

A new modern pollen dataset describing the Brazilian Atlantic Forest

Vincent Montade,^{1,2,3}  Marie-Pierre Ledru,² Thomas Giesecke,^{1,4} Suzette GA Flantua,⁵ Hermann Behling¹ and Odile Peyron²

The Holocene
1–10

© The Author(s) 2019

Article reuse guidelines:

sagepub.com/journals-permissions

DOI: 10.1177/0959683619846981

journals.sagepub.com/home/hol



Abstract

To improve our understanding of the Atlantic Forest responses to climate changes in space and time, it is essential to explore how the Brazilian Atlantic rain forest is structured as observed in modern pollen assemblages and which climate parameters determine these patterns. In this context, we compiled 196 modern pollen samples including 125 from the Atlantic Forest biome and assigned each sample to one or more eco-physiognomies. We identified seven eco-physiognomies of which four clusters of one or two eco-physiognomies were clearly distinguished, namely (1) Araucaria forest with high elevation grassland, (2) lowland rain forest, (3) semi-deciduous with riverine forests and (4) northeastern Atlantic rain forest. Climatically distinct, these clusters reflect a general temperature increase and precipitation increase from the first to the fourth cluster. Furthermore, comparison of the modern pollen dataset with the *Côlonia* pollen record from southeastern Brazil revealed that vegetation attributed to Araucaria forest with high elevation grassland showed an important variability with several shifts towards the lowland rain forest. As illustrated by comparison with the long fossil pollen record of *Côlonia*, developing such a modern training set is crucial for the understanding of responses of Atlantic Forest to environmental changes. However, additional samples are still necessary to improve characterization of different eco-physiognomies at a local scale following a defined floristic and climatic gradient. This sampling effort is becoming increasing urgent as a result of strong biodiversity loss and habitat destruction in this region.

Keywords

Atlantic Forest, Brazil, database, eco-physiognomy, modern pollen samples, pollen-climate calibration, tropical South America

Received 19 November 2018; revised manuscript accepted 2 March 2019

Introduction

The Atlantic Forest biome spreads over more than 4000 km from northeastern to southern Brazil. A complex topography and varying climate conditions are partly responsible for the biological richness of the eco-physiognomies characterizing this biome. Indeed, the Atlantic Forest represents one of the most diverse biomes in the world, harbouring a large number of endemic species (Morellato and Haddad, 2000). However, because of extensive human activity in the Atlantic Forest domain, the natural vegetation distribution is largely reduced (Morellato and Haddad, 2000; Rezende et al., 2018). Based on botanical surveys and phylogeographic studies, this biome shows a sharp separation of biodiversity between two regions, the northeastern and southern/southeastern Brazilian Atlantic Forest (Carnaval and Moritz, 2008). Furthermore, spatial analysis of past vegetation dynamics documented by fossil pollen data reveals that this biome responds to global changes though with strong differences between these two regions (e.g. Behling et al., 2000; Behling and Safford, 2010; Ledru et al., 2016; Rodrigues et al., 2016b). To improve our understanding of the Atlantic Forest responses to climate changes in space and time, it is essential to explore how the Brazilian Atlantic rain forest is structured as observed in modern pollen assemblages and which climate parameters determine these patterns. Moving from qualitative descriptions of past environmental changes to quantitative reconstructions of past environments, including vegetation cover, land use or climate variability, is a major goal of modern palaeoecology. However, most of the available techniques require modern samples for calibrating the

relationship between pollen and vegetation or climate. Such a modern pollen training set, based on the collection of modern pollen surface samples and accompanying environmental parameters, is thus essential to infer past conditions quantitatively (Birks and Birks, 1980). Extensive pollen surface sample datasets have been compiled mainly for the northern Hemisphere (e.g. Davis et al., 2013; Whitmore et al., 2005) and have been placed in the public domain (e.g. Neotoma Paleoecology Database). During the past decades, modern datasets enabled quantitative reconstructions on local to continental scales based on fossil pollen data (e.g. Bartlein et al., 2011; Mauri et al., 2015; Peyron et al., 2017; Zanon et al., 2018). However, very few studies using these techniques have been performed in the southern Hemisphere and

¹Department of Palynology and Climate Dynamics, Albrecht-von-Haller-Institute for Plant Sciences, University of Göttingen, Germany

²Institut des Sciences de l'Évolution de Montpellier, Université de Montpellier, CNRS, IRD, EPHE, France

³Ecole Pratique des Hautes Etudes, France

⁴Department of Physical Geography, Faculty Geoscience, Utrecht University, The Netherlands

⁵Department of Biological Sciences, University of Bergen, Norway

Corresponding author:

Vincent Montade, Department of Palynology and Climate Dynamics, Albrecht-von-Haller-Institute for Plant Sciences, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany.
Email: vincent.montade@gmail.com

especially in South America (but see Markgraf et al., 2002; Montade et al., 2019; Schäbitz et al., 2013; Tonello et al., 2009).

Compiling a modern pollen data training set requires several steps: initially a wide range of modern pollen samples is required to span the range of environmental values likely to be represented by the main different vegetation types from a region. The second step consists of organizing these samples and homogenizing the taxa. As modern surface sample data are needed for different applications interpreting fossil pollen data, it is beneficial to place such datasets in the public domain such as the Latin America Pollen Database (LAPD) (Flantua et al., 2015), which is available through the Neotoma Paleoecology Database (Williams et al., 2018). The most densely sampled regions for modern pollen datasets in South America are the Colombian Andes, the southeast coast of Brazil and Patagonia (see Flantua et al., 2015). In the Atlantic Forest domain (partly including the southeast coast of Brazil), many paleoenvironmental studies frequently included analysis of modern pollen rain in the vicinity of the studied lake or bog, but hitherto these data have not been combined (e.g. Behling et al., 1997; Behling and Lichte, 1997; Jeske-Pieruschka et al., 2010; Ledru et al., 1996; Montade et al., 2016). By compiling the first modern pollen dataset that covers the full Brazilian Atlantic Forest biome, our principal aim was to describe the regional vegetation and climate pattern of this biome based on modern pollen data. We also included samples from the surrounding biomes in the attempt to determine a suitable spatial extent of the pollen–vegetation–climate calibration set for the Atlantic Forest biome. As a test, we then compared this full dataset to the past variability of Atlantic Forest using the oldest continuous pollen record in this region, the *Côlonia* record, which encompasses the last glacial interglacial cycle (Ledru et al., 2009).

