma and was characterized by aquatic environments such as shallow lakes and swamps.

## LINKS BETWEEN THE MIOCENE WETLAND AND CONTEMPORARY AMAZONIAN BIOGEOGRAPHY

The role of the Pebas System in palaeobiogeographic models has been much discussed. This vast wetland is thought to have acted as a cradle of species radiation for fishes, reptiles, molluscs and ostracods (e.g. Lovejoy, Bermingham & Martin, 1998; Lovejoy, Albert & Crampton, 2006; Wesselingh & Ramos, 2010; Salas-Gismondi *et al.*, 2015; Fontanelle *et al.*, 2021). Moreover, episodic connections between the Amazonian wetland and the Caribbean Sea would have permitted immigration (and subsequent adaptation) of marine taxa into the freshwater environments, contributing to the radiation model (Lovejoy *et al.*, 1998; Lovejoy

*et al.*, 2006; Wesselingh & Ramos, 2010; Linhares *et al.*, 2017). However, Wesselingh & Salo (2006) proposed that the Pebas System also formed an environmental dispersal barrier that prevented migration and isolated terrestrial species. This idea was soon followed up by Antonelli *et al.* (2009), who noticed that dispersal of Rubiaceae, the coffee plant family, was impaired and suggested this was due to the Pebas System. Similarly, palms such as *Astrocaryum* (Roncal *et al.*, 2013, 2015) and the family Meliaceae (Koenen *et al.*, 2015) are thought to have been affected by this barrier. Antoine *et al.* (2016, 2017) presented further support for this model by showing that terrestrial mammal diversity in the fossil record of western Amazonia steeply declined during the Pebas (wetland) phase (early to mid-Miocene) and increased again in the Acre (fluvial) phase (late Miocene). Evidence from butterflies, such as *Taygetis* (Matos-Maraví *et al.*, 2013), Morphinae (Blandin & Purser, 2013), Troidini (Condamine *et al.*, 2012), Ithomiini (Chazot *et al.*, 2019), and amphibians, such as *Allobates* and dendrobatid frogs (e.g. Santos *et al.*, 2009; Réjaud *et al.*, 2020), confirm this view, as these taxa diversified after the demise of the Pebas System.

In this perspective, we propose a third model, in which the Pebas System can be seen as a permeable biogeographic system. Although the existing radiation and inhibition models remain true, we suggest that the Pebas System, with its diversity of environments, promoted dispersal of selected terrestrial and amphibious taxa. To substantiate this idea, we discuss the sedimentary record of the Pebas System and show that intermittent connectivity existed between the wetland, the Andes and the peripheral *terra firme* in western and eastern Amazonia. This connectivity consisted of fluvial channels and deltas that formed transport conduits for sediment and water supply (fresh and marine) into the wetland, but also enabled terrestrial species migration in and out of the system. Even though both the *cradle* and the *permeable* model favour speciation, the mechanisms that drive that speciation are vastly different. In the cradle model, diversification is driven by long-lived suitable conditions (time) in a large region (area). In contrast, in the permeable model speciation is driven by change, leading to a constant back and forth between gene flow and isolation.

