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REVIEW

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The onset of grasses in the Amazon drainage basin, evidence from the fossil record

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Abstract.

Poaceae (the grass family) originated in the Cretaceous, but first dominate the palynological records of the Amazon drainage basin (ADB) in the Neogene (23 to 2.5 million years ago (Ma)). However, the ecological role of grasses in the landscape during this time remains to be resolved. In this paper, we summarise the global significance of grasses and the relevance of the fossil record, and evaluate the history of the grasses in the ADB. We present a 3-stage model of the changing role of grasses, which we based on a revision of Neogene depositional environments, the palynological record, and modern grass distribution in the Neotropics. Our model comprises the following hypotheses: (H1) assumes that from c. 23 to 9 Ma western Amazonia was dominated by a megawetland (the 'Pebas system') that harboured large amounts of (aquatic?) grasses. In (H2) we propose that from c. 9 Ma Andean uplift prompted megafans (extremely large alluvial fans) that extended from the Andes into the lowlands. Meanwhile, the 'Pebas' megawetland gradually transformed into a fluvial system. In this scenario, grasses would have had a competitive advantage and were able to colonise the newly formed megafan and fluvial landscapes. Finally, in (H3) we suggest that landscape dynamics and climatic change intensified from c. 3.5 Ma, allowing for a renewed expansion of the grasses. In addition, both the fossil and molecular records suggest that from c. 5 Ma grasses were firmly established in the tropical alpine vegetation (páramo), the tropical lowland floodplains (várzeas), and savannas (cerrado). Although further study will have to confirm the precise nature of the ADB grass history, we anticipate that abiotic processes during the Neogene and Quaternary left a strong imprint in the grass phytogeography of northern South America.

Highlights

- Grasses have been a common component of the Amazon drainage basin (ADB) since at least the Neogene (23 Ma).
- A large wetland, that accommodated extensive amounts of grass remains, existed in western Amazonia from around 23 to 9 Ma.
- From c. 9 Ma, grasses were likely the successful pioneers of new habitats that formed on the Andean slopes, megafans, and the floodplains of the Amazon River.
- The rising Andes, together with environmental and climate change, favoured grass development in the ADB during the Neogene and Quaternary.
- In the last 5 million years, open surfaces in the high Andes offered comprehensive habitats for grass colonisation.

Keywords: Amazon biogeography, megafans, Miocene, Panicoideae, Pebas, Poaceae, Pooideae, Quaternary, refugia

Introduction

The earliest evidence for the existence of grasses (Poaceae, formerly Gramineae) dates back to the Cretaceous (Table 1; Prasad et al. 2005, 2011, Strömberg 2011, Samant and Mohabey 2014, Wu et al. 2018). Nevertheless, big knowledge gaps remain about the global expansion of grass-dominated habitats. In the early Miocene (c. 23 – 16 Ma), grasses started their rise to global dominance that continues until today (Kidder and Gierlowski-Kordesch 2005). The family of grasses is marked by a large taxonomic richness of over 11,500 species (Soreng et al. 2017), and highly productive grassland ecosystems occupy around 40% of

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Table 1. Age of origin of the Poaceae and their subfamilies based on phylogeny and fossils.

Poaceae, subfamilies	Ages (Ma) from phylogeny (Hodkinson 2018; Prasad et al. 2011)	Ages (Ma) from phytoliths & macrofossils (Edwards et al. 2010)	Ages (Ma) from pollen, phytoliths & cuticles (Jacobs et al., 1999; Prasad et al. 2005, 2011; Poinar et al. 2011, 2015; Wu et al. 2018)
Micrairoideae	25		
Chloridoideae	28	19	
Panicoideae	35	12	
Danthonioideae	37		
Pooideae	38	34	
Arundinoideae	39	16	
Aristidoideae	40		
Bambusoideae	43	35	
Oryzoideae	46		
Puelioideae	55		
Pharoideae	59		
Anomochlooideae	62		
Ehrhartoideae			67 - 65
Origin Poaceae	**129 - 107** PACMAD (Panicoideae - Aristidoideae - Chloridoideae - Micrairoideae - Arundinoideae - Danthonioideae)	**67 - 65** PAC? (Panicoideae - Aristidoideae - Chloridoideae) & BEP (Bambusoideae - Ehrhartoideae - Pooideae)	**70-60** Monoporopollenites annulatus pollen **97 - 110** Pooideae (or Arundinoideae, Chloridoideae, Panicoideae or Bambusoideae?) **113 - 101** Anomochlooideae?

the Earth's land surface (White et al. 2000). With their ecosystem properties, such as a high surface albedo (Sage 2004) and high carbon sequestration capacity (Fisher et al. 1994, Kidder and Gierlowski-Kordesch 2005), grasses contribute to altering climate and transforming the biosphere.

Grass development in the Amazon drainage basin (ADB) is of special interest in the light of the immense species diversity found in the area today. They occur in a wide range of ecosystems, which in northern South America comprise, amongst others, high-elevation grasslands (páramo), savanna (cerrado), tropical, subtropical, and cold to temperate grasslands, and the floodplain environments (várzeas and igapós) (Burkart 1975; see Fig. 1 & 2). Grasses are also of interest in the broader context of understanding evolution and the impact of grassland ecosystems in the past. Reconstructing the global rise of grasses, however, is hampered by the scarcity of fossil records predating the Quaternary and the interpretation of the low taxonomic resolution of grass subfamilies (e.g., Strömberg 2011).

In this review we address the following research questions:

(1) Which abiotic and biotic factors were shaping the Amazon lowlands since the Neogene (<23 Ma)?

(2) Is there conclusive evidence concerning the origin and dispersal of Poaceae in the ADB from the early Miocene onwards? And if not, what is the way forward?

(3) What can we learn from the 'forest refugia' debate when viewed in a multimillion-year time perspective?

Throughout this paper we show that grasses are abundant throughout the Neogene history of the ADB. We present a 3-stage model that proposes hypothetical scenarios in which the grasses developed in an evolving landscape. We hypothesize (H1) that in the early to late Miocene (c. 23 to 9 Ma), aquatic Poaceae occurred in a wetland system that was situated in western Amazonia. In (H2) we suggest that from c. 9 to 3.5 Ma the wetland was replaced by the Amazon River and its extensive floodplains (Hoorn et al. 2010a), while

