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The Cerrado and restinga pathways: two ancient biotic corridors in the neotropics

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Abstract

The two major rainforests of the neotropics, the Amazon and Atlantic forests, show maximum expansion during the warm and wet conditions of interglacial periods, including the current Holocene. They are connected by a network of gallery forests through the Cerrado biome. However, the extent of their expansion during glacial periods, when they were more disjunct, is unknown. During glacial periods, a pollen assemblage comprising *Podocarpus–Ilex–Hedyosmum–Myrsine* displays higher frequencies in marine, continental and coastal Brazilian pollen records. This assemblage is observed today in the high-elevation grasslands of the Cerrado and Atlantic Forest biomes and in the coastal vegetation, the restinga, of southern Brazil. We therefore reviewed the possible migration routes for these species by tracking glacial period *Podocarpus–Ilex–Hedyosmum–Myrsine* assemblages in published pollen records. The marine pollen records provide evidence of a glacial expansion of restinga, its floristic composition being continuous with the dominant regional vegetation, a cold type of shrubby grassland. There appear to be two migration routes, one involving the expansion of high-elevation grassland taxa within the lowlands, and the other low-sea level stands of coastal restinga. We conclude that the Cerrado was a node of migration between the Amazon and Atlantic rainforests, linking the Andes to the central and coastal mountains of Brazil. The Brazilian mountain ranges represent refugia of ancient taxa that colonized the continent up to the Andes and modified the floristic composition of the two rainforests during the Pleistocene glacial periods.

Highlights

- Past connections between the two main South American rainforests, the Amazon and the Atlantic forests, were explored using published pollen records and botanical surveys.

- The pollen assemblage *Podocarpus–Ilex–Hedyosmum–Myrsine* is observed today in the Brazilian high-elevation grassland physiognomy of the Cerrado and Atlantic Forest biomes, and the southern Brazil coastal forests (restinga) and Andean Forest, where it is associated with cooler climatic conditions.

- *Podocarpus–Ilex–Hedyosmum–Myrsine* is present in marine, continental and coastal pollen records from glacial periods.

- The simultaneous increase in *Podocarpus–Ilex–Hedyosmum–Myrsine* in late-glacial continental and marine pollen records suggests a shift of high-elevation grassland taxa to the lowlands with a broad expansion through the Cerrado and restinga pathways.

- The Cerrado and restinga represent ancient biotic corridors that have linked the Atlantic, Amazon and Andean forests since the early Pleistocene.

Introduction

Understanding the temporal dynamics of floristic connections between neotropical biomes helps prioritize areas for long-term and sustainable biological conservation. The South American tropics host the world's most diverse forests across a vast area, ranging from the subtropics to the equator in both the southern and northern hemispheres (Rull 2011, Raven et al. 2020). A model based on large-scale time-calibrated phylogenies suggests that, over the last 5 Ma, angiosperm dispersal rates have substantially increased interchanges between the Amazon Forest (AmF), Atlantic Forest (AtF) and Cerrado biomes (Antonelli et al. 2018). The Quaternary (the last

2.58 Ma) is characterized by the expansion and retreat of continental ice sheets, related to Milankovitch cycles (Gibbard et al. 2010), and associated with drastic changes in species diversification and biotic connections (Hewitt 2000, Jaramillo and Cárdenas 2013). In the neotropics, molecular and niche models indicate two main routes of biotic migration between the AmF and AtF biomes, one southeast–northwest (SE–NW) and the other northeast (NE) (Ledo and Colli 2017), while another study highlights the importance of the central Cerrado in evolutionary scenarios (Costa 2003) (Fig. 1). More recently a phylogeographic approach to studying mammalian migration routes has shown that the eastern route between northeastern Brazil and northern AmF may have been used more frequently than other routes during the late Quaternary (Machado et al. 2021). It has also been speculated that connections along the northern coast and through the dry vegetation diagonal (upland Cerrado–Caatinga–Chaco) were frequent during the Pleistocene, and linked to climatic variability (Werneck et al. 2011, Batalha-Filho et al. 2013a, Ledo et al. 2020). This scenario, supported by paleoclimatic studies (Auler et al. 2004, Wang et al.

2004), infers expansion of gallery forest within the dry diagonal that bridged the two rainforests.

Projections of past rainforest distributions are usually modelled under two extreme climatic events, one during the glacial epoch, the last glacial maximum (LGM), 21 ka Before Present (BP), and one during the current interglacial, the mid-Holocene, 6 ka BP (e.g., Carnaval and Moritz 2008), and sometimes under the last interglacial, 120 ka BP (e.g., Werneck et al. 2012). During the LGM, models suggest that the AtF was restricted to refugia or historically stable areas (Carnaval et al. 2009), while today's climatic conditions (warm and wet) represent the most suitable conditions for tropical rainforest expansion. However, today, the rainforests are largely separated by the Cerrado biome, and are only connected by the gallery forest network. The extent of any expansion of these rainforests during glacial periods, when, as suggested by projections and pollen records, they were more disjunct (Ledru et al. 2016), is unknown. Nor do we understand how they were connected during cooler climates. Phylogeography suggests connection routes through the central Cerrado (Sobral-Souza et al 2015) and between the Andes and the Serra Geral do Goias (Werneck et al. 2012), a mountain range located in the Cerrado and reaching an elevation of 1230 m (Fig. 2). It would be useful to know the characteristics of the vegetation during the last glacial, and when the routes suggested by the niche model studies were operational.

In Brazil, phylogeographical studies agree on a displacement trend of montane taxa to lower altitudes during cooler time periods, indicated by southeastern coastal groups of amphibians (Amaro et al. 2012) and northeastern groups of birds (Araújo et al. 2022). If montane amphibians and birds shifted to lower latitudes, it can be assumed that mountain plant taxa would also have migrated to the lowlands.

Paleoecological data are too scarce to provide continuous spatial and time trajectories over such a vast area. Consequently, pollen analysts generally rely on key indicator taxa to reconstruct vegetation dynamics during the Quaternary. The conifer *Podocarpus* is considered to be good indicator taxon for tracing past migration corridors (Ledru et al. 2007). It is often associated with three other taxa, *Ilex*, *Hedyosmum* and *Myrsine*, which are common in the Andean Forest (Bogotá-A et al. 2016), the high-elevation grassland physiognomy of the Cerrado (Oliveira-Filho and Ratter 2002), the Brazilian mountains (Fig. 2) and the AtF (Scheer and Mocochinski 2016). Because of the paucity of long-term paleoecological data, different, sometimes contradictory, scenarios of past connections and forest refugia have been presented (Fig. 1). The first scenario mentioned in the literature suggests an expansion of the conifer into the Amazon lowlands during the last glacial period (H1 in Fig. 1), attributed to a downslope shift of the Andean Forest (Colinvaux et al. 1996). However, the Andean origin hypothesis has since been rejected because higher *Podocarpus* pollen frequencies are not synchronous with higher frequencies of other Andean taxa (*Alnus*, Ericaceae), and an eastern biotic route is now preferred (H2 in Fig.1) (Piacsek et al.
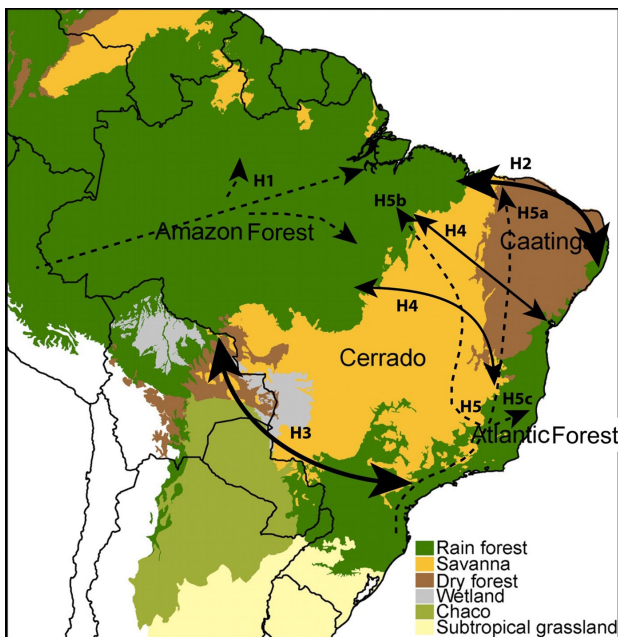