## GEOLOGICAL DRIVERS OF THE MIOCENE AMAZONIAN WETLAND

The enigmatic and rich fossil record of the Pebas Formation has delivered contradictory insights into the environmental conditions in Miocene western Amazonia, which have been debated since the 19th
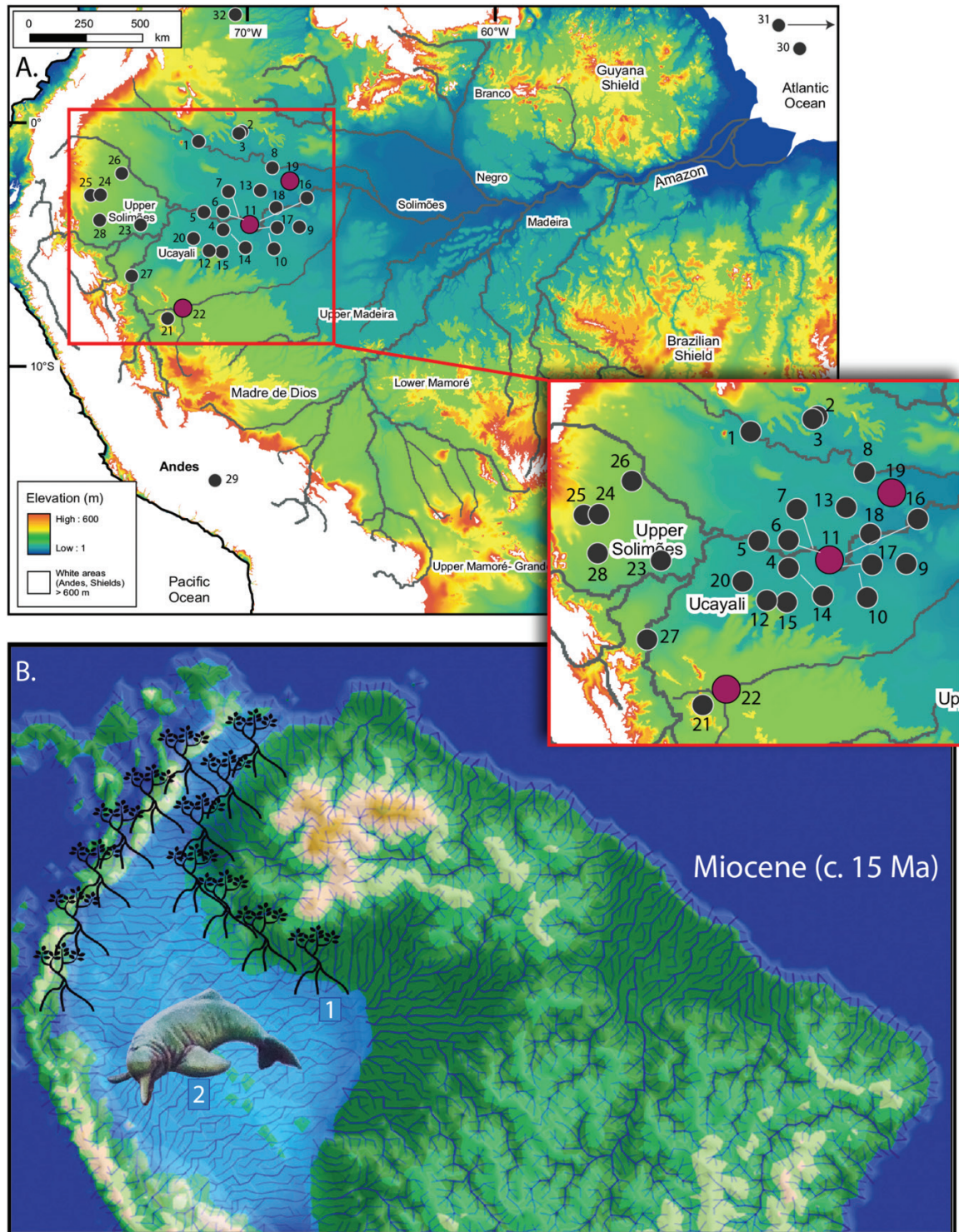
**Figure 1.** A, Main cored sites that were used to reconstruct the Neogene sedimentary history of Amazonia (Map courtesy H. Wittmann). The highlighted (magenta) locations feature in Fig. 2.2. B shows an idealized reconstruction of the Pebas System at its maximum extent during high sea level in the mid-Miocene. At the time, the area was colonized by coastal mangroves (1, icon from thenounproject.com) and selected marine organisms (2, by Orlando Grillo); see Boonstra *et al.*, 2015; Jaramillo *et al.*, 2017, Sciumbata *et al.*, 2021, for further details). This figure is readapted from Bicudo *et al.* (2020) and McDermott (2021), with permission from Elsevier, T. Bicudo, V. Sacek and L. Reading-Ikkanda.