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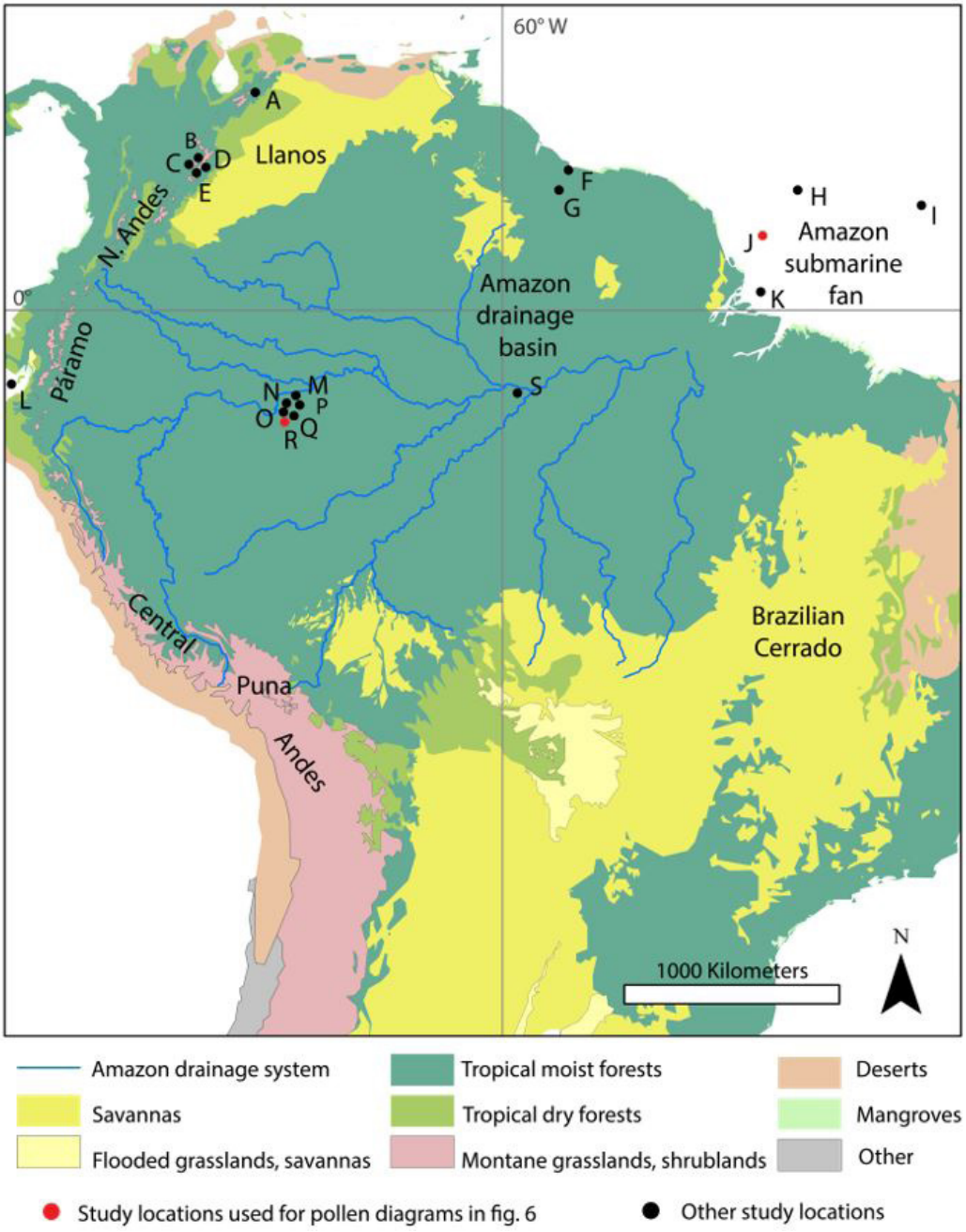

Figure 1. Grass-dominated ecosystems of northern South America, the Amazon River, and the location of the Amazon submarine fan. In red, the sampling locations with pollen diagrams (Fig. 6; Hoorn et al. 2017, Jaramillo et al. 2017). In black, the most relevant studies of fossil records referred to in the text: (A) Lorente 1986; (B) Wijninga 1996; (C) Hooghiemstra and Ran 1994, Hooghiemstra 1984; (D) Van der Hammen et al. 1973; (E) Helmens 1990; (F) Wijmstra 1971; (G) Van der Hammen and Wijmstra 1964; (H) Haberle and Maslin 1999; (I) Harris and Mix 2002; (J) Hoorn et al. 2017; (K) Figueiredo et al. 2009; (L) Grimmer et al. 2018; (M) Latrubesse et al. 2010; (N) Hoorn 1993, 1994; (O) Sá and Carvalho 2017; (P) Linhares et al. 2019; (Q) Da Silva-Caminha et al. 2010; (R) D'Apolito 2016, Jaramillo et al. 2017; (S) D'Apolito et al. 2019. Map data retrieved from Burkart (1975). Credits for the imagery layer "South America Terrestrial Ecosystems" (Esri 2014): USGS; Esri[1]. Credits for the map layer "World Drainage systems" (Esri 2010): Digital Chart of the World (DCW), U.S. National Geospatial-Intelligence Agency, Bartholemew and Times Books, Rand McNally and Company, World Resources Institute, Oxford University Press[2]. Map was created using ArcGIS® software by Esri. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used herein under license. Copyright © Esri. All rights reserved. For more information about Esri® software, please visit www.esri.com.

1 https://www.arcgis.com/home/item.html?id=45764ecdc7274509be752bfebeb268e1, last accessed 1/5/2019

2 https://www.arcgis.com/home/item.html?id=7b98eed639bb4cda85888e854a445efa, last accessed 1/10/2019

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Figure 2. Different grass environments in the present Amazon drainage basin, from top left to bottom right: (1) grasses in the high Andes, Antisana, Ecuador; (2, 3, 4, 5) grasses in the Colombian páramo; (6) grasses of the várzeas, floodplains near Manaus, Brazil; (7, 8) cerrado grasslands at Tocantins, Brazil; (9) llanos grasslands in Colombia. Image credits: Esteban Suarez (1), Henry Hooghiemstra (2, 3, 4, 5, 9), Els van Soelen (6); Marie-Pierre Ledru (7, 8).

the sub-Andean basins were filled with alluvial fan sediments derived from the rising Andes (Parra et al. 2009, Roddaz et al. 2010). In this scenario, pioneering grasses are thought to have established in the newly formed habitats on the Andean slopes and floodplains. Finally, (H3) proposes that from c. 3.5 Ma grasses were favoured by Quaternary climatic change, relief formation in the Andes, and the intensified erosion that followed.

Our three hypotheses are based on a review and discussion of existing palynological records and place the evolution of grasses in the ADB (Fig. 1) in the light of past changes in environment, vegetation, climate, and geography (e.g., Hoorn 1994, D'Apolito 2016, Jaramillo et al. 2017, D'Apolito et al. 2019) (see Fig. 1). A visual summary of the modern distribution of Poaceae in the Neotropics (based on Bremond et al. 2012) further helped with formulating an expectation

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of which Poaceae subfamilies could have occurred in the different Neogene depositional environments (Fig. 3).

We also briefly discuss the 'forest refugia theory', which concerns decades of debate about the occurrence and evolution of grasses in the ADB during the Quaternary ice ages (e.g., Haffer 1969, Colinvaux et al. 2001). Furthermore, we evaluate the role of fire, adaptations in the photosynthetic pathway of grasses, and changes in the atmospheric carbon dioxide concentration during the global rise of grasses.

The ultimate goal of this review is to provide an overview of deep time (since 23 Ma) fossil records that should be complementary to molecular records as the latter don't capture extinction or species decline (Crane et al. 2004). Finally, we discuss the challenges that arise when answering these questions and give an outlook on opportunities for future research.

Materials and methods

We searched the literature on the history of grasses and their global context, with special attention on the ADB. The present geographic distribution of Poaceae species richness in the Neotropics is summarised in Bremond et al. (2012) and includes Poaceae species records and their elevational ranges from Colombia, Peru, Ecuador, and Bolivia. We used this dataset and subdivided it into categories: 'Lowlands', including taxa with exclusive occurrence up to 1000 m.a.s.l. (meters above sea level), 'Forest', with taxa at or above 1000 m.a.s.l. and below 3600 m.a.s.l., and 'Open vegetation' including taxa at or above 3600 m.a.s.l. Taxa occurring across zones were lumped into two separate categories and all duplicates were removed (see Supplementary Materials, table S1). The overall Poaceae species richness in the Neotropics, according to subfamily and based on the entire dataset from Bremond et al. (2012), was plotted separately. In the context of the Humboldt year, we use the Naturgemälde (von Humboldt and Bonpland, 1807) to show the prevailing Poaceae subfamilies according to the elevational gradient (Fig. 3).

Palynological data from Hoorn et al. (2017) and Jaramillo et al. (2017) were used to represent the Neogene to Pleistocene record of the Poaceae in Amazonia, and to visualise the proportion of grasses (including '*Monoporopollenites annulatus*') versus other angiosperms. The palynological diagrams were created with Tilia (version 2.6.1, www.TiliaIT.com), and the source data can be found in the Supplementary Materials (tables S2, S3).