Figure 1. A map of the Brazilian biomes (from IBGE 2004) showing the hypothesized connection routes between the Atlantic and the Amazon Forest. H1 represents a migration route for Andean taxa through the Amazon basin (from Colinvaux et al. 1996); H2 a coastal northeastern route; H3 a southeastern–northwestern (SE–NW) bridge; H4 a route through the interior of the Caatinga (for H2, H3, H4 see Ledo and Colli 2017); H5 a route that starts in southern Brazil with three ramifications, H5a from southern–southeastern to northeastern Brazil, H5b from southeastern Brazil to southern AmF, and H5c coastal southern and southeastern up to 18°S (from Pinaya et al. 2021).

2021). To explain a late-glacial simultaneous expansion of *Podocarpus* in central and northeastern Brazil, another pollen-based reconstruction has discarded the hypothesis of a shift in the Andean Forest taxa to lower elevations and instead suggests a unidirectional central route connecting southern–southeastern Brazil and northeastern Brazil (H5a, b, c in Fig. 1) (Pinaya et al. 2019).

Today, the *Podocarpus–Ilex–Hedyosmum–Myrsine* assemblage is observed in only three locations, two in Brazil and one in the Andes. (1) In southern Brazil, the assemblage is found in upper montane grasslands with cooler temperatures, with a mean annual temperature (MAT) of 13.4°C, and higher precipitation levels (Scheer and Mocochinski 2016). However, *Hedyosmum brasiliense*, the only species of *Hedyosmum* in Brazil, is rarely observed except in the coastal forest of Paraná State[1]. It has never been recorded in the cerrado *sensu strico* botanical surveys (Ratter et al. 1996). (2) In the high-elevation grassland physiognomy of the Cerrado biome, the only location where the assemblage is found is the Serra do Espinhaço in central Brazil (Fig. 2), where it is assigned to rainforest and semideciduous forest, at a minimum elevation of 750 m asl (Oliveira-Filho and Machado 1993, Oliveira-Filho and Fontes 2000). In another montane range, Chapada Diamantina (Fig. 2), *Hedyosmum* is observed in shady and fire-protected environments such as at the foot of the montane, together with *Clethra scabra* Pers. and *Drimys brasiliensis* Miers (Couto et al. 2011). (3) The assemblage is a characteristic of the Andean Forest, at an elevation of between 2300 and 3200 m above sea level (asl), with a MAT ranging between 8 to 13°C and higher precipitation levels (Bogotá-A et al. 2016). *Podocarpus* grows between 1000 and 3200 m, *Hedyosmum* between 2500 and 3400 m, *Ilex* between 2600 and 3600 m, and *Myrsine* between 2400 and 3300 m (Bogotá-A et al. 2016). Based on these three localities, we assume that the *Podocarpus–Ilex–Hedyosmum–Myrsine* assemblage is a characteristic of cooler temperatures than found in the lowlands, with a MAT of ~13°C.

Modern pollen rain calibrations do not consider *Hedyosmum* as a key taxon for the AtF (Montade et al. 2019); when *Myrsine*, *Ilex* and *Podocarpus* are observed simultaneously in pollen spectra, they are assigned to *Araucaria* forest, along with *Araucaria* pollen grains and less than 10% Poaceae (Montade et al. 2019). One of the rare pollen calibrations for the upper montane grassland and forest does not report this assemblage, just *Myrsine* (Portes et al. 2020a) while, during the whole Holocene, *Hedyosmum*, *Ilex* (single grains) and *Myrsine* (less than 10%), with no *Podocarpus*, are clearly present in the pollen record (Portes et al. 2020b). Pollen rain calibrations for the Cerrado report 10% *Hedyosmum* in the gallery forest physiognomy (Cassino and Ledru 2021), in agreement with botanical surveys (Oliveira-Filho and Ratter 1995).
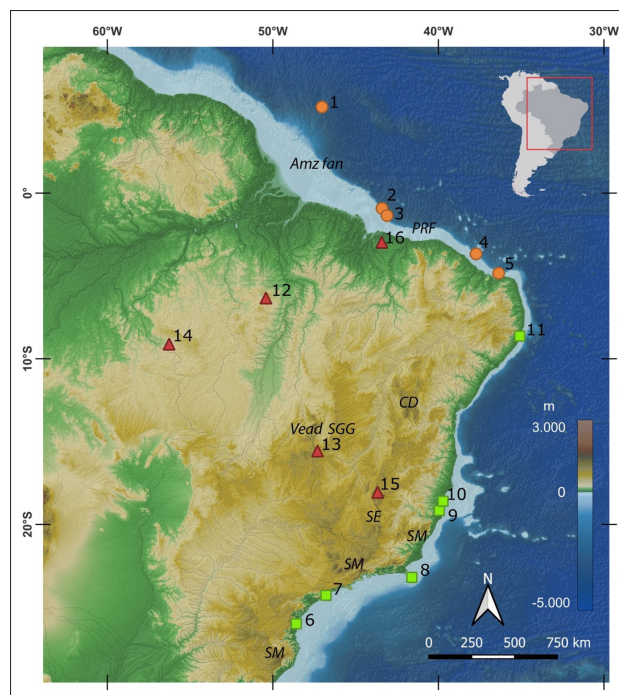
Figure 2. A topographic map of Brazil[2] showing the location of the records discussed in the text. (refer to Table 1 for the sites indicated by orange circles, to Table 2 for sites indicated by red triangles, and to Table 3 for the sites indicated by green squares). Amz fan, Amazon fan; PRF, Parnaíba River fan; Vead, the Veadeiros mountain range; SGG, the Serra Geral do Goias or Goias mountain range; CD, the Chapada do Diamantina or Diamantina mountain range; SE, the Serra do Espinhaço or Epinhaço mountain range; SM, the Serra do Mar mountain range along the coast between central and southern Brazil.

The 1.5 Ma pollen record of Colônia, located in the Serra do Mar near the city of São Paulo, covers several glacial–interglacial cycles, and the pollen assemblage *Podocarpus– Ilex–Hedyosmum–Myrsine* is well represented throughout the record, indicating an ancient presence of these cool-adapted taxa in southeastern Brazil (Rodríguez-Zorro et al. 2020, 2022). In addition, the last glacial marine pollen records located offshore in northeastern Brazil (NEB) have produced several scenarios that could explain the increase in cool-adapted pollen assemblages during glacial periods. For example, an increase in fluvial transport as a result of river input in the Amazon basin, or transport by the rivers running through NEB, from ~1000 m asl to the coast, could have led to the deposition of *Podocarpus*, *Hedyosmum*, *Ilex*, *Myrsine* and *Alnus* up to the northeastern continental shelf (Behling et al. 2000, Dupont et al. 2010, Bouimetarhan et al. 2018, Piacsek et al. 2021). In contrast, an expansion of *Podocarpus–Ilex–Myrsine* observed on the continent close to NEB marine records during the late glacial (Ledru et al. 2006) suggests another cause for the occurrence of a cool climate-

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Table 1. A summary of the pollen data from northeastern marine records. Site locations are indicated in Fig. 2.