century (see for overview Räsänen *et al.*, 1998; Gingras *et al.*, 2002; Wesselingh, 2006a; Hoorn *et al.*, 2010b). Even today, interpretations differ and range from fluvial, fluvio-lacustrine to para-marine megalake settings (see Jaramillo *et al.*, 2017, for overview). The main geological drivers responsible for generating and sustaining the Pebas System are thought to be related to Andean uplift (Fig. 2.1) causing flexural subsidence in the foreland basins east of the Andes (e.g. Hoorn 1993; Sacek, 2014) (Figs 2.2A, B, 3), dynamic subsidence (topography change due to plate–mantle interaction) (Shephard *et al.*, 2010, Eakin, Lithgow-Bertelloni & Dávila, 2014; Bicudo *et al.*, 2019; Bicudo, Sacek & de Almeida, 2020), high precipitation rates (> *c.* 3 m per year) related to orographic barrier formation (Poulsen, Ehlers & Insel, 2010; Sepulchre, Sloan & Fluteau 2010; Barnes *et al.*, 2012) and global sea-level change (Hoorn, 1993). During the mid-Miocene, global temperatures and global sea levels (Miller *et al.*, 2020; Westerhold *et al.*, 2020; Fig. 2.2D) were high, and the balance between sediment influx and subsidence was maintained for millions of years (Fig. 2.2B). Towards the end of the mid-Miocene (*c.* 10 Ma) the eventual demise of the Pebas System was probably caused by a combination of geological processes including a drop in global sea level, the formation of a topographic barrier between Amazonia and the Caribbean (i.e. Vaupés arch; Mora *et al.*, 2010) and continued sediment infill pushing the flexural low further eastwards over time (Sacek, 2014) (Figs 2.2B, C, 3). As a result, the Pebas System transitioned into a fluvio-lacustrine system also known as Acre phase (Hoorn *et al.*, 2010a, b), and this transition coincided with the genesis of the transcontinental Amazon River (Figs 2.2C, 3) and the formation of the submarine Amazon fan along the Brazilian Equatorial Margin (Figueiredo *et al.*, 2009, 2010; Hoorn *et al.*, 2017; van Soelen *et al*, 2017) (Figs 1A, 2.2C). The dissection of the Amazonian landscape by rivers created new opportunities for terrestrial taxa to colonize the *c.* 1 000 000 km$^2$ that were previously occupied by wetland.

## BRIDGING THE CARIBBEAN AND AMAZONIA

The first arrival of marine-derived fish lineages into Amazonia dates to the Palaeogene (Lundberg *et al.*, 2010; Bloom & Lovejoy, 2011, 2017), but the Miocene Pebas System is thought to have been a prime motor of diversification in selected marine fish lineages by providing a patchwork of habitats differing in salinity levels (Lovejoy *et al.*, 2006; Bloom & Lovejoy, 2011, 2017). During the Miocene, marine incursions into the Pebas System established a biogeographic connection between the Caribbean and western Amazonian environments through the Llanos basin (Boonstra *et al.*,

2015; Jaramillo *et al.*, 2017). This marine connection must have converted sections of the freshwater shore of the Pebas system into brackish environments and promoted the colonization of such littoral stretches by marine coastal biota (Lovejoy *et al.*, 2006; Wesselingh & Salo, 2006; Linhares *et al.*, 2017), providing exceptional conditions for coastal species to adapt and speciate in continental freshwater environments (Lovejoy *et al.*, 2006; Bloom & Lovejoy, 2011, 2017). Once sea waters regressed, such originally coastal species may have become an integral part of the freshwater Amazonian diversity (Lovejoy *et al.*, 2006; Bernal *et al.*, 2019). These speciation dynamics should have been especially important for mesohaline species such as those found in estuaries that, due to their adaptation to a wide range of salinities, may have been more predisposed to adapt to freshwater habitats (Bernal *et al.*, 2019). The legacy of these speciation events is observable today in the fauna and flora that inhabit the Amazon: fish, river dolphins and rainforest plant taxa show morphological affinity with typical coastal species (Lovejoy *et al*., 1998; 2006; Cassens *et al.*, 2000; Bianucci *et al.*, 2013; Bernal *et al.*, 2019; Benites *et al*., 2020; Sciumbata *et al.*, 2021).