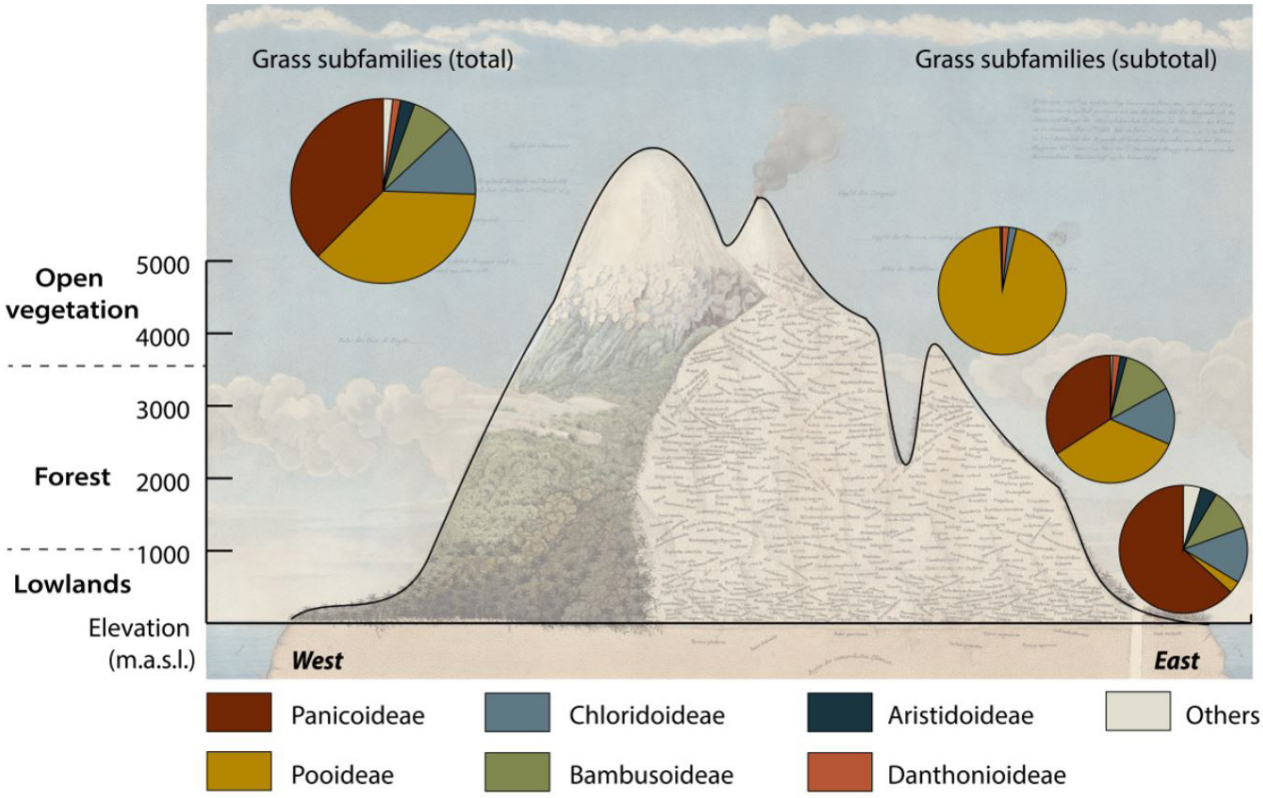

Figure 3. Profile of the Cordillera Occidental (Ecuador) showing species richness of the Neotropical Poaceae subfamilies according to their exclusive elevational range: Neotropical lowlands (0-1000 m.a.s.l.), Andean forests (≥1000 m and <3600 m.a.s.l.), and open vegetation/highlands (≥3600 m.a.s.l.). The summary pie chart (top left) shows the total species richness/Poaceae subfamily; the smaller pies show species restricted per biome (right side). Data retrieved from Bremond et al. 2012. Background image: 'Naturgemälde' (von Humboldt and Bonpland, 1807).

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Poaceae: Historical records, evolution, and the role of fire

Evidence from the fossil record

Direct evidence of Poaceae from the fossil record is based on macrofossils, such as fossilised leaves, stems, and reproductive structures in palaeo-faunal records. However, microfossil remains such as pollen (Fig. 4.1-4) and phytoliths (i.e., plant silica bodies; see Fig. 4.5) (Strömberg 2011) are also common in the fossil record. Most grasses are anemophilous and produce large amounts of pollen, but phytoliths are often better preserved in dry grassland sediments (Prasad et al. 2005). The low taxonomic resolution of fossil Poaceae pollen complicates the interpretation of grasses in fossil records. Recent progress herein has been achieved by using morphometric analysis (Schüler and Behling 2011), combining digital image processing with morphometry data analysis (Guimarães et al. 2017), scanning electron microscopy (SEM; Waikhom et al. 2014, Mander and Punyasena 2015), confocal microscopy (Salih et al. 1997), and chemotaxonomy (Julier et al. 2016).

Indirect evidence of grass presence in the past is derived from climatic reconstructions, fossil soil analysis, and stable isotope analysis of soil carbonates tracing back C3 and C4 grasses (Strömberg 2011). Aridity affects the isotopic signal of plants, making it possible to distinguish open from closed canopy habitats (Zanazzi and Kohn 2008). The presence of charcoal in fossil records is a direct indicator of fire activity in the past, another disturbance factor that promotes grassland dynamics over time. Phylogenetic reconstructions give further indications regarding the evolution of different grass lineages (e.g., Bouchenak-Khelladi et al. 2010, 2014a, Soreng et al. 2017, Hodkinson 2018; Table 1).

For a long time, the functional morphology of mammals (e.g., powerful chewing muscles, long legs, large body size, high-crowned tooth morphology) was also thought to be an indicator of grasslands (MacFadden et al. 1996). However, the present understanding is that these rather give indications about habitat openness, feeding height, and levels of aridity instead of being an indicator of grasslands (Flynn et al. 2003, Janis et al. 2004).

Origins and global evolution

The earliest signs of grass presence reach back to the Early Cretaceous and are based on epidermal fragments and phytoliths (Anomochlooideae?) that are dated at 113 – 101 Ma. These remains were obtained from the dentition of a hadrosauroid found in northwest China (Wu et al. 2018). The age of this finding roughly coincides with that of grasses found in amber from Myanmar (Poinar et al. 2011, 2015;Table 1). Other authors report Late Cretaceous and Paleogene records, which are based on phytoliths that were found in 67 to 65 Myr old dinosaur coprolites from Pisdura in central India (Prasad et al. 2005, 2011;Table 1). The latter is in agreement with molecular dating finding evidence of earliest grasslands around 75 Ma (Christin et al. 2014). Nevertheless, in view of the new findings from China and Myanmar this age will need to be pushed back further.

Most grass species form part of two lineages called the BEP (Bambusoideae, Ehrhartoideae, Pooideae) and the PACMAD (Panicoideae, Arundinoideae, Chloridoideae, Micrairoideae, Aristidoideae, Danthonioideae; Strömberg 2011). Habitats of pristine Poaceae are assumed to have originated around 57 Ma from closed canopy habitats, with ancestors of Pooideae and Bambusoideae originally being mesophytic, and adapted to average climatic and edaphic conditions. BEP ancestors probably colonized closed, dry and woody habitats of Africa in the early Eocene. Adaptation of the subtribe of Pooideae towards more open, mesophytic habitats is dated considerably later, to around 38 Ma (Bouchenak-Khelladi et al. 2010).

The PACMAD clade is thought to have originated between 53 and 45 Ma, in closed canopy and forested environments, and gradually adapted to a mix of closed and open habitats (Bouchenak-Khelladi et al. 2010). Phytoliths support the hypothesis of the late Eocene as the moment of first adaptive shifts within

Figure 4. Pollen of fossil and extant Poaceae taxa from the Amazon drainage basin. (1) *Cortaderia haplotricha* (Danthonioideae), Scanning Electron Microscope, extant taxon from the Sierra Nevada del Cocuy, Colombia; (2) *Chusquia spencei* (Bambusoideae), Light Microsocope (LM), extant taxon from Zulia, Venezuela; (3) *Monoporopollenites annulatus*, Pleistocene, Amazon submarine fan, LM; (4) *M. annulatus*, early Miocene, Santa Teresa, Marañon River, Peru, LM (image credits: Carina Hoorn & Matteo Sciumbata), (5) Phytolith picture of cf. *Panicum* spp. (Gramineae) early-middle Miocene, Apaporis River, Colombia (image credits: Gaspar Morcote-Rios).