Environmental settings (climate and vegetation)

The most important atmospheric circulation pattern leading to long-term climate variability in the Brazilian Atlantic Forest is the South American summer monsoon. Today, the monsoon is activated by the land sea gradient during the austral summer when the Intertropical Convergence Zone shifts southward. The North–South orientation and the concave shape of the Andean mountains in relation to the Intertropical Convergence Zone regulate the trajectory for moist fluxes over the South American continent. Air masses cross the Amazon basin in southwestern direction where they are diverted by the Andes towards the southeast into what is called the South Atlantic Convergence Zone with its modern location between Sao Paulo and Rio de Janeiro (Flantua et al., 2016). The South Atlantic Convergence Zone system has a high inter-annual variability, inducing regional flooding or drought according to the strength of the South American summer monsoon or the geographic position of the South Atlantic Convergence Zone (Garreaud et al., 2009). The strength and average position of this system has changed in the past in response to the precession cycle of the Earth's orbit (Cruz et al., 2005). Today, the main area under the precipitation from the South American summer monsoon is located in southeastern Brazil where a short dry season is observed (June to August) while in northeastern Brazil a long dry season occurs from June to January (Flantua et al., 2016).

The three main biomes from northeastern to southern Brazil are the Caatinga characterized by a xeric scrubland and thorn forest, the Cerrado (a tropical savannah) and the Atlantic Forest (Figure 1; see Figure 7 in Hoorn et al., 2017), with the main focus of this paper on the latter. The Atlantic Forest biome spreads all along the eastern part of Brazil, extending 4000 km from north to south. Between 3° and 19°S this biome is relatively narrow and bordered by the Caatinga biome while between 30° and 19°S its East–West extent is wider and bordered by the Cerrado biome.



Figure 1. The distribution of biomes or vegetation units in eastern South America and the location of 196 modern pollen samples with the selection of the 125 samples (red dots) related to the Atlantic Forest biome (including the northeastern Atlantic rain forest). AF: Atlantic Forest; AFN: northeastern Atlantic rain forest.

Five main eco-physiognomies associated with the Atlantic Forest are described according to their botanical characteristics: (1) high elevation grassland, (2) Araucaria forest, (3) coastal Atlantic rain forest, (4) semi-deciduous forest and (5) riverine forest.

1. The *high elevation grassland* eco-physiognomy is commonly observed in southeast Brazil at mountain ranges above elevations of 1800 m and represents a highly fragmented biome which harbours rich floras and high endemism (Safford, 1999a, 2007; Scheer and Mocochinski, 2016). The landscape consists of a series of cool-humid, mountaintop grass and scrubland areas with 11% of the plant species directly shared with the Andes (Safford, 1999b). It is also the highest, coolest plant community in the cold-humid tropics of eastern South America (Safford, 1999b). Among the main plant families are Asteraceae, Polypodiaceae, Melastomataceae, Orchidaceae, Poaceae, Lamiaceae, Lycopodiaceae, Cyperaceae, Ericaceae and Rubiaceae, and among the most represented genera are *Baccharis*, *Leandra*, *Tibouchina*, *Polygala*, *Peperomia*, *Habenaria* and *Senecio*. Tree taxa such as *Escallonia*, *Weinmannia* and *Myrsine* are also frequent in the Andean forest, while *Lagenocarpus triquetus* (Boeckeler) Kuntze (Cyperaceae) and *Croton muellerianus* L.R.Lima (Euphorbiaceae) are among the most common herbs (Scheer and Mocochinski, 2016). Differences can be observed in composition of this eco-physiognomy, in particular in some places as in mountaintops, only one species can be largely dominant (Safford, 1999b).
2. The *Araucaria forest* is a mixed evergreen forest with *Araucaria angustifolia* (Bertol.) Kuntze as the dominant tree and well adapted to cool and wet climate. Today, the northernmost limit for *A. angustifolia* (Bertol.) Kuntze is 18°S (Hueck, 1966). Several isolated pockets exist in

valleys between 1300 and 2000 m a.s.l. and at the cloud forest-grassland ecotone with *Araucaria* in the mountain ranges between 23° and 18°S. Its main distribution is located today in southern Brazil in the States of Parana and Santa Catarina between 24 and 28°S.

3. The *coastal Atlantic rain forest* is the most diverse forest type of the Atlantic Forest biome and occurs on coastal ranges up to 1000 m a.s.l. with high precipitation rates sometimes exceeding 3000 mm yr⁻¹. Species composition and taxa abundances differ between northern and southern low elevation rain forests (Oliveira-Filho and Fontes, 2000). Among the main species are *Inga edulis* Mart., *Lecythis pisonis* Cambess., *Melanoxylon brauna* Schott, *Pourouma guianensis* Aubl., *Pseudopiptadenia contorta* (DC.) G.P.Lewis & M.P.Lima, *Swartzia acutifolia* Vogel, *Thyrsoedium spruceanum* Benth. Among the main genus are *Eugenia*, *Miconia*, *Ocotea*, *Myrcia*, and *Inga*. Elevational differences are observed, where *Ilex* and *Myrsine*, for instance, are characteristic for higher elevations. Many species of epiphytic plants such as Orchidaceae and Bromeliaceae characterize this forest.
4. The *semi-deciduous Atlantic forest* forms a transitional zone between the humid Atlantic rain forest near the Atlantic coast, and the drier Caatinga scrubland, and Cerrado of the interior (Hoorn et al., 2017). The transition from rain forest to semi-deciduous forest is gradual and complex, and not necessarily linked to a coastal-hinterland climate gradient. The semi-deciduous Atlantic forest is characterized by a 2- to 4-month dry season and extends mainly across the central plateau above 600 m a.s.l. (Hencker et al., 2012). One main characteristic is the dominance of pioneer and heliophilous species (*Aparisthium cordatum* (A.Juss.) Baill., *Apuleia leiocarpa* (Vogel) J.F.Macbr., *Copaifera langsdorffii* Desf., *Dalbergia nigra* (Vell.) Benth., *Inga cylindrica* (Vell.) Mart., *Machaerium nyctitans* (Vell.) Benth., *Plathymenia reticulata* Benth., *Tapirira guianensis* Aubl., *Toulisia laevigata* Radlk.) and secondary species (*Ocotea divaricata* (Nees) Mez, *Pseudopiptadenia contorta* (DC.) G.P.Lewis & M.P.Lima and *Siparuna reginae* (Tul.) A.DC.) (Oliveira-Filho and Scolforo, 2008). The Fabaceae and Myrtaceae are among the most representative botanical families followed by Melastomataceae and Rubiaceae (*Gallesia*, *Esenbeckia*, *Metrodorea*), Asteraceae, Euphorbiaceae. The shrubby layer of vegetation is mainly composed of Asteraceae, Orchidaceae and Bromeliaceae.
5. The *riverine forest*, the smallest eco-physiognomy, is a semi-deciduous forest with permanent moist soils. Among the main families are Fabaceae, Piperaceae and Annonaceae and the main species *Inga edulis* Mart. and *Matayba guianensis* Aubl. The shrub layer is poor with the dominance of *Celtis brasiliensis* (Gardner) Planch.