Taken together, Miocene marine incursions probably represented a migratory pathway for coastal biota into western Amazonia by connecting the biogeography of the latter with that of the Caribbean. In this view, marine incursions may have acted as a selective evolutionary driver that had substantial consequences for the modern species composition of the Amazonian landscape (Lovejoy *et al.*, 2006; Bloom & Lovejoy, 2011, 2017; Jaramillo *et al.*, 2017; Bernal *et al.*, 2019; McDermott, 2021).

## THE PEBAS SYSTEM AS A PERMEABLE BIOGEOGRAPHIC SYSTEM

Extensive geological datasets from the Pebas and Solimões formations indicate that the Miocene wetland system hosted a variety of sub-environments including shallow lakes, fluvial channels, swamps and lowland forests (see also Hoorn 1994; Latrubesse *et al.*, 1997, 2010; Wesselingh *et al.*, 2006a; Hoorn *et al.*, 2010a, b) in which sand, clay and lignites were deposited (Fig. 2B).

Sediment deposition and paleoenvironments in the Pebas System were regulated by orbital cyclicity that built successions ranging from subaquatic/lake during flood or transgressive cycles (*sensu* Wesselingh *et al.*, 2006b; Vonhof & Kaandorp, 2010; Hoorn *et al.*, unpubl. data) to swamps and soils during dry or regressive cycles. Seasonal freshwater cyclicities were recognized in mollusc shells (Kaandorp *et al.*, 2005), akin to the flood pulse found in the modern *varzea* system (Junk, 2013),
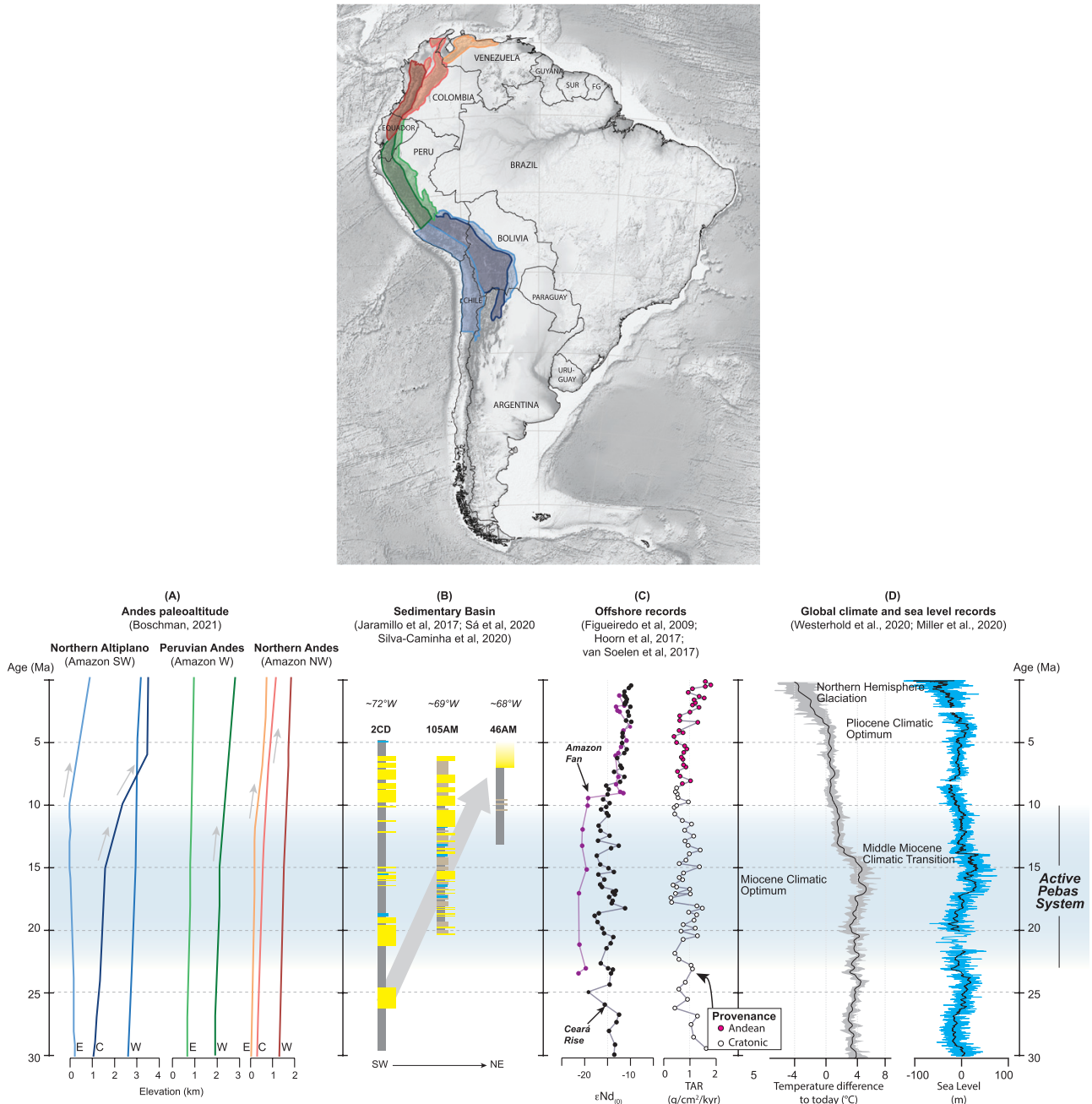
**Figure 2.** 1 (top). Northern (red and orange), Peruvian (green) and Central (blue) Andes; regions correspond to uplift curves of Fig. 2.2A. 2 (bottom). Synthesis of geologic data for the Amazon and global climate for the last 30 Ma. Global and regional climatic, environmental and provenance reconstructions through time. A, Temporal constraints on the evolution of Andean