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Figure 5. The Amazon delta is a sediment body formed at the intersection of continental Amazonia and the Atlantic (see Figure 1). Sediments transported by the Amazon River are partially deposited here, whereas most of the sediments are deposited further down into the Atlantic Ocean in a submarine fan system called the 'Foz do Amazonas' or mouth of the Amazon. Growth of the fan is dependent on glacial and interglacial phases. During global sea-level low-stands (glacials), clastic sediments originating from the drainage basin bypass the shelf and are directly transported into the growing submarine fan. In times of global sea-level high-stands (interglacials), there is hardly any deposition in the Amazon fan system. Sediment deposition instead occurs in terrestrial riverine and lacustrine environments and on the continental shelf (Hoorn 1997, Figueiredo et al. 2009) (image rights: NASA MODIS Rapid Response team).

the PACMAD clade towards more open habitat and arid adapted grasses in Africa (Strömberg 2005). Still, closed-habitat grasses remained dominant during the late Oligocene and the early Miocene. The preferred habitats of subfamilies such as the Anomochlooideae, Pharoideae, and Puelioideae are shaded tropical or warm temperate forest understories both in the past and in the present (Bouchenak-Khelladi et al. 2010).

Grasses count among early and mid-succession life forms that excel in fast colonization of newly opened and dynamic spaces (Connell and Slatyer 1977, Junk and Piedade 1997). Linder et al. (2017) attribute the success of grasses to four functional properties. Firstly, their high dispersal ability facilitates the spread over all continental landmasses. Secondly, their ability to establish themselves in pristine spaces formed by landscape changes enabled grasses to become the dominant species in the vegetation (Levick et al. 2015). Next to that, their morphological and phenotypical traits allow grasses to adapt and quickly establish in a wide range of environments, from forest understoreys to aquatic habitats, rain forests, deserts, and mountains (Linder et al. 2017). Lastly, grasses developed tolerances towards disturbances, a benefit that woody plants often lack (Linder et al. 2017).

Expansion of C4 grasses and the role of fire

The global expansion of grass-dominated habitats occurred over several major phases in which modifications in the photosynthetic pathway played an important role. Photosynthesis is the process through which vascular plants use solar energy to transform water and carbon dioxide into sugars, a mechanism that developed prior to 2800 Ma in a CO_2-rich atmosphere (Hayes 1994). Many grasses use the C4 (Hatch-Slack or Kranz) photosynthetic route (Watson and Dallwitz 1992), which allows a more efficient water and CO_2 use (Leegood 2002) compared to the original C3 (Calvin-Benson) and the CAM (Crassulacean Acid Metabolism) photosynthetic pathway. Today, C4 plants and their efficient carbon fixation make up only 3% of vascular plant species but contribute around one third of the global terrestrial photosynthesis (Linder et al. 2017). Plants using the ancient way of C3 photosynthesis still predominate at high latitudes and elevations, and in regions with cool-season precipitation (Strömberg 2011).

Work by Keeley and Rundel (2005) differentiates between the evolution of C4 photosynthesis triggered by low atmospheric carbon dioxide concentrations (Boom et al. 2001, Sage 2004) and the global expansion of C4 grasslands. The development of C4 photosynthesis

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during the Oligocene (c. 30 Ma) is seen as one of the '*most dramatic examples of biome assembly in the geological record*' (Edwards et al. 2010). Large-scale expansion of C4 grasslands, however, didn't take place before the late Miocene and Pliocene (c. 8 to 3 Ma; Edwards et al. 2010, Strömberg 2011, Bouchenak-Khelladi et al. 2014b) and is probably connected to a combination of environmental factors. Climate may also have played a role, with late Miocene global cooling resulting in increased seasonality and changes in precipitation patterns (Osborne and Beerling 2005).

Fire as an ecological disturbance factor is considered to be an essential driver for C4 grassland expansion (Keeley and Rundel 2005, Beerling and Osborne 2006, Osborne 2008, Edwards et al. 2010). Biomass produced in areas with sufficient precipitation during the growing season provided fuels for wildfires, while reduced fuel moisture after the dry season supported wildfire ignitions (Keeley and Rundel 2005). In latitudes with warm atmospheric temperatures, the high light environment created by regular fires supported the rapid replacement of wood biomes by C4 grasslands (Keeley and Rundel 2005, Bond 2008). Low atmospheric carbon dioxide concentrations additionally resulted in slow tree growth and recovery after fire disturbance events (Bond et al. 2003).

Present and past distribution of Poaceae in the Amazon drainage basin

Modern distribution of Poaceae in the ADB

Grasses have distinct climatic and environmental preferences (Sage et al. 1999). In the Andes, Pooideae and Danthonioideae are commonly found at high elevations (Luteyn 2019), whereas Panicoideae prevail along the modern Amazon River margins and lakes (Kricher 2011). Other subfamilies of grasses, such as Anomochlooideae, Pharoideae, and Bambusoideae inhabit the Amazonian forests (Judziewicz and Clark 2007).

Bremond et al. (2012) compared the modern elevational distribution of Poaceae across the Neotropical Andes with climatic data. They found, among other things, that mean annual temperature is the key factor that controls C4 distribution in the Neotropics. We visually summarised their dataset with species richness (based on elevation specific taxa), and plotted per subfamily according to elevational range. In terms of species richness, the Pooideae subfamily overwhelmingly dominates the grass páramo within the open vegetation (≥3600 m.a.s.l.), whereas the Andean forest (≥1000 and <3600 m.a.s.l.) has a mixed composition with predominantly Pooideae, Panicoideae, Chloridoideae, and Bambusoideae. Finally, the Neotropical lowlands (<1000 m.a.s.l.) have a composition mainly formed of Panicoideae, Chloridoideae, Bambusoideae, and Aristidoideae. Our figure gives a good indication of the Poaceae composition that can be expected along the elevational gradient in the sedimentary record (Fig. 3). Consequently, this helps us to formulate our expectation for the grass composition in past environments.

The fossil record and the environmental preference of grasses

In a catchment as large as ADB, fossil pollen is sourced from a wide range of habitats and environments over time (Hoorn et al. 2017). Nevertheless, grass pollen and phytoliths can be very helpful in discriminating the provenance within the drainage basin.

Grasses were able to adapt to different habitats, yet their morphological traits mostly remained uniform below family level (e.g., Julier et al. 2016). This is something that applies even more to fossil Poaceae pollen (Bush 2002). Moreover, the sediment cores from which palynological samples are collected usually are taken in aquatic environments, which can result in a bias towards these environments (Bush 2002). If a majority of taxa within the ecosystem are insect pollinated, Poaceae can easily appear overrepresented in records (Bush 2002).

In the course of the 'forest refugia' debate, the Poaceae pollen presence in fossil records was often interpreted as an indicator of regional aridity. However, floating grasses and marshes can equally contribute to the presence of Poaceae in the pollen rain (Bush 2002). Gosling et al. (2009) measured up to ~50% of Poaceae in samples collected at the mud-water interface from modern Neotropical lakes. Assigning subtribes correctly and comparing these to their modern dispersion is therefore an important tool for the interpretation of fossil pollen records.

In savanna ecosystems Poaceae pollen range from less than 20% (Ledru 2002, Gosling et al. 2009) to around 75% in true cerrado (Salgado-Labouriau 1973). Very high (50 – 90%) amounts of Poaceae pollen in palynological records give strong evidence for the existence of savanna habitats (Salgado-Labouriau 1979, Bush 2002). However, aquatic environments can also feature large amounts of grass pollen (e.g., Behling et al. 2001, Sá et al. 2016). And to complicate matters further, savannas and aquatic environments are both characterized by different species of the subfamily of the Panicoideae. Instead, and as we saw above, Poaceae pollen from the high Andean slopes overwhelmingly pertains to the Pooideae. SEM analysis can potentially contribute to identification of grass subfamilies in pollen samples and is thus an essential step in determining the source habitat of fossil grass pollen.