Material and methods

Due to the limited number of modern pollen samples in the study region, we decided to combine samples characterized by different sampling methods. This dataset consists of 196 modern samples with 141 soil surface samples, 22 pollen traps, 7 river bed samples and top cores from 5 lake 20 peat bog and 1 swamp (Appendix S1, available online). Most of the samples are distributed from northeastern to southern Brazil and are primarily comprised of samples from the Brazilian Atlantic Forest biome with additional samples from the surrounding biomes (Figure 1). Although not exhaustive, the modern pollen samples from the surrounding biomes are helpful to explore the consistency of the different eco-physiognomies of the Atlantic Forest and how these eco-physiognomies may be defined by their pollen assemblages

and their indicative pollen types within a regional context. We assigned biomes and eco-physiognomies to all the samples based on information provided by the collectors. We harmonized the classifications and identified the following main vegetation biomes: Atlantic Forest (AF), Cerrado (CE), Caatinga (CA), Restinga (RE), Grassland (GRASS) and Mangrove (MA). In addition, we labelled AFN to the northeastern Atlantic rain forest due to its high floristic and palynological specificity. We then assigned the following eco-physiognomies within the AF biome: high elevation grassland (HEG), Araucaria forest (ArF), coastal Atlantic rain forest (RAIN), riverine forest (RF) and semi-deciduous forest (SDF). After homogenizing the pollen identification and aggregating rare occurrences into family level, a total of 146 pollen taxa was obtained (Appendix S2, available online). Most of the taxa names were chosen following the LAPD nomenclature list (Marchant et al., 2002a). We excluded exotic and aquatic pollen taxa, and all samples with a pollen sum lower than 100.

We used a multivariate regression tree analysis on the full dataset (196 samples) with the vegetation eco-physiognomy as explanatory variables for two reasons (Figure 2): first to explore whether the description of the vegetation eco-physiognomy corresponds to discernible clusters in the pollen composition of the samples, and second to reduce the assignment of multiple eco-physiognomies to a unified grouping. We used dummy variables with values of 0 and 1 to represent the affiliation of samples to one or more vegetation types. The size of the regression tree was guided by cross-validation and visual inspection of trees with similarly low standard errors. Analyses were carried out using the R-package MVPART (De'ath, 2013), with Hellinger transformed pollen proportions. Based on the groups obtained with a tree of 10 leaves, we analysed which taxa best described the different groups using the indicator index (IndVal) of Dufrene and Legendre (1997) as implemented in the R-package LABDSV (Roberts, 2016) and reporting taxa with a *p* value ≤ 0.05.

We then selected the modern pollen samples from AF and AFN (125 samples, see Appendix S1, available online) and visualized the abundance of the main pollen taxa in a diagram using the R-package RIOJA (Juggins, 2015) (Figure 3). We further mapped percentages for the major pollen taxa (Figure S1, available online). To determine if and how the variation in pollen proportion reflects the climate pattern in AF and AFN, we carried out a correspondence analysis with the R-package VEGAN on the set of 125 modern samples from AF and AFN (Oksanen et al., 2018). We chose the environmental parameters annual precipitation (P_{ANN}) and minimum temperature of July (T_{07}) generally corresponding to the coldest month and projected them on the axes 1 and 2 of the correspondence analysis (Figure 4). Finally, we projected the position of the samples from the Colônia pollen record (Ledru et al., 2009), representing the last 130 kyr BP, on axes 1 and 2 of the correspondence analysis (Figure 5). Environmental data were obtained from WorldClim global climate data (Hijmans et al., 2005) using the software NewLocClim 1.10 (Grieser et al., 2006).

For each dataset (196 and 125 samples), we reduced the data matrix to taxa that occur in at least three samples with an abundance above 1% in order to remove noise in the numerical analyses and we square root transformed the pollen data to stabilize the variance.

Results

Multivariate regression tree: Discernible eco-physiognomies from pollen data

The multivariate regression tree, performed on the 196 samples, results in a useful grouping of the samples; however, with an R^2 of 0.39 the assignment of samples to the groups is not very strong. The length of the vertical branches indicates the amount of variance explained by a particular split (Figure 2). The strongest