topography. Andean elevations are provided for several Andean ranges from the south-west to north-west headwaters of the Amazon (see Fig. 2.1, based on Boschman, 2021). B, Compilation of broad sedimentological observations summarizing key facies changes through time (see Fig. 1A for core locations; *blue = marine*; *grey = clay*; *yellow = sand*). The positioning of the stratigraphic cross-sections is an approximation based on relative constraints based on palynostratigraphy (see Espinosa, D'Apolito & de Silva-Caminha, 2021, and references cited). C, Temporal variations in εNd in the Amazon Fan (red, after Hoorn *et al*, 2017) Ceará Rise (black, after van Soelen *et al.*, 2017) and terrigenous accumulation rates (TAR) at the Amazon outlet near the Ceará Rise. D, Global Cenozoic smoothed mean temperature difference from today (black line) and 20 kyr binned data (grey cloud) (Westerhold *et al.*, 2020) and mean sea-level curve (black) and raw data (blue) (Miller *et al.*, 2020) showing key global climatic events, mid-Miocene sea-level highstand and long-term late Cenozoic cooling and sea-level fall.

although Miocene sediments lack plant taxa typical of *varzea* ecosystems. In terms of nutrient influx, aquatic ferns such as *Azolla* Lam. and algae such as *Botryococcus* Kützing and *Pediastrum* Meyen suggest that cyclic changes, from oligotrophic to eutrophic lake conditions, were regulated by Andean sediment input and productivity in the system. In addition, repetitive occurrence of marine palynomorphs and mangrove pollen (Hoorn, 2006; Boonstra *et al.*, 2015; Espinosa, D'Apolito & da Silva-Caminha, in press; Hoorn *et al.*, unpubl. data) point at conditions shifting from brackish to freshwater due to the waxing and waning of the marine incursions (Fig. 3D). These allocyclic processes highlight the permeability of the system.