Site number	Site	Last glacial pollen assemblage	Reference
1	Amazon fan, 5° 12'N, 47° 1.8'W	*Alnus* <1%, *Podocarpus* and *Hedyosmum* ~5%, *Ilex* single grains	Haberle and Maslin 1999
2	core GeoB 1248, 0°55.2'S, 43°24.1'W	Poaceae 20–30%, *Ilex* <1–4%, *Podocarpus* 2–7%, *Alchornea* 1–4%, *Hedyosmum* 1–11%, *Ilex* 1.5–4%, Ericaceae ~1%, *Myrsine* single grain –1.3%, Melast/Comb 2–5% *Alnus* <1– 8%	Piacsek et al. 2021
3	GeoB16205-4 1°21.110S, 43°05.800 W	Poaceae >20%, *Podocarpus <2%, Alchornea* ~5% *Hedyosmum* and *Ilex* (2–8%), no *Myrsine*, Melast/Comb 4–8%	Bouimetarhan et al. 2018
4	GeoB 3104-1, 3°40'S, 37°43'W	Poaceae >20%, no *Podocarpus, Alchornea* ≤5% *Hedyosmum* ≤5%, Melast/Comb ~5%	Behling et al. 2000
5	GeoB 3910-2, 4°15'S 36°21'W	Poaceae 15–20%, *Podocarpus* <1%, *Alchornea* (≤ 1%), *Hedyosmum* (2–3%), *Ilex* and *Myrsine* <1%	Dupont et al. 2010

Table 2. A summary of the pollen data for selected late glacial continental records from the Cerrado and Cerrado–AmF ecotones. Site locations are represented in Fig. 2.

Site number	Site	Late glacial pollen assemblage	Reference
12	Carajas 6°20'S, 5°25'W 600–800 m asl	*Poaceae* 40%, *Podocarpus* single grain, *Myrsine 11%, Ilex* and *Hedyosmum* <5%,	Absy et al. 1991, Hermanowski et al. 2012
13	Lake Feia 15°34'S, 47°18'W 900 m asl	Poaceae 53%, no *Podocarpus, Hedyosmum* 5%, *Ilex* 3%, *Myrsine* 1,7%, *Weinmannia* and *Drimys* single grain, Melastom/Comb 4%	Cassino et al. 2020
14	Lago do Saci 9°07'S, 56°16'W 185 m asl	Poaceae 30 – 52%, *Podocarpus* and *Ilex* 4%, Melastom/Comb 22%	Fontes et al. 2017
15	Pinheiro mire 18°3'44.42"S, 43°39'42.37"W 1240 m asl	*Podocarpus* <5%, *Ilex* single grain, *Myrsine* 2%, *Drimys* single grain, *Araucaria* single grain	Horák-Terra et al. 2020
16	Caço Lake 2°58'S, 43°25'W 120 m asl	Poaceae < 10%, *Podocarpus* 4 – 10%, *Ilex* 4%, *Myrsine* 4 – 10%, Melastom/Comb 10 – 20%	Ledru et al. 2001, 2006

related pollen assemblage across the neotropical lowlands.

The aim of this study is to characterize the Brazilian vegetation during glacial periods, with a focus on the *Podocarpus–Ilex–Hedyosmum–Myrsine* pollen assemblage. First, the marine, continental and coastal pollen records where this assemblage has been recorded are reviewed, then, based on the palynological results and published phylogeographical studies, hypothetical scenarios for connecting corridors in Brazil (Fig.1) are discussed. Finally, we present a new scenario relating low-sea level stands during glacial periods to the expansion of coastal vegetation or restinga, and the lowland expansion of what is today the high-elevation grassland physiognomy of the Cerrado biome.

Marine pollen records

Pollen data from marine sediment cores of the continental margins can be used to reconstruct past vegetation and climate changes. However, pollen grains can be transported from their sources over long distances by fluvial and atmospheric transport processes (Muller 1969, Hooghiemstra et al. 2006). Calibration between modern deep oceanic pollen spectra and estuarine and continental surface pollen spectra shows a good correspondence between estuary and oceanic samples, thus reflecting the regional vegetation of a continent (Sánchez Goñi et al. 2018). Fluvial transport of pollen and spores is especially high in humid tropical areas (Govin et al. 2014), favoring rich sediment and pollen deposition

along the continental margin. In South America, the Amazon River receives several tributaries, most of which originate in the Andes. Therefore, when conifer *Podocarpus* pollen grains are identified in marine sediments deposited within the Amazon fan (Fig. 2 site number 1), either expansion of the Andean Forest into the lowlands (Haberle and Maslin 1999), and/ or stronger precipitation driving an increase in the southward transport of the Amazon River plume and fluvial deposition (e.g., Bouimetarhan et al. 2018), can be inferred. A study of terrigenous fractions in marine cores located in the Amazon fan has divided the elements into two based on their Andean or lowland origin (Govin et al. 2014). In recent decades, marine cores retrieved from northern and northeastern Brazil continental shelves (Fig. 2) have been used to reconstruct paleohydrological changes in the tropics. East of the Amazon fan, core GeoB 1248 (0°55.2'S, 43°24.1'W) was located about 160 km from the modern coastline and 280 km from the Parnaíba River fan (Fig. 2 site number 2), and covers the last 130 kyr (Piacsek et al. 2021). The main basin in the area, the Parnaíba hydrographic basin, supplies the sediment and pollen. A glacial expansion of cold montane forest taxa (*Ilex*, *Podocarpus*, *Hedyosmum*, Ericaceae, *Myrsine*, *Weinmannia* and *Alnus*) (Table 1) was originally attributed to transport of the Andean Forest taxa into the lowlands via the Amazon River plume (Piacsek et al. 2021). However, as the taxa do not all vary synchronously, two different groups of pollen transport and deposition have been defined by Piacsek et al. (2021). An entomophilous taxa group, with *Ilex*, *Hedyosmum*, Ericaceae, *Myrsine* and *Weinmannia*, could have been transported from the Andes to the mouth of the Amazon River, while an anemophilous taxa group, including *Podocarpus* and *Alnus*, may be linked to long-distance wind transport, although there are differences between the two pollen taxa. *Alnus* is a common tree in the high Andes, and a high pollen producer, and can be dispersed over large distances by wind (Reese and Liu 2005). *Podocarpus* is also an Andean component that could follow the same transportation route as *Alnus*. However, high frequencies of *Podocarpus* are associated with (1) reduced iron (Fe)/potassium (K) ratios, an indicator of weaker fluvial transport, thus reducing the likelihood of fluvial transport, and (2) low *Alnus* frequencies, thus refuting wind transport from the Andes. In addition, when the frequency of *Podocarpus* is low (<3%) or absent, high Fe/K ratios are concomitantly observed. Thus, the authors inferred that *Podocarpus* was present at a closer location than the Andes, as a result of wind transport from northeastern montane forest refugia (Piacsek et al. 2021).

Another marine core, GeoB16205-4 (1°21.110S, 43°05.800W, ~1955-m water depth) was retrieved off the Parnaíba River fan (NEB) (Fig. 2 site number 3), and pollen analyses focused on the last cold episode of the Pleistocene, the Younger Dryas (Bouimetarhan et al. 2018). The observed increase in terrestrial discharge into the western equatorial Atlantic Ocean, together with the deposition of a pollen assemblage associated with the formation of a dense tropical forest characterized by *Alchornea*, Arecaceae, *Celtis*, *Hedyosmum*, *Ilex*, Melastomataceae and *Podocarpus*, could be related to wetter regional climatic conditions than Andean fluvial transport through the Amazon basin (Bouimetarhan et al., 2018), in agreement with Piacsek et al. (2021). To enable these repeated abrupt short-term developments of a "dense" forest, the authors inferred the existence of eastern corridors comprising forest mosaics that joined at different locations within the Caatinga biome (Bouimetarhan et al. 2018).