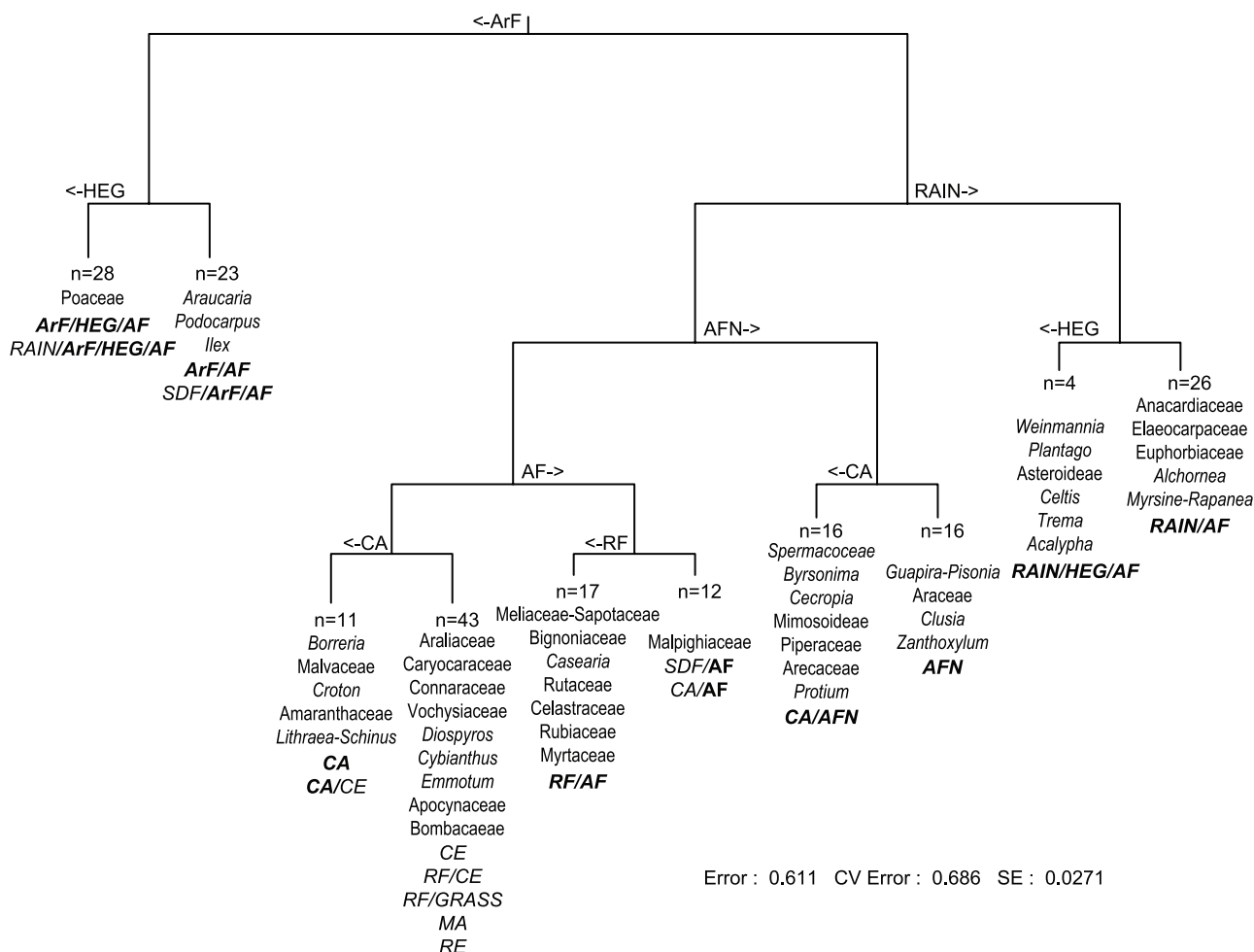


Figure 2. Multivariate regression tree of the taxonomically harmonized dataset of 196 samples with biome and eco-physiognomy as the explanatory variables and samples were assigned to more than one biome or eco-physiognomy. AF: Atlantic Forest; AFN: northeastern Atlantic rain forest; ArF: Araucaria forest; CA: Caatinga; CE: Cerrado; GRASS: grassland; HEG: high elevation grassland; MA: mangrove; RAIN: coastal Atlantic rain forest; RE: Restinga; RF: riverine forest; SDF: semi-deciduous forest. The biome and eco-physiognomy determining a particular split is indicated near each node. Numbers below the leaves indicate the number of samples contained and the list of taxa represents the result of the indicator taxa (IntVal) analysis that was performed separately, showing all taxa with at least a 95% significance of being an indicator for the particular group. Capital letters indicate the biomes and eco-physiognomies included in the group and bold letters indicate the biomes and eco-physiognomies common to each group.

division is the grouping of samples coming from Araucaria forest (ArF; most left branch), which is stronger than the separation of samples for Caatinga (CA) or Cerrado (CE). Within the first samples from the ArF, samples of open environments of high elevation grassland (HEG) are well separated and are characterized by Poaceae as an indicator taxon. Samples from coastal Atlantic rain forest (RAIN), northeastern Atlantic rain forest (AFN) and remaining samples of Atlantic Forest (AF) make another clear division. The largest group is mainly composed of samples coming from CE (43 samples), where also the single samples from Restinga (RE, coastal dune vegetation), Mangrove (MA) and Grassland (GRASS) fall into this group. Here, indicator taxa correspond primarily to Cerrado and not to the other eco-physiognomies. With samples from the semi-deciduous forest (SDF, 12 samples), only one sample is associated with CA; consequently, the indicator taxa mainly correspond to the SDF. Even though the cross-validated (CV) error is relatively high, all groups are characterized by significant indicator taxa in the IndVal analysis.

Pollen diagram: Description of eco-physiognomies

The pollen diagram (Figure 3) presents the 35 main taxa of the 7 groups belonging to the Brazilian Atlantic Forest as defined by the regression tree analysis (Figure 2):

The high elevation grassland mixed with Araucaria forest (ArF/HEG/AF, 28 samples) is generally dominated by high Poaceae frequencies of more than 30% associated with Asteroidae (ca. 19%). Arboreal pollen such as *Myrsine-Rapanea* and Myrtaceae are frequently recorded with values above 5%. A frequent occurrence of *Araucaria*, *Weinmannia*, *Clethra* and *Plantago* also characterizes this group and some samples contain high frequencies of Mimosoideae (>5%).

The Araucaria forest (ArF/AF, 23 samples) shows the highest frequencies of *Araucaria* and *Podocarpus* is frequently above 5% with maxima of 80%. These taxa are mainly associated with Poaceae, Asteroidae, *Ilex* and Myrtaceae with mean percentage values ranging from 12% to 8%.

The coastal Atlantic rain forest (RAIN/AF, 26 samples) is mainly represented by Anacardiaceae, *Myrsine-Rapanea*, *Alchornea* and Myrtaceae frequently above 10%. The characteristic taxa Euphorbiaceae and Elaeocarpaceae are abundant in several samples.

The coastal Atlantic rain forest is also mixed with high elevation grassland (RAIN/HEG/AF, four samples). Although with lower mean value than in the ArF/HEG/AF group, Poaceae (27%) still dominates with Asteroidae and *Myrsine-Rapanea*. Here, these taxa are associated with *Weinmannia*, Myrtaceae,



Figure 3. Pollen diagram showing the percentages of the main pollen taxa for the 125 surface samples from Atlantic Forest biome (including Atlantic rain Forest from the north). AF: Atlantic Forest; AFN: northeastern Atlantic rain forest; ArF: Araucaria forest; HEG: high elevation grassland; RAIN: coastal Atlantic rain forest; RF: riverine forest; SDF: semi-deciduous forest. The coloured pollen taxa refer to taxa with significant indicator value for the selected groups indicated in the regression tree (see Figure 2). The code on left side refers to the modern pollen samples with their respective eco-physiognomies (see Appendix S1, available online).