At the margins of the wetland, environmental conditions positively favoured the grasses (Poaceae). These grasses reached relatively high proportions (D'Apolito *et al.*, 2016), suggesting growth along the lake shores, although influx from open vegetation in the montane sediment source area cannot be excluded (Kirschner & Hoorn, 2020). Members of Mauritiinae (Arecaceae) such as *Grimsdalea magnaclavata* Germeraad, Hopping & Muller (a taxon only known from its fossil pollen record), also thrived on the shores of the Pebas System, alternating with stands of *Mauritiidites* van Hoeken-Klinkenberg (with affinities with *Lepidocaryum* Mart. and *Mauritia* L.f.) (Bogotá-Ángel *et al.*, 2021). Mangrove pollen were documented from discrete intervals, but in places they constitute the dominant taxon, suggesting they periodically formed part of the local vegetation (Hoorn, 2006; Boonstra *et al.*, 2015). Moreover, mangrove pollen and marine palynomorphs were accompanied by at least 14 associated species (Sciumbata *et al.*, 2021), providing further support for the hypothesis of Bernal *et al.* (2019) that coastal taxa may have immigrated into and subsequently adapted in Amazonia. Further away from the wetland shores, a more diverse vegetation existed that transitioned to *terra firme*. The shores of the Pebas System also hosted a reptile diversity that might have been the highest of the (Neogene) Neotropics, and possibly globally (Riff *et al.*, 2010; Scheyer *et al.*, 2013; Salas-Gismondi *et al.*, 2015; Cidade, Fortier & Hsiou, 2019). However, the demise of the Pebas System at the end of the Miocene was unavoidably paired with the extinction of most of the taxa belonging to these groups.

Our permeable biogeographic model posits that features of the Pebas System, such as its landscape heterogeneity and cyclic flood-fill packages, created dispersal opportunities for some taxa (i.e. permeability) at the same time as serving as a dispersal barrier for others such as terrestrial mammals and *terra firme* plants. The system would have also favoured taxa living along niche gradients (e.g. aquatic vs. terrestrial;

brackish vs. freshwater; eutrophic vs. oligotrophic) that were increasingly common during Pebas times and taxa capable of adapting to the cyclic, probably orbitally paced, landscape variability. Amphibians, such as the frog *Pristimantis*, would have found the dynamic Pebas landscape permeable as flood-fill cycles created new aquatic and terrestrial migratory pathways, perhaps explaining their increased diversification during Pebas times (Waddell *et al.*, 2018). Similarly, these advantages applied to bats (Sánchez *et al.*, 2018) and insects such as damselflies (Sánchez-Herrera *et al.*, 2020), which speciated in the wetland system and endured after the system progressed into a fluvial system. Further, marine incursions into the Pebas System favoured selected taxa like fish and marine mammals, whereas other taxa might have survived (see the earlier section on the biogeography) without receiving a diversification boost. We conclude that the Pebas System must have been a permeable biogeographic system, in which only selected taxa benefitted.