Phytolith analysis is an alternative method when reconstructing the Poaceae fossil record along the Andes-Amazonian elevational gradient. Studies in archeobotany and palaeoecology have shown promising phytolith yields in Quaternary sediments (e.g., Piperno, 1988, 1997). Initial tests on pre-Quaternary sediments have also produced modest assemblages (Morcote-Rios, pers. comm.). Further insights into grassland dynamics might result from the application of models to estimate vegetation composition based on pollen deposits in lakes (Sugita 2007a,b).

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Andes to Amazon, grass occurrences across the ADB in the past 23 million years

The pioneering nature of grasses, as described in the earlier sections, might be one of the causes why grasses were able to evolve in the ADB. In this section, we review the highly dynamic landscape context that set the scene for the evolution of grasses in order to identify suitable areas for grass colonization within the ADB.

Earliest evidence of grass environments in the ADB and its immediate periphery

Palynological data from terrestrial and marine sediment cores are an important source to reconstruct Amazonian palaeovegetation and to estimate the past extent of grasses in the drainage basin (Fig. 1). Terrestrial sediment cores drilled in the seventies (Maia et al. 1977) have provided an invaluable source of information on Amazonian Neogene history, vegetation, and Poaceae occurrences (Hoorn 1993, 1994, Silva-Caminha et al. 2010, D'Apolito et al. 2016, Jaramillo et al. 2017, Leite et al. 2017, Sá and Carvalho 2017, Linhares et al. 2019).

Along the Brazilian Equatorial Margin, an almost complete Neogene stratigraphy of the Amazon River sediments is recorded in a hydrocarbon exploration well that was drilled on the upper continental slope of the Amazon submarine fan (Figs 1 & 5; Figueiredo et al. 2009, Hoorn et al. 2017). This large offshore sediment apron, located in Pará, Brazil, forms the most distal extent of the Amazon River and provides a more continuous stratigraphy than in the continental sedimentary basins (Hoorn et al. 2017). The sedimentary record provided an insight into changes of past Amazonian landscapes and the terrestrial biomes. A detailed palynological study of these samples suggests that changes in sediment and pollen source area are related to an expanding drainage basin (Hoorn et al. 2017). Notably, from the late Miocene onwards, this study shows increasing amounts of grasses. As the proto-Amazon River transforms into the river that we know today, the record gradually changed from coastal plain and tropical lowland taxa towards increasing portions of montane forest and Andean taxa of treeless environments (Hoorn et al. 2017).

Outside the ADB, the earliest grass pollen records were observed in samples from the Oligocene to lower Miocene deposits in the Guiana Coastal Basin (Fig. 1; Van der Hammen and Wijmstra 1964). Grasses were relatively prominent contributors to this palynological record, ranging from 10% to 40% of the total sum during the lower to middle Miocene, and 5 to 20% in the Pliocene (Fig. 1; Wijmstra 1971). Modest percentages of grass pollen (c. 10%) also occur in Oligocene sediments of the coastal basins situated near the Merida Andes (Venezuela). However, in the early Miocene grass percentages already reach up to 70%, with late Miocene to Pleistocene deposits including up to 95% grasses (Fig. 1; Lorente 1986).

The Pebas megawetland (c. 23 – 9 Ma)

The development of the Pebas megawetland is of particular importance for understanding origins of Poaceae pollen in the ADB. This sedimentary system, represented by the Pebas and Solimões geological formations, initiated in the early Miocene (c. 23 Ma) and lasted until the late Miocene (c. 9 Ma). The Pebas megawetland was characterized by shallow lakes, floodplains, and a swamp environment extending over large parts of Western Amazonia, probably fragmenting pre-existing pristine rainforest (Hoorn 1994, Wesselingh et al. 2001, 2006, 2010, Wesselingh and Salo 2006, Hoorn et al. 2010a,b, Hoorn and Wesselingh 2010). Grasses, ferns, fern allies, and aquatic taxa all were frequent (Hoorn 1993, 1994, D'Apolito 2016). D'Apolito (2016) reports high grass pollen percentages from c. 18 to 11 Ma (Fig. 1 & 6). Initial results from phytolith research further point at the presence of Panicoideae in this time interval (Gaspar Morcote-Rios, pers. comm; Fig. 4.5). Although the taxonomic affinity of these Poaceae still needs to be investigated further, it is likely that most of the species were associated with aquatic environments. Nowadays, grasses in these environments are mostly formed by genera such as *Echinochloa* and *Paspalum* that belong to the Panicoideae (Piedade et al. 2010). Nevertheless, the incipient eastern Andes is an additional possible source area for Poaceae pollen in the wetland.

The wetland gradually turned into a dynamic fluvial system that was characterized by channel and overbank deposits (Iriondo 1993, Latrubesse et al. 1997, 2010, Lundberg et al. 1998, Wesselingh and Salo 2006, Riff et al. 2010, Hoorn and Wesselingh 2010, Hoorn et al. 2010b). In western Amazonia, these fluvial sedimentary deposits are well represented in the upper part of the Solimões Formation. The Poaceae in this part of the formation probably originated in fluvial floodplain environments characterized by floating meadows and gallery forests (Latrubesse et al. 2010, Silva-Caminha et al. 2010; Jorge et al., 2019). Nevertheless, an Andean origin is also plausible as these sediments have their principal source area in the Andes (Hoorn 1993).

The Amazon River and megafan formation in the Andean foothills (c. 9 Ma)

The onset of the Amazon River as transcontinental river (i.e., the river that flows from the Andes to the Atlantic) occurred no later than c. 9.4 to 9 Ma (Hoorn et al. 2017). However, at the beginning, sediment discharge was relatively modest and vastly increased in the Pliocene-Pleistocene (Figueiredo et al. 2009, Hoorn et al. 2010b, Hoorn et al. 2017). This timing coincides with the Andes almost reaching its modern elevation (Gregory-Wodzicki 2000, Anderson et al. 2015, Garzione et al. 2017).

Large megafan palaeo-drainage networks (Fig. 7) developed in the Central Andes, following mountain uplift and climate change (Räsänen et al. 1987, 1992, Horton and Decelles 2001, Wilkinson et al. 2010). These megafans are the principal conduct of