Alchornea, Moraceae-Urticaceae and Melastomataceae with percentages around 4%.

The northeastern Atlantic rain forest (AFN, 16 samples) shows pollen assemblages dominated by Myrtaceae with *Guapira-Pisonia*, Melastomataceae and *Spermacoceae* with mean percentage values ranging from 13% to 9%. Frequent occurrences of *Byrsonima*, *Alchornea*, *Zanthoxylum*, Moraceae-Urticaceae, Fabaceae, Arecaceae and *Ilex* also characterize this group.

The semi-deciduous forest (SDF/AF, 12 samples) is also characterized by the dominance of Myrtaceae with Poaceae and Asteroideae with values generally above 10%. These taxa are associated with Malpighiaceae, Mimosoideae, Arecaceae, Moraceae-Urticaceae frequently above 4% and Rubiaceae, *Zanthoxylum* at low abundance (<4%).

The riverine forest (RF/AF, 17 samples) is dominated by Myrtaceae with Asteroideae and Poaceae showing mean percentage values from 18% to 10%. A frequent occurrence (>4%) of Rubiaceae, Arecaceae, Amaranthaceae and Meliaceae-Sapotaceae is also observed. Occurring in half of the samples, *Gallesia* and Fabaceae reach also values frequently above 4% in this group.

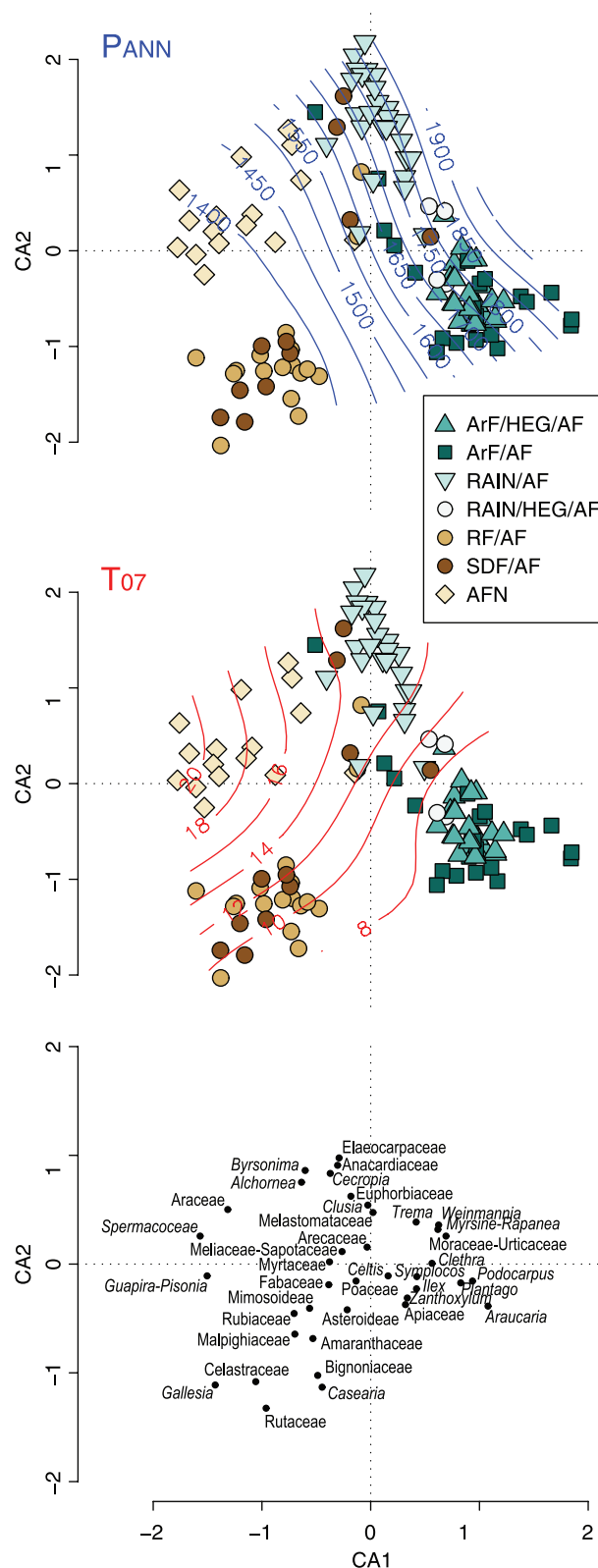
Ordination: Climatic and vegetation consistency of eco-physiognomies

The first axis of the correspondence analysis (Figure 4) describes the environmental gradient from the Araucaria forest in the south associated with low winter temperatures and high precipitation to the northeastern Atlantic rain forest with high winter temperatures and lower precipitation. Four main clusters with samples from one or several eco-physiognomies are discernible. One main cluster is formed by the two types of grasslands (ArF/HEG/AF and RAIN/HEG/AF) together with samples from the Araucaria forest (ArF/AF). Characterized by *Araucaria*, *Podocarpus* and *Plantago*, these samples occur under low T_{07} and high P_{ANN} . Samples from the coastal Atlantic rain forest (RAIN/AF), the second cluster, are separated along the second axis and associated with an increase in Elaeocarpaceae, Anacardiaceae and *Byrsonima*. While P_{ANN} values remain high for this cluster, T_{07} values increase in comparison with the previous cluster. Samples from semi-deciduous and riverine forest (SDF/AF and RF/AF) are separated along the second axis, where they form a well-defined third cluster characterized by Rutaceae, Casearia, *Gallesia*, Celastraceae and Bignoniaceae. The fourth cluster with samples from northeastern Atlantic rain forest (AFN) is characterized by *Spermacoceae*, *Guapira-Pisonia* and Araceae and associated with the warmest winters.