The hypothesis of the Pebas System as a permeable biogeographic system is supported by the diverging diversification histories of coastal and aquatic taxa, which often thrived during Pebas times, and terrestrial taxa like land mammals that decreased in diversity. The hypothesis of the permeable system implies that the Pebas System was not predominantly a dispersal driver or inhibitor, but rather species dispersal was selectively favoured or inhibited in similar proportions. However, we note that the three hypotheses (cradle, barrier, permeable) are not mutually exclusive, but may be relevant for different groups of taxa. Since we only have data for a small fraction of the total Neogene diversity, the magnitude of permeability is not yet resolved. Furthermore, the extent and longevity of possible barriers and conduits in the Pebas System remains unclear, making it difficult to infer their effect on different taxa. Future work can address these gaps from a variety of perspectives. For instance, improved age constraints on sedimentary sequences will allow comparisons of spatial landscape heterogeneity at a given point in time. More comparative study of dispersal and diversification across taxa from distinct niches will help build a conceptual model of the traits that favour versus inhibit dispersal in Pebas conditions. Additionally, such a theoretical framework can be advanced with species dispersal simulations that represent Pebas-like conditions, including its heterogeneity and cyclicity. By integrating new data, improved age constraints on existing data, and models that link geological and biotic processes, future work will unravel the
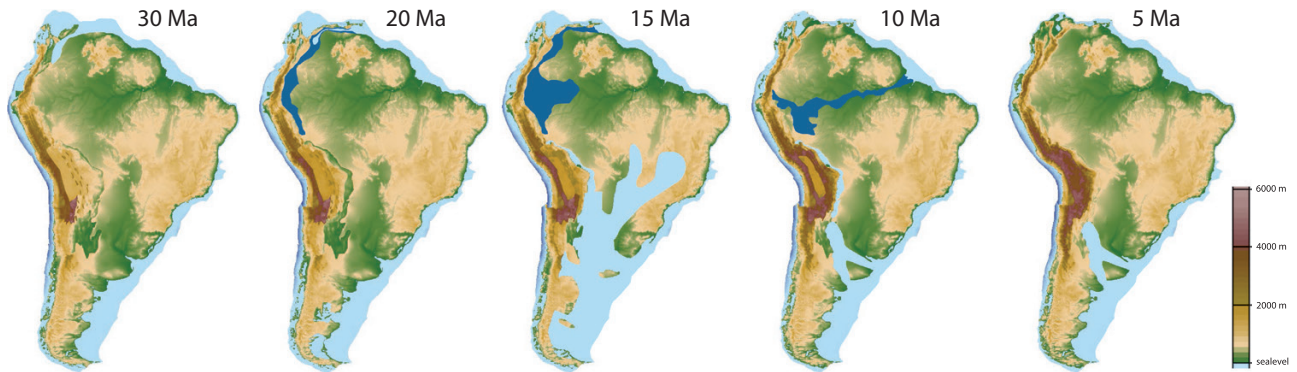
**Figure 3.** Palaeogeographic reconstruction of South America and the Miocene Amazonian wetland. Elevation in the Andes is based on Boschman (2021), marine incursions (light blue) and lakes (dark blue) based on Wesselingh & Hoorn (2011) for Amazonia and Hernández *et al.* (2005) for south-eastern South America.

biogeographic consequences of the Pebas System and the implications of selective dispersal for ecology and diversity through geologic time.

## CONCLUSIONS

At present, the origins of Amazonian biodiversity are not fully understood. Many efforts are devoted to phylogeographic models, but advances in regional geology are an important information source that is insufficiently tapped. In this perspective we assess the role of the Miocene Amazonian wetland (Pebas System) in current biogeographic models and summarize key data from geological records. We show that the palaeobiogeography of Amazonia was determined by two-way migratory pathways between Amazonia, the Andes and the Caribbean and between western and eastern Amazonia. Moreover, we conclude that cyclic deposition driven by orbital forcing and sea-level change were important determinants of sediment deposition and species evolution.

The permeable biogeographic model that we propose for the Pebas System uses these geological features to understand distinct, taxon-dependent biogeographic trends. It does not address the extent to which the Pebas System is responsible for the modern biodiversity of western Amazonia, but rather presents a framework for explaining Miocene diversification patterns, the relicts of which may persist today. Furthermore, our new hypothesis may help design future data collection while also contributing to their interpretation in light of the multifaceted depositional history of the Pebas System.

## ACKNOWLEDGEMENTS

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Neogene tropical South America data (referenced to Figure 2 of main text).