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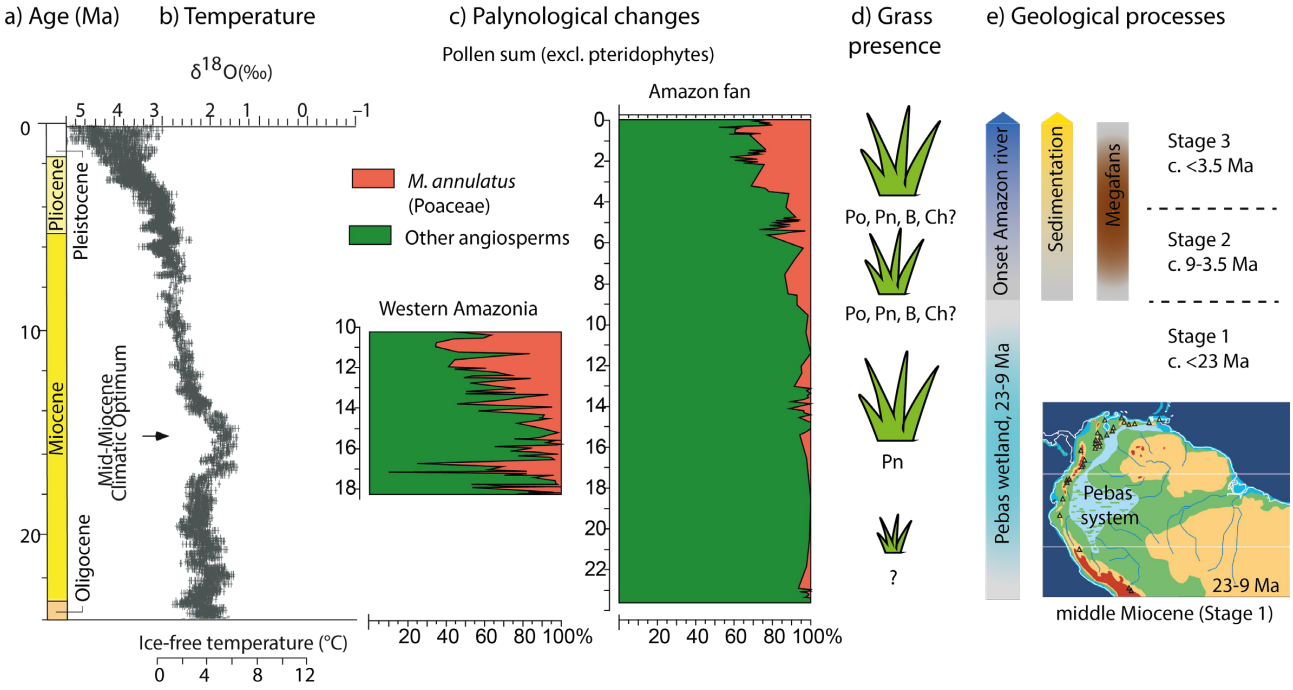

Figure 6. The grass history in the ADB from palynological records. a) **Age** in million years; b) **Temperature curve for the Neogene** (Zachos et al. 2008); c) **Palynological summary diagrams** represent the Miocene of western Amazonia (Jaramillo et al. 2017) and the Neogene to Quaternary record in the Amazon submarine fan (Hoorn et al. 2017). **Stage 1:** c. 23 to 9 Ma, the Amazon fan receives sediments from eastern Amazonia, with a low input of grass pollen; in western Amazonia an extensive wetland environment with (aquatic, Panicoideae?) grass dominance. At this time, the Central Andes Plateau has an elevation of c. 2 km (Garzione et al., 2017). **Stage 2**: c. 9 – 3.5 Ma: The Amazon River connects the Andes and Atlantic. Grasses were more abundant in the Amazon fan, possibly from the Andean slopes, megafans, and the Amazon River floodplain. Between 8 and 5 Ma both the Eastern Cordillera (Colombia) and the Central Andes Plateau were c. 4 km high (Anderson et al., 2015; Garzione et al., 2017) and accommodated high Andean forest, and from c. 5 Ma open vegetation. **Stage 3:** Sediment and grass pollen increase from 3.5 Ma and especially from 2.5 Ma. The likely source is the high Andes, with its extended páramo during the glacials (Flantua and Hooghiemstra 2018, Flantua et al. 2019), but also the megafans and lowland floodplains. The Andes was close to its present height. d) **Grass presence and diversity** becomes increasingly enriched as a result of biome development in the highlands and lowlands of the Neotropics. Po: Pooideae, Pn: Panicoideae, B: Bambusoideae, Ch: Chloridoideae. e) **Geological processes:** bars represent the environments through time. Pebas wetland by Hoorn et al. (2010), onset of megafans by Parra et al. (2009), Roddaz et al. (2010), and onset of Amazon River and sediment discharge by Hoorn et al. (2017). The pictogram shows the extend of the Pebas system in western Amazonia before its transition from a wetland into a fluvial system (redrawn from Hoorn et al. 2010b).

sediment discharge into the sub-Andean foreland basins and western Amazonia (Latrubesse et al. 1997, Wilkinson et al. 2010). Several megafans have been identified along the eastern Andean Cordillera, and with their distinct avulsive behaviour they form a dynamic and dominant element in the landscape of the ADB (Wilkinson et al. 2010). Deep canyon incisions in the Central Andes are dated as 9 to 5 Ma (Schildgen et al. 2007) and coincide with increased sedimentation rates in the sub-Andean zone from 7.9 to 6 Ma (Uba et al. 2007). Further rapid incision in the Andes occurred around 4 to 3 Ma (Lease and Ehlers 2013).

We propose that megafan formation deeply modified the sub-Andean and western Amazonian landscapes, to the point that pioneering taxa, such as the grasses, would have had a competitive advantage. The taxa that we anticipate could have conquered these environments are Panicoideae, Bambusoideae, Chloridoideae, and perhaps also Pooideae.

Jorge et al. (2019) report abundant Poaceae in the late Miocene sediments of the Solimões Formation and relate these occurrences to fluvial and megafan/avulsive river environments. The Poaceae remain high in the late Pliocene to early Pleistocene fluvial sediments near Manaus (c. 3.6 to 1.9 Ma; D'Apolito et al. 2019). Altogether, this indicates that from late Miocene onwards the floodplains of the Amazon River provided new and unique habitats that favoured grass colonization. Finally, during the Pleistocene, glacial and interglacial stages respectively resulted in river incision and inundation of the floodplain areas (Irion and Kalliola 2010).

At present, the floodplains of the Amazon River are characterized by seasonally flooding (várzeas) with continuous deposition and erosion (Räsänen et al. 1987,

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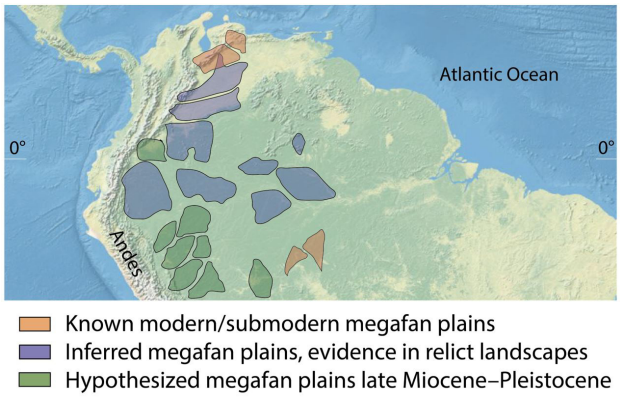

Figure 7. Modern, inferred, and hypothesized megafan plains of the Northern South America (adapted from Wilkinson et al. 2010). Megafans are a continental feature linked to large drainage networks adjacent to eroding mountain belts. Their triangular fan shape contains a high volume of unconfined fluvial sedimentary materials (Horton and Decelles 2001). In their distributary form, megafans form a strong contrast to the tributary systems characterizing the modern Amazon Basin (Cordeiro and Rossetti 2015). Megafans form on low-slope terrain with a highly migratory primary channel and floodplain areas (Horton and Decelles 2001).

Irion et al. 1997, Junk and Piedade 1997; Fig. 2). Like in the late Miocene, these environments typically trap pollen transported by river from the Andean highlands and from the overbanks in the fluvial system.

Origins of the páramo in the high Andes (c. 5 Ma)

The onset of the páramo, a grass steppe in the northern Andean highlands (2800 – 4200 m) is first reported by van der Hammen and Cleef (1986) and dated as late Pliocene to Pleistocene. This date was later corroborated by Bermúdez et al. (2015) in the Maracaibo basin (Venezuela), who reported grasses and typical páramo elements (e.g., *Valeriana*, *Huperzia*, among others) in sediments dated at 5 ± 2 Ma.

Recently, new evidence obtained from the Amazon submarine fan pushed the age for the Andean páramo further back to early Pliocene. The appearance of pollen grains of *Jamesonia* and *Huperzia* (c. 9 Ma), followed by *Valeriana* and *Polylepis-Acaena* (c. 5.4 Ma), are indicative of a high Andean vegetation that correspond with an elevational range of at least 3200 – 4000 m (Hoorn et al. 2017). Grimmer et al. (2018) suggested an even earlier onset of the páramo at c. 6 Ma, based on palynological data from the Ocean Drilling Program (ODP) Hole 1239A in the Ecuadorian Pacific. Nevertheless, their record does not show evidence for significant open vegetation, and grass pollen contribution remains low, making the interpretation of their source area difficult to interpret.