Discussion and conclusion

Regional to local classification of the Atlantic Forest biome

Based on 196 modern pollen samples, of which 125 are from the Atlantic Forest biome, our dataset combines a diverse range of sample types (e.g. surface soils, surface lake/bog sediments, artificial pollen traps or river beds). Pollen preservation and spatial and temporal resolution of modern pollen rain samples partly differ according to the sampling methods. For example, in soil samples, pollen can be more easily destroyed by mechanical or chemical corrosion than in lake/bog sediments or in pollen traps (Jantz et al., 2013; Wilmshurst and McGlone, 2005). This can lead to under-represented grains with thin exine or over-represented grains with thick exine. Spatial resolution of pollen rain recorded in modern samples is also different between lake sediments and soil samples or pollen traps. Pollen traps and soil samples generally reflect a very local signal of the vegetation (Behling et al., 1997; Montade



the lake (Mayle and Iriarte, 2014). Concerning the temporal resolution, an artificial pollen trap may capture pollen over a short period (e.g. 12 months) which may not necessarily be representative of pollen production over several years or decades, as this is provided by other surface sample types (Behling et al., 1997; Jantz et al., 2013).

Although the different sampling methods used in our dataset certainly add some noise in our results, the multivariate regression tree allows to separate the main vegetation eco-physiognomies based on their pollen content (Figure 2). Within the Atlantic Forest biome, as described in the ordination, four main clusters are identified (Figure 4): (1) *Araucaria* forest (ArF) mixed with high elevation grassland (HEG), (2) coastal Atlantic rain forest (RAIN), (3) semi-deciduous and riverine forests (SDF and RF) and (4) northeastern Atlantic rain forest (AFN). These clusters show a clear correspondence to regional climate variables, differentiating sites from north to south and from coast to inlands. These gradients are reflected by sites belonging to AFN, SDF and RF situated in the north or inlands with lower P_{ANN} and higher T_{07} compared with samples from ArF, HEG and RAIN located in the south near the coasts or in mountain areas (Figure 4). This pattern is consistent with botanical surveys performed in southern/southeastern Brazil that show that tree composition changes substantially between lowland rain forest, montane rain forest and semi-deciduous forest related to decreasing rainfall inland and decreasing temperatures with elevation (Oliveira-Filho and Fontes, 2000). Furthermore, although corresponding to rain forest, samples from northeastern Brazil are well differentiated from samples of central/southern Atlantic Forest regions. Not surprisingly, this result is also in good agreement with botanical surveys and phylogeographic studies that show a sharp separation of biodiversity between these two regions of the Atlantic Forest biome (Carnaval and Moritz, 2008; Neves et al., 2017).

As previously shown from core top samples from southern Brazil, Poaceae represents a major pollen taxon (Rodrigues et al., 2016a), which may serve as an indicator of HEG at proportions exceeding 27%. Even though grasses are also a major component of other eco-physiognomies, the proportion of Poaceae pollen alone generally allows differentiating between open and closed vegetation types. However, at a local scale in mountain areas, it remains difficult to distinguish rain forests (ArF or RAIN) from HEG which are sometimes growing in the same environmental conditions in southern/southeastern Brazil. This is illustrated by the first main cluster in our data with ArF and HEG eco-physiognomies both characterized by high P_{ANN} and low T_{07} . Although characterized by different indicator taxa (Poaceae for HEG and *Araucaria*, *Podocarpus*, *Ilex* for ArF), these two eco-physiognomies clustering together in the ordination indicates a high degree of similarity (Figure 4). A common feature is the important abundance of herbs (mainly Poaceae and Asteroideae) which is related to grasslands generally building a mosaic pattern with the *Araucaria* or the rain forest in mountain areas (Safford, 1999a). Numerous samples from this main cluster were often collected within these vegetation mosaics between *Araucaria* forests or montane rain forests and grasslands along transects of few hundred metres long (Behling and Lichte, 1997; Jeske-Pieruschka et al., 2010). Close similarities between these samples from adjacent eco-physiognomies are thus explained by this sampling strategy. These strong vegetation gradients over short distances are partly related to threshold responses of vegetation to abiotic factors present in the landscape (Behling et al., 2007). Different micro-climate conditions could also influence distribution of these eco-physiognomies; global climate datasets, however, have insufficient spatial resolution to detect such local scale variabilities in environmental parameters. This mosaic patterns with development of grasslands differ from usual vegetation gradients in temperate latitudes such as in Eurasian grasslands, where development of grasslands (named Steppes) occurs with cold and dry conditions and climatically

clearly distinct from forested environments (Overbeck et al., 2007). However, compared with the other eco-physiognomies, HEG and ArF are well distinguished by *Araucaria*, which is the single most typical taxon characterizing a large eco-physiognomy. With high percentages in ArF, *Araucaria* also occurs frequently in HEG with values above 1%. This taxon is represented by one single species in Brazil, *A. angustifolia* (Bertol.) Kuntze, which requires permanent moisture and cool temperatures. *A. angustifolia* (Bertol.) Kuntze is a wind-pollinated tree. Although pollen from this tree can be dispersed over several kilometres, most of pollen are generally dispersed within a few hundred metres (Bittencourt and Sebbenn, 2007). In this context, this pollen taxon is considered as an excellent indicator of ArF (e.g. Ledru, 1993) which is consistent with the IntVal analysis that indicates *Araucaria* as the best indicator taxon for ArF (Figure 2).

The eco-physiognomy of RAIN, the second cluster, differs from the previous ArF and HEG eco-physiognomies by low frequencies of herbs and a higher diversity and frequencies of arboreal pollen with Anacardiaceae, Elaeocarpaceae, Euphorbiaceae and *Alchornea* associated with Myrtaceae, Arecaceae, Melastomataceae and Moraceae-Urticaceae. Here Anacardiaceae is the strongest indicator for this eco-physiognomy. In these samples, this pollen taxon is mainly represented by *Tapirira guianensis* Aubl., which is a pioneer tree abundant in the rain forest and frequently growing in forest edge habitats (Oliveira et al., 2004). Although a total of 26 samples are available from the RAIN, this eco-physiognomy is strongly underrepresented as 22 samples are pollen traps coming from three botanical plots in close proximity (Behling et al., 1997). This probably results in a high degree of sample redundancy. Furthermore, pollen traps may have partly influenced pollen proportions in comparison with other sample methods mainly characterized by soil and lake/bog samples. While this eco-physiognomy occurs close to ArF and HEG habitats, the much lower elevation results in higher T_{07} with similar P_{ANN} values as HEG and ArF. However, as evidenced in botanical surveys, rainfall seasonality in lowland rain forests on the coast is lower than in mountain rain forests (Oliveira-Filho and Fontes, 2000). While our results are consistent with vegetation and climatic conditions, additional sample locations from coastal Atlantic rain forests are required to confirm this vegetation/climate pattern by using pollen assemblages.