East of the Parnaíba River fan, the marine core GeoB 3104-1 (3°40'S, 37°43'W, 767-m water depth) was located 90 km east of the city of Fortaleza (Ceará State) on the upper continental slope (Behling et al. 2000, Jennerjahn et al. 2004) (Fig. 2 site number 4). The sea surface temperature (SST) showed a seasonal amplitude of ~ 2°C, and the shortest distance to today's coastline was 70 km (Fig 2). The main source for the fluvial input of terrigenous material, including pollen and spores, into the marine deposits was the Jaguaribe River, which is 610 km long and flows into the Atlantic Ocean about 80 km south of the core site. The Jaguaribe River originates in the Serra da Pedra Branca at 700 m asl, and in the Chapada do Araripe at 900 m asl (Castro et al. 2020). Today, four types of climate (humid, subhumid, semiarid and arid) (Gatto 1999) and eleven classes of vegetation are seen in the hydrographic basin of the Jaguaribe River, with moist forest and woody savanna (cerradão) observed at higher elevations in the Chapada do Araripe (Costa and Araújo 2007). Late-glacial pulses of moisture were characterized by an increase in terrigenous elements, abundant moss and ferns, and low frequencies of Melastomataceae/Combretaceae, *Alchornea* and *Hedyosmum* pollen taxa (Table 1) (Jennerjahn et al. 2004). Moist forest ferns and mosses were not observed during the Younger Dryas episode, and a drier climate was thus inferred.

Further to the east, GeoB 3910-2 was located at 4°15'S 36°21'W, at a depth of 2362 m, in front of the 447-km long Piranha River (also called the Açu River), the westernmost of three small rivers that reach the ocean between 38 and 36°W (Fig. 2 site number 5) (Dupont et al. 2010). The Piranha River originates in southeastern Paraíba State on the Borborema plateau, where the highest summit reaches 1197 m asl (Pico do Jabre) near the border with Ceará, and flows north–northeast through Paraíba and Rio Grande do Norte states to empty into the Atlantic Ocean near Macau (Dupont et al. 2010). During the late glacial, between 18 and 15 ka the pollen record associates the expansion of *Hedyosmum*, *Alchornea*, *Podocarpus*, *Myrsine* and *Ilex* (Table 1) and maximum titanium (Ti)/calcium (Ca) ratios with wetter conditions and stronger fluvial transport during the more humid period, between 16.5 and 15 ka. The Piranha River is located east of all the montane refugia, thus rejecting a SE–NW wind transport for *Podocarpus*, and the hypothesis of a *Podocarpus* growing among inland vegetation was preferred by the authors (Dupont et al. 2010). After

15 ka, the return of arid conditions was associated with the expansion of Poaceae and Cactaceae.

In summary, *Podocarpus* has been observed in three out of four NEB marine records (Table 1) for the last glacial. These records are not linked to Amazon fan sediment deposition, and SE–NW wind transport can be discounted for the easternmost pollen records, which are not located along this wind route, making the hypothesis of a local expansion of cool-adapted forest taxa more likely. However, *Podocarpus* is rare or absent in the two easternmost marine cores (Table 1), thus rejecting the hypothesis of a broad lowland expansion of *Podocarpus* in NEB during the last glacial period.

Continental pollen records

Since the 1980s, pollen grains of *Podocarpus* have been commonly used as an indicator for the Andean Forest (Liu and Colinvaux 1985, van der Hammen and Hooghiemstra 2000). Thus, when the presence of *Podocarpus* was observed in northern Amazonia during the last glacial, a cooler Amazon Forest with Andean elements was inferred (Colinvaux et al. 1996).

On the eastern edge of the Amazon basin (Fig. 2 site number 12), the late-glacial expansion of cool-adapted forest elements was characterized by *Podocarpus–Ilex–Hedyosmum–Myrsine* and Poaceae (Table 2), with no matching modern analog (Absy et al. 1991, Hermanowski et al. 2012). Similarly, in the AmF–Cerrado ecotone, the Lago do Saci pollen assemblages (Fig. 2 site number 14) suggest an open savanna, with cold elements represented by *Podocarpus*, *Ilex*, Melastomataceae and Poaceae (Fontes et al. 2017) (Table 2), pushing the hypothetical invasion of Andean taxa further east.

In the central region of Brazil, in the Cerrado, the Lagoa Feia pollen record (Fig. 2 site number 13) shows the late glacial expansion of *Hedyosmum*, *Ilex*, *Myrsine*, *Weinmannia*, *Drimys,* Poaceae and Melastomataceae (Cassino et al. 2020). Also, in the central region, at higher elevations in the Serra do Espinhaço, both *Podocarpus* and *Myrsine* are observed in the local vegetation today (Oliveira-Filho and Machado, 1993). The pollen record for Pinheiro mire (Fig. 2 site number 15) shows an expansion of a cool and moist forest during the late glacial, with *Drimys*, *Araucaria, Podocarpus, Ilex* and *Myrsine* present (Horák-Terra et al. 2020).

In western NEB, the Caço Lake pollen record (Fig. 2 site number 16) shows an expansion of cool and moist forest taxa during the late glacial, with *Podocarpus*, *Ilex*, *Myrsine*, Melastomataceae/Combretaceae and Poaceae present (Table 2) (Ledru et al. 2002, 2006).

On the basis of these results, two different scenarios are possible: on the one hand, Andean Forest taxa could have colonized the Brazilian central region from the west through the Amazon basin; on the other hand, the high-elevation shrubby grassland that grows on the top of the mountains in the Cerrado and AtF could have expanded into the lowlands (Oliveira-Filho and Fontes, 2000). Considering the evidence of high-elevation shrubby grasslands expansion and that the

expansion of *Podocarpus* in the Amazon basin can also be inferred from drier soil conditions, the Andean origin could be questioned (D'Apolito et al., 2017).

Coastal pollen records

During the Quaternary, significant changes in the geomorphology of the coastline and associated vegetation types from southern to northeastern Brazil occurred (e.g., Cohen et al., 2020). The formation of mangrove ecosystems was associated with an increase in fluvial activity as a result of sea-level fall in the late Holocene (Angulo et al. 2006) and the emergence of tidal flats and the expansion of terrestrial vegetation (Cohen et al. 2020). Numerous pollen records along the Brazilian coast testify to significant changes in coastal vegetation assemblages during the late Quaternary. We reviewed some of the more informative records along a latitudinal gradient from south to north (Table 3).

The Babitonga Bay pollen record, covering the last 2000 years (Santa Catarina State) (Fig. 2 site number 6), was retrieved from a mangrove tidal flat in an estuarine complex, and shows a progressive increase in *Podocarpus–Ilex–Hedyosmum–Myrsine* (Table 3) simultaneous with the development of the mangrove. These taxa are part of the ombrophilous forest (a type of rainforest in the AtF biome) observed today near the coring site (França et al. 2019, Azevedo et al. 2021). At ~25°S, *Podocarpus sellowii* grows in the current lowland rainforest behind the mangrove and is well represented in modern pollen rain (Montade et al. 2019).

Further north, a modern pollen rain study between the forest at the foot of the Serra do Mar mountain range and the mangrove of Itanhaem (São Paulo) (Fig. 2 site number 7) revealed the presence of *Podocarpus*, *Ilex*, *Myrsine*, *Weinmannia* and Ericaceae in samples collected within the mangrove/restinga belt, in agreement with phytosociological surveys (Amaral et al. 2006).