Wijninga (1996) first observed grass pollen in the Miocene sedimentary record of the Bogotá Basin (Fig. 1; e.g., Tequendama member, Tilata Formation; Eastern Cordillera, Colombian Andes). He found relatively low grass occurrences (10 – 20%) with one peak of 50% in the Miocene. Instead, records of the Pliocene Tilata, Subachoque and Sabana formations (Bogotá Basin) included grass percentages of 30 – 90% (Van der Hammen et al. 1973, Hooghiemstra 1984, Hooghiemstra and Ran 1994, but also see Torres et al. 2013 for an updated age model). Helmens (1990) further remarks on the effect of Pliocene tectonism on vegetation and refers to the erratic behaviour of herbs such as *Borreria*, which increase dramatically as a consequence of the roughness of the terrain.

The tropical lowland savanna (cerrado, 10 – 4 Ma)

The cerrado forms a vast savanna grassland extending over an area of around 2 million km^2 and is partially situated in the ADB (Fig. 1; Marquis 2002, Gottsberger and Silberbauer-Gottsberger 2006, Pinheiro and Monteiro 2010). The first grass taxa related to savannas are reported from the mid-Miocene (Jacobs et al. 1999, Strömberg 2011). This age is confirmed by phylogenetic evidence, which suggests that the cerrado biome formed under the influence of regular fire activity from a persisting closed-canopy ecosystem. The savanna lineages started to diversify as early as 10 Ma (Simon and Pennington 2012) and the cerrado ecosystem is thought to be fully formed around 4 Ma (Simon et al. 2009).

Quaternary palynological records and the 'forest refugia' theory

The 'forest refugia' theory formulated an explanation for the immense species diversity in Amazonia. As Haffer (1969) and Prance (1982) argued, forests fragmented and retracted during Quaternary glacial periods, giving space to grassland vegetation dominating the landscape, and building a reservoir for present-day's high diversity and endemism in plant and animal species. Haffer's (1969) hypothesis, however, wasn't based on basin-wide palynological records or climatic reconstructions, but on his observations of modern bird distributions. It claims rapid allopatric speciation originating as recently as the Pleistocene as a key mechanism applying for a wide range of forest taxa (Rocha and Kaefer 2019).

Some authors proposed that the palynological records confirmed the 'forest refugia' theory (e.g., Absy and Van der Hammen 1976, Absy et al. 1990). However, other researchers used palynology to confirm the stability of Amazonian rainforests in the Quaternary and found a lack of evidence for the replacement of a whole biome (Colinvaux et al. 2001, Bush and de Oliveira 2006, but see Hoorn 1997).

New research in palaeoclimatic modelling now indicates that tropical rainforests in Amazonia were stable over the long-term (Leite et al. 2016). This agrees with the fossil record, which suggests that the origin of modern Amazonian biodiversity is rooted deeply in the past and goes at least as far back as the Miocene (Hoorn et al. 2010a), or even beyond that (Maslin et al. 2005). Nevertheless, big knowledge gaps remain, and it is virtually unknown what happened in the tropical lowlands from late Miocene to late Pleistocene.

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Discussion: what is the driver of Neogene grass evolution in the Amazon drainage basin?

Landscape dynamics set the scene for grass expansion

In this section we bring previously presented lines of evidence together and evaluate our 3-stage model concerning origin and dispersion of grasses in the ADB.

Our first hypothesis (H1) assumed that the Pebas megawetland system, with its mosaic of shallow lakes, rivers, swamps, and floodplains, harboured abundant aquatic and floating meadow grasses throughout the Miocene (c. 23 – 9 Ma). The fluvial input into this system possibly assembled a proto-várzea (seasonally inundated floodplain) vegetation with e.g., Panicoideae, but possibly also included Poaceae taxa from the Andean slopes. A flood pulse, similar to that proposed for the modern large river-floodplain system (Junk et al. 1989), may have regulated freshwater input into the Pebas system (Kaandorp et al. 2005). Perennial grasses such as described by Junk (1997a) would have formed part of the plant community. Recent numerical models by Bicudo et al. (2019) provide a further basis for this scenario and explain the sedimentary basin development that accommodated such a wetland. These authors suggest that várzea gradually extended from the eastern Andean slopes into Amazonia, as the wetland development progressed.

The wetland gradually drained and made place for the fluvial landscapes of the incipient Amazon transcontinental river. This fluvial landscape is thought to have initiated in western Amazonia from c. 9 Ma and enabled colonization by a mix of grass-dominated and forest vegetation (Latrubesse et al. 2010). Similarly, the numerical models of Bicudo et al. (2019) propose a transition towards a mosaic of forest, floodplain grasslands and lakes. On account of this massive change in the geographic landscape, our second hypothesis (H2) suggests that during this period, extensive mountain uplift and megafan formation triggered high-energy fluvial environments (9 to 3.5 Ma), opening up large open spaces in the Andean foothills and slopes where grasses were important pioneer species. A study on the Chaco megafan showed that the vegetation still includes a mix of forest, savanna, and swampland vegetation (Iriondo 1993).

Finally, (H3) proposes that from 3.5 Ma, a combination of landscape dynamics and climatic change created more open surfaces that favoured the pioneering grasses. In the Andes, climatic fluctuations led to an extended Pleistocene páramo (Flantua and Hooghiemstra, 2018; Flantua et al. 2019), which also must have favoured increases in grass coverage. Meanwhile, in the Amazon lowlands Quaternary climatic fluctuations led to alternatingly dryer and wetter conditions, represented respectively by deep fluvial incision and high sediment discharge (Irion and Kalliola 2010).

Biogeographical context

Linder et al. (2017) stated that '*the success of grasses is best understood in context of their capacity to colonise, persist, and transform environments*'. By placing the onset of Poaceae in the biogeographical context of the ADB, we propose that landscape changes in the Andes and in Amazonia were provoking the expansion of grasses in the ADB.

As explained above, the late Miocene landscape in the ADB was highly dynamic, with increased sedimentation rates, alluvial megafans, canyons, and incisions. Strong fluvial dynamics influenced the swampy wetland that gradually drained after 9 Ma (Hoorn et al. 2017). Furthermore, lateral erosion and meandering rivers actively created floodplains in the landscape (Salo et al. 1986). It is thus thinkable that grasses, acting as pioneers and exceptionally suited for colonizing new environments, were successful here. A larger share of grasses probably colonised the tectonically active slopes and megafans in the Andean forelands (H2).

In the European Alps, a landscape with a large fan-shaped alluvial system has been identified and is presumably similar to the one in the ADB. Here, large megafans were identified that formed during glacial–interglacial cycles and are of great importance for catchment-to-basin delivery and detention of sediments (Fontana et al. 2014). Assuming that similar processes occurred in the ADB, we propose megafans were a central and important element of landscape dynamics. Eroded canyon flanks resulting from increased sediment transport provided ideal habitats for fast colonizers. Fluvial megafan systems also contained permanently vegetated islands (Horton and Decelles 2001). Regarding previously described late Miocene landscape dynamics, it is quite likely that grasses were successfully spreading. Megafan environments and mosaic landscapes probably harboured a mix of grass-dominated vegetation and gallery forests with a wet-dry seasonal climate (Junk 1997b, Latrubesse et al. 2010).

Rossetti et al. (2014) suggest that megafan development and accompanying sedimentary dynamics are of great importance regarding vegetational developments in northern Amazonia. Inside late Quaternary megafans, almost half of the surface might have consisted of *grass campinarana*, a vegetation type that occurs in wetlands characterized mainly by Poaceae, and that is related to slow vegetational succession processes (Martins and Mattes 1978, Cordeiro and Rossetti 2015). Outside of the megafan, grasses and shrub landscapes can easily make up 13% of vegetation. According to Navarro et al. (2010), Poaceae are one of the dominant taxa on alluvial fans of dynamic Quaternary wetlands. Poaceae were likely key elements of primary vegetational succession.