Samples of SDF and RF corresponding to the third main cluster are also characterized by high values of herbs (mainly Asteroideae and Poaceae). However, compared with the first cluster (HEG and ArF), these samples are associated with high proportions of Arecaceae, Rubiaceae, Fabaceae or Amaranthaceae, and high frequencies of Myrtaceae (>15%) are frequently recorded in these eco-physiognomies. Arecaceae represent an important arboreal taxon which is associated with palm trees frequently growing in these eco-physiognomies and generally rare in ArF or HEG (Oliveira-Filho and Fontes, 2000). Growing more inland (mainly for SDF), most of these samples occur under lower annual rainfall and similar T_{07} than RAIN/AF which is consistent with botanical surveys from southern Brazil (Oliveira-Filho and Fontes, 2000). Although clustered together in the ordination, some differences in pollen assemblages can also be observed between SDF and RF. In SDF, for example, high percentages of Myrtaceae occur together with high percentages of Mimosoideae and Malpighiaceae, thus constituting a specific assemblage. Malpighiaceae is also reported as the only good indicator of SDF in the IntVal analysis.

The fourth cluster, characterized by AFN samples, shares similarities with the second (RAIN) and the third cluster (SDF and RF). This is well illustrated by high frequencies of Myrtaceae, Melastomataceae or *Alchornea*. On the other hand, AFN samples also reveal some differences with the second and third cluster as shown by high percentages of *Guapira-Pisonia*, the strongest indicator for this eco-physiognomy (Figure 2). This taxon corresponding to heliophilous trees is generally associated with other

heliophilous or pioneer tree taxa such as Melastomataceae (mainly represented by *Miconia* in AFN) or *Clusia* (Montade et al., 2016). *Spermacoceae* or *Byrsonima* are also recorded with high frequencies in several samples from the AFN. *Byrsonima* trees are abundant in the AFN (Cavalcante et al., 2000). *Spermacoceae*, a good indicator of the Caatinga (see CA/AFN in Figure 2), is frequently associated with species which are generally growing at the forest edge of the AFN and is also considered as a good indicator of disturbances (Marchant et al., 2002a). With higher T_{07} and lower P_{ANN} compared with other clusters of eco-physiognomies, pollen assemblages from the AFN reflect environment under high environmental stress associated with strong inter-annual variability in precipitation characteristic for northeastern Brazil.

To broadly reproduce potential natural vegetation from modern and fossil pollen assemblages, the biomisation approach was implemented for South America (Marchant et al., 2009). This method is based on the assignment of pollen taxa to one or more plant functional types (PFTs) which are then used to evaluate the degrees of affinity between pollen spectra and different biomes (Prentice et al., 1996). From Marchant et al. (2009), within the Atlantic Forest domain, three main biomes are distinguished using this method. In comparison with our results, the tropical rain forest distributed along the coast broadly corresponds to our second cluster (RAIN) and the tropical seasonal forest to our third cluster (SDF and RF). The Atlantic rain forest from the northeastern Brazil is not represented. Another problem is that the eco-physiognomy of the Araucaria forest with high elevation grasslands in southern Brazil is assigned by the biomisation method to a warm temperate evergreen broadleaf forest. Under humid conditions and not tolerant of freezing, this assigned biome differs from natural vegetation where frosts are common during the winter (Safford, 1999b). Furthermore, Rodrigues et al. (2016a) demonstrated that because of high percentages of Poaceae in high elevation grassland, modern pollen samples from eco-physiognomies were partly assigned to Cerrado using the proposed biomisation (Marchant et al., 2009). Being mainly implemented and further developed in biomes with a strong Andean influence, such as those in Colombia (Marchant et al., 2002b), vegetation gradients differ substantially from those in southern Brazil which could explain the observed incorrect identification of biomes or eco-physiognomies. Consequently, reconstruction methods can be more precise when using vegetation schemes based on eco-physiognomies which are better distinguished based on pollen assemblages.

Modern versus temporal variability of Atlantic Forest

Improving our understanding of natural vegetation dynamic of the Atlantic Forest also requires comparison of the spatial variability of eco-physiognomies evidenced here by our modern pollen data with the temporal variability of Atlantic Forest evidenced by fossil pollen records.

To do that, we selected the Colônia pollen record which is the longest pollen record in southeastern Brazil (Flantua et al., 2015) and encompasses the last glacial interglacial cycle (Ledru et al., 2009). Showing important shifts between grasslands and montane rain forest during the last 130 kyr BP, we plotted the fossil pollen assemblages from Colônia passively onto the correspondence analysis of the modern samples (Figure 5). Most of fossil pollen samples are shifting between ArF/HEG and RAIN and only few pollen samples occur in the SDF/RF eco-physiognomies. According to our projected climatic parameter (P_{ANN} and T_{07}), this indicates some variability in terms of temperature while annual precipitation remains in the same ranges except when some fossil pollen samples fall in the SDF/RF. These last samples belong to the deepest part of the core which might correspond to the last interglacial period and show that conditions were drier and warmer at that time. As mentioned in the previous part, with the same ranges of annual precipitation, rainfall seasonality is lower