Further north, in the state of Rio de Janeiro, sediment core CF10-04B was collected from the continental shelf of Cabo Frio (Fig. 2 site number 8) (Table 3). The *Podocarpus–Ilex–Hedyosmum–Myrsine* assemblage was present during the last 6500 years, along with mangrove indicator taxa, suggesting that the forest occupied a narrow strip of the coastal region (Barreto et al. 2020). Latitude 22°S is the northernmost record of *Podocarpus* as a coastal forest tree[3].

On the northern coast of Espírito Santo State, the Nativo do Flamengo pollen record (Fig. 2 site number 9) represents a peat-covered wetland depression where *Myrsine rubra* M.F Freitas. & Kin.-Gouv. is a frequent species in the modern environment, growing up to the margins of the wetland. During the last 2000 years, mangrove has developed simultaneously with the expansion of *Myrsine*, *Ilex* and *Hedyosmum*, while *Ilex* (Table 3) was observed in sandy soils formed prior to the expansion of mangrove (Buso Junior et al. 2019).

[3] http://specieslink.net, last access 25/01/2023.

In the Doce River delta, the limits between mangrove, restinga and herbaceous vegetation are clear (França et al. 2013, 2016). Pollen analyses of five sediment cores collected between the mangrove tidal mudflat and the restinga (Fig. 2 site number 10) show that, over the last 7000 years, changes in vegetation cover have followed changes in relative sea level. At ~7000 yr BP, the pollen assemblage is characterized by *Hedyosmum*, *Rhizophora* and *Podocarpus*, whereas, during the last century, Ericaceae has expanded along with *Mimosa*, Melastomataceae, Moraceae/Urticaceae and *Hedyosmum* (Table 3).

In the Formoso River estuarine system in NEB (Fig. 2 site number 11), today's landscape comprises AtF, and includes perennial sandy strand–plain forest, mangroves and beach formations, with Myrtaceae as the most widely represented family (Martins et al. 2021). Studies of sediment cores link the expansion/retraction of herbaceous plain/forest with variations in sea level (Martins et al. 2021).

Before 7000 cal yr BP, the AtF was characterized by *Mimosa*, Anacardiaceae, Euphorbiaceae, Fabaceae, Ericaceae, Apocynaceae, Rubiaceae and Malpighiacaeae. Herbaceous taxa were mainly represented by Cyperaceae, Poaceae and Amaranthaceae. An increase in the AtF tree taxa *Mimosa*, Melastomataceae/Combretaceae, Arecaceae and Fabaceae was observed when the mangrove started to expand, although Cyperaceae and Poaceae remained predominant. During the last century, pollen assemblages have been characterized by tree and shrub taxa, including Ericaceae, Fabaceae, Malpighiacaeae,

Table 3. A summary of the pollen data from selected late Holocene coastal records, with their associated climatic information. Site locations are represented in Fig. 2.

Site number	Site	Pollen assemblage	Modern climate	Reference
6	Babitonga Bay 26°S 48°35'W	Poaceae 12–77%, *Podocarpus* 1–10%, *Hedyosmum* 2–11%, *Ilex* 1–7%, *Myrsine* 1–8%	MAP1 600– 1 900 mm MAT 18–20 °C Dry season May–Oct	França et al. 2019, Azevedo et al. 2021
7	Itanhaem 24°16'59"S, 46°47'20"W	Poaceae 15–25%, *Podocarpus* single grain–3%, *Alchornea* 7–10%, *Ilex* <1–5%, *Myrsine* <5%, *Weinmannia* 1–5% Ericaceae single grain, Melast/Comb 5–10%	MAP 2 000–2 500 mm MAT 20 °C Dry season July–August	Amaral et al. 2006
8	Cabo Frio 23.2°S, 41.6°W	Poaceae 5–25%, *Podocarpus* single grain –2%, *Ilex* and *Myrsine* <5%, *Hedyosmum* 1–10%, *Alchornea* 15–30%	MAP 600–700 mm MAT 23 °C	Barreto et al. 2020
9	Nativo do Flamengo 19°09'48.6"S, 39°56' 22.3"W	Poaceae 25–50%, *Myrsine* 3–20%, *Ilex* 5–10%, *Hedyosmum* 3%, Melast/ Comb 3–10%	MAP 1 215 mm MAT 23.3 °C, Dry season June– September	Buso Junior et al. 2019
10	Doce River Delta 18°36' to 19°05'S, 39°43' to 48'W	Poaceae >30%, *Alchornea* single grain, *Hedyosmum* < 5%, Ericaceae (0–4%), Melastom/Comb 1–2%,	MAP 1 400 mm MAT 20–26 °C Dry season April–Sept	França et al. 2013, 2016
11	Formoso river estuarine 08.63037S 35.07951W	Ericaceae 0–4%, Fabaceae 0–3.5%, Malpighiacaeae 1–3%, *Mimosa* 0–4%, Melastomataceae 1–2%, *Cecropia* 0–2%, Meliaceae <1%, Myrtaceae <1%).	MAP 20 00 mm MAT 25 ∘C Dry season Oct– Dec	Martins et al. 2021

Mimosa, Melastomataceae/Combretaceae, *Cecropia*, Meliaceae and Myrtaceae (Table 3).

Coastal pollen records suggest a close relationship between continental and coastal environments, with both transgressive and regressive marine events. They also show that the *Podocarpus–Ilex–Hedyosmum–Myrsine* assemblage is well represented, although at different frequencies as a function of latitude.

The restinga

The Brazilian coastal region is ~9000 km long and is divided into five main bioclimatic regions (Fig. 3): the AmF or equatorial coast (1); the northeastern coast from Maranhão to northern Bahia (2); the eastern coast from southern Bahia to Espírito Santo (3); the southeastern coast (Espírito Santo to São Paulo) (4); and the subtropical coast (Parana to Rio Grande do Sul) (5) (Lacerda et al. 1993). The restinga or coastal forest grows almost continuously along the 9000 km coast, on sandy, acidic and nutrient-poor soils usually associated with sand ridges created during marine transgressions and regressions. These sand ridges include beaches, dunes, sandy strands, depressions between cords, lake margins and mangroves (Araújo 1992, Lacerda et al. 1993), forming the dominant regional ecosystem. The floristic assemblages include many species from neighboring forests, including the AtF, Cerrado and AmF (Fig. 3).

For example, today the coastal regions of Ceará State and the Parnaíba River delta are dominated by restinga formations, with floristic elements of Cerrado and Caatinga (Santos-Filho et al. 2015, Serra et al. 2016). In addition, the floristic composition of NEB restinga differs from the southern (e.g., Santos et al. 2012, Korte et al. 2013), southeastern (e.g., Guedes et al. 2006, Pereira et al. 2001) and central-eastern (e.g., Pereira and Assis 2000, Assis et al. 2004) restinga, according to their associated regional climatic patterns and SST.

In southern Brazil (zone 5 in Fig. 3), mean annual SST ranges from 18°C in July to 26°C in January (Florianópolis, Santa Catarina[4]). Among the dominant genera forming the restinga are *Myrcia* (Myrtaceae), *Myrsine*, *Ilex* and, less frequently, *Hedyosmum brasiliense* and Ericaceae (*Gaylussacia brasiliensis*), with *Podocarpus sellowii* in the northern part of the Santa Catarina State at latitude 27°S[5] (Korte et al. 2013).