Another habitat where grasses could have occurred, and diversified, is the ground vegetation layer under closed forest canopies (Linder et al. 2017). Here grasses are more protected from wind and for that reason partly insect-dominated (Soderstrom and Calderon 1971). This implies that these forest grasses only contributed minor amounts of pollen to the Amazon submarine fan. Other forest taxa did not increase in the Amazon fan record, which suggests that forests were a less dynamic biome. Macrofossil evidence

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from the late Pliocene of south-western Amazonia confirms this scenario as grass pollen previously attributed to open grasslands is now interpreted as having originated in closed-canopy, wetter bamboo forests (Olivier et al. 2009).

Global climate as indirect driver of vegetation dynamics

The growth of the Antarctic continental ice sheet was initiated in the Oligocene, persisted throughout the Miocene, and was only interrupted by the mid-Miocene climatic optimum (c. 17–15 Ma; Zachos et al. 2001;Fig. 6). Around 15 Ma, coinciding with the increase of the (aquatic?) grasses in western Amazonia, a global shift in oxygen isotope records of benthic foraminifers indicates the end of the global warm climate period, with rapid deep water cooling and expanding of the East Antarctic Ice Sheet (Pagani et al. 1999a). With the continued global cooling and ice sheet expansion about 14 Ma, CO_2 levels increased, reaching pre-industrial levels around 10 Ma (Pagani et al. 1999b). The whole of the late Miocene and the beginning of the Pliocene were characterized by the fall of global sea levels (Haq et al. 1988) and climatic variability, including pronounced seasonality and fluctuation of the monsoonal climate in Amazonia (Uba et al. 2007).

As some of the climatic changes are connected to geographical rearrangements on the continent, we suggest that the climate indirectly played a major role during the evolution of grasses. With the progressive rise of the Andes, moist air masses started to rain out at the eastern flanks of the Andes and discharged in highly migratory water channels. Records of fossil freshwater bivalves indicate that seasonal precipitation patterns controlled by the Inter Tropical Convergence Zone (ITCZ) existed since the Middle Miocene Climate Optimum (c. 16 Ma) in western Amazonia (Kaandorp et al. 2005).

The long-term climate cooling trend from 13 Ma to present is reflected in the sedimentary composition at the Ceara Rise, a sea mount near the mouth of the Amazon River (Fig. 1; Harris and Mix 2002). Arid climatic conditions are typically represented by the ratio of oxide minerals goethite and hematite, with high values being indicative of high precipitation levels. Harris and Mix (2002) showed that up to 8 Ma (except for the interval 12 to 10 Ma) precipitation rates were relatively high, followed by a shift to drier conditions from 8 Ma. The transition from Neogene to Quaternary coincided with the rise of Poaceae pollen, as observed in the Amazon submarine fan record (Hoorn et al. 2017), and also with a general increase in terrigenous Andean sediment (Lammertsma et al. 2018; Mason et al., 2019). The further decline in the ratio of oxide minerals from 4.5 Ma, indicative of aridification, is paralleled by a rise in Poaceae and the introduction of high Andean taxa.

Although grass pollen percentages fluctuated across the basin and their taxonomic composition remains unresolved, it is clear that by 4 Ma, grassland biomes occurred from the high Andes to the lowland savannas. Notably, between 2.6 and 0.8 Ma, grass pollen percentages seem to have reached even higher levels than in post-glacial times (Hoorn et al. 2017). Although this points towards larger grass occurrences than at present, it is, as yet, not possible to be sure of their provenance. Finally, in the last 50,000 years the Poaceae pollen representation has remained low, whereas high Andean taxa are relatively abundant (Haberle and Maslin 1999).

The 'forest refugia' theory in a multimillion-year time perspective

After closer testing of palaeo-botanical records, the 'forest refugia' theory today is seen as falsified by a majority of scientists. According to Colinvaux and Oliveira (2000) the main reason for how the theory had evolved into a paradigm was incorrect interpretation of pollen diagrams with varying portions of taxa indicating landscapes and climate. The authors suggest that previously analysed shares of grass pollen were not high enough to justify the presence of savanna grasslands. Furthermore, it is argued that the Amazon lowlands were continuously forested since beginning of the Pleistocene (e.g., Colinvaux et al. 2001, Leite et al. 2016).

The existence of grasslands in Pleistocene Amazonia was strongly refuted. However, in the light of this review, it is worth noting that both parties in the 'forest refugia' debate ignored the possibility that grasses were abundantly present at an earlier time, and already formed an important component of the vegetation in the ADB. Their perspective was biased towards the time period of their studies and the meaning of grasses in older records was ignored. While overly focusing on climate, the debate side-lined landscape developments, biogeographical and successional dynamics in the ADB, which are closely linked with evolving vegetation.

Although the theory is seen as disproved today, in a multimillion-year time perspective, the grasses clearly played an important role in large parts of western Amazonia during both the Neogene and the Quaternary. To fully understand their history it is therefore crucial to further assess the fossil record and place vegetation changes in the perspective of geographic changes during the late Neogene, ranging from accelerated Andean uplift, megafan development, and the formation of the Amazon River and its extensive floodplains.

It seems clear that rainforest in the Quaternary didn't withdraw giving space to grasslands. However, the sheer size of the ADB harbours a wide range of environments, and taxa of the whole basin get fluvially transported towards the Amazon submarine fan. The above-presented lines of evidence strongly support our hypothesis of landscape changes provoking the Miocene expansion of grasslands in the western ADB with Poaceae as important components of primary vegetation succession. Further palynological studies will help to determine the botanical affinity of these grasses in greater detail.

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Conclusion

In this paper we addressed the question whether landscape dynamics and/or climate change could be the driving force behind increasing shares of Poaceae in the ADB during the Neogene. We used fossil records to reconstruct the latest Oligocene to Pleistocene palaeovegetation, geography, and climate in Amazonia and show that in this time span grasses were able to occupy a broad range of environments within the palaeo-landscape.

The onset of extended Poaceae occurrence in the ADB seems to occur earlier than elsewhere on the globe, and their development is thought to be connected to Andean uplift and the formation of the Pebas megawetland system (c. 23 to 9 Ma). We expect that Poaceae in this environment relate to the modern aquatic Panicoideae that occur at present in the temporarily flooded areas of the basin. Furthermore, the highly dynamic landscapes related to the rising Andes likely provoked the success of grasses. Best supported by literature, and hence most plausible, is that landscape dynamics were the main factor contributing to the grass evolution in the ADB. Between 9 to 4 Ma, the colonization of the dynamic Andean highlands, incipient forelands, and Amazon River floodplain, as well as the establishing Brazilian cerrado, all contributed to the fossil palynological records.

Grass evolution in the ADB, however, should also be seen in context with the long-term climatic cooling trend that initiated in the late Miocene and culminated in the Quaternary. Together, landscape changes, sea level fall, and changing base level of the Amazon River all were responsible for creating the scenario in which grasses could thrive.

We advocate for more palynological studies in the ADB to investigate the exact nature, origin, and age of the Poaceae pollen in terrestrial and marine records. Such data will contribute to our understanding of the development of grass-dominated vegetation in the ADB. In addition, we need to resolve how accurately the amounts of grass pollen in palynological records reflect prevailing biomes. Even more important will be to determine fossil grass pollen at subfamily and tribe levels. Different methods have been recently suggested but remain to be successfully applied to long-term palynological records. New palynological studies across the basin will reveal further aspects about the onset of grasses in the ADB.

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Conflict of interest

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Supplementary Materials

The following materials are available as part of the online article from https://escholarship.org/uc/item/3r85x2b8#supplemental

Supplementary Table S1. Occurrence of grass subfamilies along the elevational gradient.

Supplementary Table S2. Pollen diagram Amazon submarine fan.

Supplementary Table S3. Pollen diagram western Amazonia.

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