In the southeastern restinga (zone 4 in Fig. 3), the mean annual SST is 23.5°C, with a minimum of 17°C in July and a maximum of 24.5°C in February (Bertioga São Paulo[6]). Phytosociological surveys show the presence of *Ilex* (in both flooded and non-flooded restinga), *Hedyosmum* (in non-flooded restinga), *Podocarpus sellowii* (in the coastal forest that grows immediately behind the restinga) and *Myrsine* (in non-flooded restinga) (Guedes et al. 2006). Pollen analyses of surface sediment samples taken along a transect from
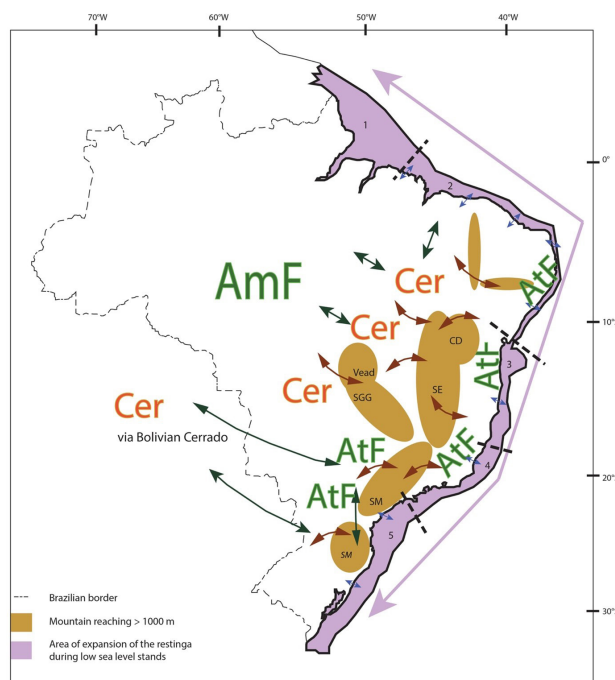
Figure 3. A graphic representation of glacial/interglacial corridors showing the restinga pathway along the coast (long purple arrow) and between the restinga and the continent (small blue arrows), and the Cerrado pathway from high-elevation grassland to the lowlands (red arrows) and across the lowlands (green arrows). AmF, Amazon Forest; AtF, Atlantic Forest; Cer, Cerrado. The LGM coastline reconstruction is based on Peltier (2004). Bold dashed lines and numbers refer to the five bioclimatic regions of the restinga described in the text. For the abbreviations used for the mountain ranges, see Fig. 2.

mangrove to restinga to lowland AtF on the coast of São Paulo have revealed the presence of *Podocarpus*, *Ilex*, *Myrsine and Hedyosmum* (Amaral et al. 2006). Today, *Podocarpus sellowii* is observed in the lowland forest behind the restinga, between latitudes ~27°S and 23°S[7], with SST ranging from 18°C to 22°C in winter and from 24.5°C to 27°C in summer. *Ilex*, *Myrsine*, *Hedyosmum*, *Podocarpus sellowii* and Ericaceae are also observed in the restinga of Rio de Janeiro (Araújo 1988, Souza et al. 2008), where the mean winter SST is 21.7°C, maximum summer SST 26.9°C and mean annual SST 24.9°C (Ubatuba Rio de Janeiro[1]). *Myrsine* and Ericaceae (*Agarista revoluta*) are observed in the restinga of Barra de Maricá Rio de Janeiro (Pereira et al. 2001). Another species of Ericaceae, *Gaylussacia brasiliensis*, has been observed in an open restinga at Setiba (Espírito Santo, mean SST 24.7°C) (zone 3 on Fig.3), although without *Ilex*, *Myrsine* and *Hedyosmum*. *Gaylussacia brasiliensis* is able to colonize several Brazilian biomes, from coastal to high-elevation fields, although it has only been identified to family level in pollen records.

To the north (zone 2 in Fig. 3), only one species of *Myrsine* (*Myrsine guianensis* (Aubl.) Kuntze, identified to genus level in the pollen record) has been observed in the restinga of Macaipe (Pernambuco), which has a mean annual SST ranging between 26.7°C and 28.7°C (Almeida Jr et al. 2011). Today, both Ericaceae (*Gaylussacia brasiliensis)* and *Myrsine guianensis* are observed in the restinga to the south (Rio Grande do Sul) and to the north (Rio Grande do Norte) (Zickel et al. 2007).

The most widely represented families in the restinga of the Barreirinhas formation, up to19 km inland in the state of Paraíba, are Fabaceae, Rubiaceae, Sapotaceae and Myrtaceae (Zickel et al. 2021). In the non-flooded restinga of Rio Grande do Norte, none of these has been observed, and Myrtaceae dominates (Almeida Jr and Zickel 2012).

In the northern coastal restinga (zone 2 on Fig.3), in the states of Maranhão and Piauí, the mean annual SST is stable at 28°C (minimum 27°C, maximum 29°C) (city of Parnaíba, Piauí[8]). The restinga is characterized by a mixture of AtF and AmF species, dominated by Fabaceae, Poaceae, Cyperaceae and Euphorbiaceae (Santos-Filho et al. 2010, 2015). These families have also been recorded in restinga in the states of Ceará, Rio Grande do Norte and Pernambuco (see references cited above). In addition, 85.2% of the species listed in Piauí State have been recorded in other coastal areas of NEB, while the remaining 14.8% are only recorded in the Piauí restinga (Santos-Filho et al. 2015). The difference in mean annual SST between the restinga of Bertioga (São Paulo) and Parnaíba (Piauí) is 4.5°C, with a seasonal amplitude of 7.5°C and 2°C, respectively (see references cited above).

During the last glacial, the mean SST in NEB was 3–5°C lower than today (Stute et al. 1995), and the lower sea level exposed a wide strip of land (Peltier 2004) that likely favored the expansion of restinga. The lower SST also allowed the expansion of *Podocarpus*, *Hedyosmum*, *Ilex*, *Myrsine* and Ericaceae, an assemblage commonly observed today at the latitude of São Paulo and in marine records located offshore in northwestern and eastern NEB (Fig. 2) dating to the last glacial (Piacsek et al. 2021), although *Podocarpus* has not been observed in the marine records for offshore Ceará State (Behling et al. 2000).

Discussion and Conclusions

The *Podocarpus–Ilex–Hedyosmum–Myrsine* pollen assemblage is observed today in different physiognomies of the Brazilian Cerrado and AtF biomes, either in the southern coastal forest or in high-elevation grasslands. During the late Holocene, the same assemblage is observed in coastal pollen records and during the last glacial in central and northern Brazil pollen records. The last downward shift of *Podocarpus–Ilex–Hedyosmum–Myrsine* from central Brazilian mountains occurred during the late-

[8] http://www.cptec.inpe.br, last access 25/01/2023.

glacial cooling (Cassino et al. 2020). The low sea levels that occurred during each glacial cycle (Lisiecki and Raymo, 2005) exposed a vast area of land that became covered with restinga, which was submerged again during the interglacials (Fig. 3).

The different scenarios

There are three main scenarios for past connections and pathways between the AmF and AtF (Fig. 1). Firstly, a west–east pathway has been attributed to Andean Forest expansion of *Podocarpus–Ilex–Hedyosmum–Myrsine* (ex *Rapanea*) into the lowlands during glacial periods (H1 in Fig. 1) (Colinvaux et al. 1996). Under this scenario, the western AmF extended eastwards and the northern AtF extended westwards along the northern coast of Brazil (Costa 2003). However, marine records show that other Andean pollen taxa, Ericaceae and *Alnus*, did not follow this assemblage, and that there were two distinct groups of taxa corresponding to different routes (Piacsek et al. 2021).

Secondly, a southern pathway could have enabled a connection between the AmF and southeastern AtF. During glacial periods, the dominance of a winter rainfall regime (Rodríguez-Zorro et al. 2020) favored the expansion of cool and moist forest taxa from the highlands into the lowlands of the central region of Brazil (H4, H5b in Fig. 1), and from the southern coast toward the southernmost part of AmF (H3 in Fig. 1) (Carnaval and Moritz 2008, Sobral-Souza et al. 2015, Werneck et al. 2012). During glacial periods, this trajectory favored the expansion of *Podocarpus–Ilex–Hedyosmum–Myrsine* from the Brazilian mountain tops into the lowlands, where they sheltered during the interglacials. This pathway is also called the "old pathway" (Batalha-Filho et al. 2013a), or SE–NW route (Ledo and Colli, 2017), although NW seems inappropriate as it discounts the presence of a southeastern AmF. A paleoecological record from southeastern Brazil shows that the downward shift of a cool-adapted forest (with *Araucaria*) enabled the expansion of an arid upper montane grassland (with *Acaena* and *Ephedra*) at higher elevations during the early Pleistocene (Rodríguez-Zorro et al. 2022).

Thirdly, the coastal pathway scenario, first considered by Por (1992), enables a connection between the AmF and AtF in the northern coastal region (H2 in Fig. 1); this was later called the "young pathway" and acknowledged to have functioned in the late Quaternary (Batalha-Filho et al. 2013a, Machado et al. 2021). Ecological niche modeling using thirteen woody species showed that NEB forested areas were restricted to the coast during the last interglacial (Silveira et al. 2019).

During the late glacial, *Podocarpus–Ilex–Hedyosmum–Myrsine* expanded from central Brazil up to northern Maranhão (Table 2), thus calling the first scenario into question. Given the limitations of the first scenario, NEB marine records have been used to infer either an eastern pathway (Bouimetarhan et al. 2018) or a new atmospheric pathway from the montane summits (~1000 m asl) of NEB (Piacsek et al. 2021). However, phylogeographical studies show that high-

elevation formations (*brejos de altitude* in Portuguese) in NEB were not connected during the Pleistocene (Batalha-Filho et al. 2013, Dantas et al. 2015). In addition, only one montane refugium today hosts *Podocarpus* in the northernmost part of NEB (Baturité, Ceará State), and phylogeographical studies have failed to reveal any connecting routes from this single refugium (Silveira et al. 2019) or ancient connections with eastern (restinga and/or AtF) rather than western (AmF) Brazil (Andrade et al. 2007, 2009). Both marine and terrestrial pollen records show high *Podocarpus* frequencies (Tables 1 and 2), suggesting that the sources were not located far from the sediment core (Ledru et al. 2006, Montade et al. 2019).

None of the three above scenarios can fully explain the northeastern pathway, nor the potential for southern restinga tree taxa to migrate to northern coastal regions along a coastal pathway. Indeed, the expansion of the cool-adapted assemblage *Podocarpus–Ilex–Hedyosmum–Myrsine* is favored by the plasticity of the restinga and its ability to include taxa belonging to neighboring vegetation types. Thus, we infer that during the glacials, when *Podocarpus–Ilex–Hedyosmum–Myrsine* assemblages expanded from the mountain summits toward central Cerrado, they were also connected to the restinga as observed today in southern Brazil (Fig. 3). Finally, our review shows that there were two routes for movement of the cold-adapted taxa assemblage, one along the coast between the southern and northern coastal regions, restricted by sea-level variations but profiting from the liberation of new strips of land, and another between the highlands and lowlands across the continent and reaching the coast of Brazil (Fig. 3).

The restinga pathway

Today, the coastal region of NEB and the Parnaíba River delta are covered by narrow restinga with sandy soils and open herbaceous, shrubby and arboreal plant formations (zone 2 in Fig. 3) (Silva and Britez 2005, Santos-Filho et al. 2010, 2015, Serra et al. 2016), with a mean annual SST of 28°C and a seasonal amplitude of 2°C (27°C to 29°C) (Parnaíba, Piauí[9]). Modern coastal pollen rain studies and phytosociological surveys of southeastern Brazil, between latitudes 27°S and 22°S (zones 5 and 4 in Fig. 3), show the presence of *Podocarpus*, *Ilex*, *Myrsine*, *Weinmannia*, Ericaceae and sometimes *Drimys*, with a mean SST of 23.5°C, minimum of 17°C (July) and maximum of 24.5°C (February) (see above). These assemblages are similar to those attributed to montane taxa in the marine pollen records of the last glacial period (Table 1).

Model reconstruction of LGM SST shows a cooling of between 1.0°C and 2.4°C in the tropics (15°S–15°N) (Otto-Bliesner et al. 2009, Paul et al. 2021) and a seasonal difference in the SST in the western tropical Atlantic (west of 10°W and north of 20°S) up to 3.9°C higher than it is today (Niebler et al. 2003). In present-

day NEB, the seasonal SST amplitude is ~3°C, with the warmest SST (27.6 ± 0.3°C) occurring in austral summer and the coldest (24.3 ± 0.1°C) in austral winter (Locarnini et al. 2013). Reconstruction of SST in NEB for the past 322 kyr shows 23.8°C to be the coldest recorded $SST_{Mg/Ca}$ (Hou et al. 2020), which is similar to present-day SST between latitudes 27°S and 22°S in southeastern Brazil.

We infer that, during the glacial periods, the cool-adapted taxa assemblage that grows in the restinga in southeastern Brazil today expanded to lower latitudes via a coastal route during low-sea level stands (Fig. 3). Moreover, the restinga included taxa from the closest neighboring biome (Buso Junior et al. 2019), which means that, for NEB, there is no modern analog for the cool-adapted forest formation that was distributed across the Cerrado biome, from central to northern Brazil, during glacial periods. From the late-glacial until the early Holocene, SST reconstructions reveal a progressive increase of ~3.2 ± 1.1°C (Wilson et al. 2011), likely associated with the progressive retreat of the cool-adapted taxa to their present-day distribution in the high-elevation habitats of central Brazil, montane ranges in NEB and southern coastal regions (Fig. 3). The existence of a drier and saline microregion in the northern coastal region of NEB, between Foz of Parnaíba (Piauí State) (2.9096°S, 41.7537°W) and Jaguaribe (Ceará State) up to Guamaré in the Rio Grande do Norte State (5.1076°S, 36.3197°W), where, in some areas, the Caatinga reaches the ocean today, could have prevented the expansion of a moist forest and the coastal dispersion of the cool-adapted taxa (*Podocarpus* is not observed in the marine pollen records from this area), thus blocking the eastern route of migration. In addition, the phylogeography of *Podocarpus* and *Anthurium* indicates that the population of Baturité (Ceará State) is genetically isolated from nearby populations in NEB, and, for Araceae, populations of Baturité appear to be closer to southeast Brazilian populations (Andrade et al. 2009, Dantas et al. 2015), thus reinforcing the hypothesis of an ancient eastern route across the continent for northern NEB.

The importance of the Cerrado pathway

Our study shows that, rather than a direct connection that would assemble the AtF and AmF, both low glacial sea levels and spatial displacement of specific suitable climatic conditions favored the expansion of a cool-adapted restinga and the formation of ecological corridors between highly biodiverse rainforests. However, if this scenario explains the discrepancies observed between NEB marine and terrestrial records, it does not correspond with the SE–NW route of migration, or old pathway (Batalha-Filho et al. 2013a). Indeed, Brazilian montane ranges, sometimes called "Brazilian cordilleras", are older than those in the Andes (Ab'Sáber 2000) and could have been an alternative source, rather than the austral–Antarctic source identified for the Páramos (Sklenár et al. 2011), of numerous species that later expanded and diverged during the progressive uplift

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[9] http://www.cptec.inpe.br, last access 25/01/2023.

of the Andes (Antonelli et al. 2009) through Cerrado pathways to the south and north of the Amazon basin (Simon et al. 2009). The eastern Brazilian mountains have been designated the origin of some Andean birds (Chaves et al. 2015), and two central Brazil mountain ranges, Serra do Espinhaço and Chapada dos Veadeiros (Fig. 2), qualify as hotspots of evolutionary diversity (Fenker et al. 2020). During the Pleistocene glacial intervals, the high-elevation grassland physiognomy of the Cerrado biome was more widespread than today, when only the core region is expanding north (Maranhão State), with some enclaves seen in NEB (southern Ceará State) and northern and southern AmF (Fig. 4) (Ackerly et al. 1989, Ritter et al. 2010, Oliveira-Filho and Carvalho 1993, Sarmento and Soares 1971).

During drier and cooler climatic conditions, pollen records from the AmF show the westward expansion of the high-elevation grassland taxa of the Cerrado biome (Absy et al. 1991, Fontes et al. 2017), along with changes in central Cerrado floristic composition (Horák-Terra et al. 2020), highlighting the importance of the Cerrado in building bridges between the Brazilian rainforests. The southern AmF and Cerrado, in the Beni province of Bolivia, reach the foothill of the Andes, and likely represent an ancient expansion of the biome (Fig. 4). Divergence times between Bolivian and Brazilian Cerrado lineages show connections dating back to the Pliocene (Batalha-Filho et al. 2013b), thus also suggesting a Cerrado origin for the Andean Forest taxa (Cabanne et al. 2019). In addition, the floristic composition of the Cerrado today reflects numerous exchanges with the different biomes that have been molecularly dated to 4–5 Ma (Simon et al. 2009; Collevatti et al. 2015). The high-elevation grassland formations (*campos rupestre* in Portuguese) have also been molecularly dated to these time periods (e.g., Inglis and Cavalcanti 2018), suggesting an ancient past expansion of cool-adapted taxa in tropical South America, hence assigning high-

elevation grasslands to a biogeographical island system (Flantua et al. 2019) during interglacials. Interestingly, the phylogeographical history of the Cerrado tree species *Tabebuia aurea*, with an ancient lineage dated to 4 Ma and a west to east dispersal route, suggests a continuous migration route during the Andean uplift. The most ancient lineages of several plant species that today grow in the high-elevation grasslands of the Cerrado, e.g., *Chamaecrysta coriacea* (Rando et al. 2016), *Calliandra* (Souza et al. 2013), *Paepalanthus* (Trovó et al. 2013), *Minaria* (Ribeiro et al. 2014), *Hoffmannseggella* (Antonelli et al. 2010) and *Diplusodon* (Inglis and Cavalcanti 2018), have all been molecularly dated to 5 Ma.

Hence, the Cerrado enclaves that are located outside the core region of central Brazil today (Fig. 4) could all have been connected in past glacial periods, when rainforest distribution was reduced. Some of them likely reconnected during regression of the rainforests, as did the Bolivian Cerrado, thus reopening the corridor connecting the southeastern AtF and southern AmF (Mayle et al. 2000). This southern pathway (also called the South American dry vegetation diagonal, e.g., Mogni et al. 2015) connected the Andean foothills to southeastern AtF (Antonelli et al. 2009), as evidenced in the pollen record of Colônia by the presence of Cerrado taxa (*Caryocar* and *Mauritia*) in southeastern Brazil dating back to the early Pleistocene (Rodríguez-Zorro et al. 2022), and the presence of a Cerrado-like vegetation with cold-adapted taxa in eastern Bolivia during the Pleistocene (Mayle et al. 2000). Moreover, Amazon fan pollen records dating back to the late Miocene show that the simultaneous expansion of grasses and tropical mountain taxa (*Podocarpus–Ilex–Hedyosmum–Myrsine*) transported by the Amazon River and its tributaries started in the late Miocene and continued into the Pleistocene (Hoorn et al. 2017, Kern et al. 2022) which is in full agreement with our study.

Implications for conservation

The complexity of the impact of climate dynamics on the distribution of flora among different Brazilian biomes (phytogeographic domains, *sensu* Vieira et al. 2022), in association with anthropogenic disturbances, requires updated policies and efficient legislation to conserve biodiversity and maintain ecological processes at secular and millennial scales. Given the accentuated process of degradation of the Brazilian biomes, areas suitable for the protection of relict taxa associated with past climate dynamics are already threatened by extinction.

To confront global change scenarios, a new approach based on flexible spatial networks, that combines the protection of fixed areas with transient areas, has been proposed to define priority regions for conservation (D'Aloia et al. 2019). This model could be incorporated into policies and legislation to help moderate changes in land use and the redistribution of biodiversity caused by ongoing climate change.

Among the Brazilian biomes, the restinga, AtF and Cerrado are some of the most critically endangered.
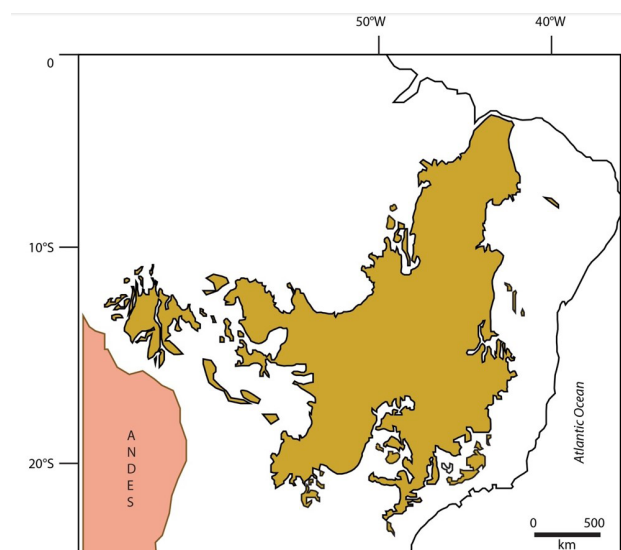

Figure 4. A map showing the current distribution of the Cerrado in South America (from Vieira et al. 2022).

Five centuries ago, the epicenter of European colonization was the coastal zone, which today is the region with the highest urban population densities in Brazil and, consequently, the source of major anthropogenic disturbances. To mitigate these disturbances, in 2009 the Pact for the Restoration of the Atlantic Forest, one of the most threatened biodiversity hotspots globally (Crouzeilles et al. 2019), was created as a movement to restore 150 000 km^2 of degraded/deforested land by 2050, and pledged 10 000 km^2 for the Bonn Challenge in 2020[10] (www.bonnchallenge.org). The Pact is based on three main strategies: (1) promoting positive governance, communication and restoration; (2) lobbying public policies; and (3) establishing monitoring systems. However, for such activities to be effective, past climate dynamics need to be included in spatial network models so that future policies and legislation guarantee conservation of the plant relics and refugia needed to mitigate future climate changes of either anthropogenic or geological origin. This is the only way to guarantee effective conservation at secular and millennial scales. Like the restinga and AtF, the Cerrado biome (*sensu* Vieira et al. 2022) also contains a wide variety of vegetation types known for their high biodiversity that are currently jeopardized by the expansion of agriculture.

Vieira et al. (2022) pointed out that the first official federal government map that included all the Brazilian Cerrado enclaves was only published in 1993, which has strongly affected land-use regulation because Brazilian government programs, or even laws, are generally specific to each biome.

Today, only 8.36% of the Cerrado is included in the Conservation Units (UC), far from the target of 17% by 2020 (Brasil 2020); and from 2016 to 2019, the average annual rate of deforestation was proportionally 78% higher than in AmF and, in 2019, had affected 49.9% of the Cerrado (Vieira et al. 2022).

Thus, as we face both climate deregulation and high anthropogenic pressure on the natural resources of the Brazilian biomes, it is crucial we improve our scientific knowledge of migration corridors and past connections, and convince stakeholders that the political division of biomes, for example AtF versus Cerrado, should be reconsidered if we want to protect tropical biota and allow the exchange of species and migrations to continue, as it has over time and across climates to form the tropical biodiversity we see today.

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Author Contributions

MPL and FSA developed the research idea and wrote the manuscript.

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