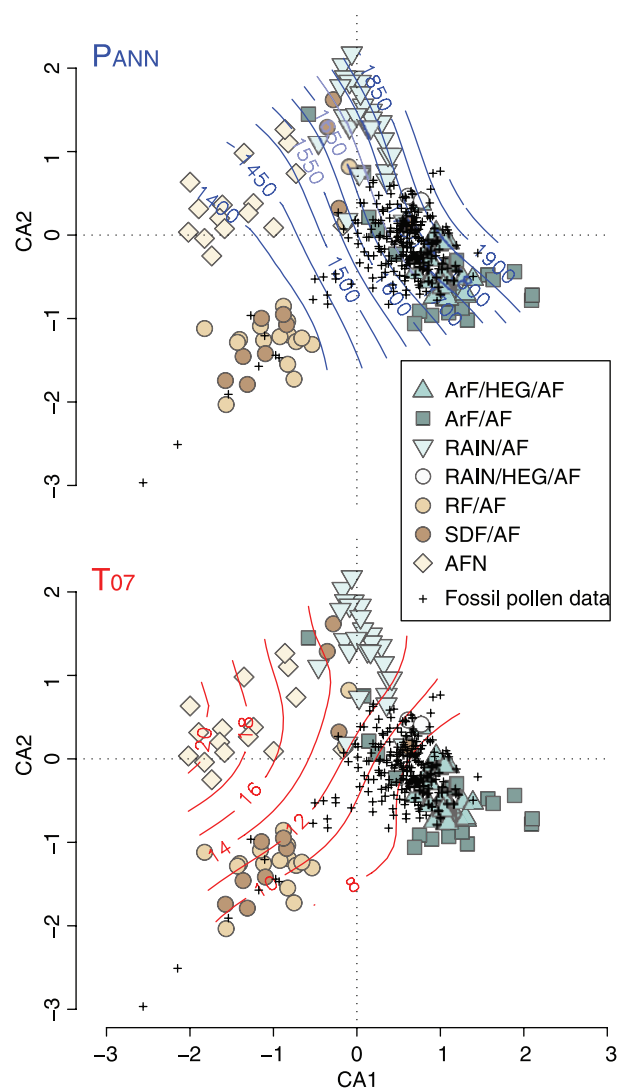


Figure 5. Fossil pollen data from Colônia (Ledru et al., 2009) passively plotted on the axes 1 and 2 of the correspondence analysis performed on the 125 modern pollen samples from the Atlantic Forest biome (including the northeastern Atlantic rain forest).

AF: Atlantic Forest; AFN: northeastern Atlantic rain forest; ArF: Araucaria forest; HEG: high elevation grassland; RAIN: coastal Atlantic rain forest; RF: riverine forest; SDF: semi-deciduous forest.

The isohyets represent the annual precipitation (P_{ANN}) and the minimum temperature of July (T_{07}) associated with the sample locations.

in coastal Atlantic rain forest than in mountain rain forest from southern Brazil. A variability of the dry season length evidenced by the shifts of fossil pollen samples between ArF/HEG and RAIN might be related to changes in South American summer monsoon as recorded in southern Brazil by speleothems (Cruz et al., 2007). Climatic interpretations of the Colônia pollen record were partly based on fluctuations of herbs (mainly Poaceae) against arboreal tree taxa which reflected high elevation grassland against forest. Based on our modern pollen dataset this interpretation can be changed suggesting a variability between mountain environments (including Araucaria forest and high elevation grassland) versus a coastal or lowland rain forest. However, this new interpretation still needs to be taken with caution. For example, under markedly different boundary climate conditions, the fossil pollen assemblages may be without modern analogues. In particular, plant–climate interactions being sensitive to atmospheric CO_2 concentration (Prentice and Harrison, 2009), pollen assemblages were probably partly influenced by the low atmospheric CO_2 concentrations during the late glacial as shown in

tropical Africa (e.g. Izumi and Lézine, 2016; Jolly and Haxeltine, 1997). Consequently, under high atmospheric CO₂ concentrations, modern pollen samples are not necessarily good analogues of fossil pollen samples during periods under low atmospheric CO₂ concentrations, such as the last glacial period. Furthermore, as most of samples of RAIN in our training set come from adjacent locations, additional samples from this eco-physiognomy are thus strongly necessary. Unfortunately, Atlantic Forest has undergone a huge forest loss, and with only about 10–15% of the original area remaining (Ribeiro et al., 2009), it is urgent to collect additional samples (in particular in lowland rain forests) from biomes with a high risk of complete deforestation in the next coming decades (Rezende et al., 2018).

Therefore, to improve the database in the future we advise to not only increase the number of samples but also define a more adapted sampling strategy that could include, for instance, the eastern to western vegetation assemblages of southern Brazil following a defined floristic and climatic gradient. This will strongly help to improve our understanding of the significant changes in floristic composition related to climate variability during the last millennia to succession of the glacial/interglacial cycles of the Atlantic Forest, the second forest in biodiversity after Amazonian forest in South America.

Acknowledgements

This research is part of the projects from ‘Dimensions of biodiversity’ FAPESP (BIOTA 2013/50297-0), NSF (DEB 1343578), NASA, ‘UV-Trop’ INSU LEFE and ‘TROPICOL’ Fondation BNP Paribas ‘Climate Initiative’. We are grateful for the very constructive comments from Frank Mayle and one anonymous referee that help us to improve this article. This is an ISEM publication n°2019-088.

Funding

V.M. benefitted from postdoc grants from FUNCAP, Brazil; EPHE, France; and DFG, Germany. S.G.A.F. acknowledges support by ERC grant 741413 Humans on Planet Earth (HOPE).

Supplemental material

Supplemental material for this article is available online.

ORCID iD

Vincent Montade  <https://orcid.org/0000-0002-8518-2610>

References

- Bartlein PJ, Harrison SP, Brewer S et al. (2011) Pollen-based continental climate reconstructions at 6 and 21 ka: A global synthesis. *Climate Dynamics* 37(3–4): 775–802.
- Behling H and Lichte M (1997) Evidence of dry and cold climatic conditions at glacial times in tropical southeastern Brazil. *Quaternary Research* 48(3): 348–358.
- Behling H and Safford HD (2010) Late-glacial and Holocene vegetation, climate and fire dynamics in the Serra dos Órgãos, Rio de Janeiro State, southeastern Brazil. *Global Change Biology* 16(6): 1661–1671.
- Behling H, Arz HW, Pätzold J et al. (2000) Late Quaternary vegetational and climate dynamics in northeastern Brazil, inferences from marine core GeoB 3104–1. *Quaternary Science Reviews* 19(10): 981–994.
- Behling H, Negrelle RRB and Colinvaux PA (1997) Modern pollen rain data from the tropical Atlantic rain forest, Reserva Volta Velha, South Brazil. *Review of Palaeobotany and Palynology* 97(3): 287–299.
- Behling H, Pillar VD, Müller SC et al. (2007) Late-Holocene fire history in a forest-grassland mosaic in Southern Brazil: Implications for conservation. *Applied Vegetation Science* 10(1): 81–90.
- Birks HJB and Birks HH (1980) *Quaternary Palaeoecology*. London: Edward Arnold.
- Bittencourt JVM and Sebbenn AM (2007) Patterns of pollen and seed dispersal in a small, fragmented population of the wind-pollinated tree *Araucaria angustifolia* in southern Brazil. *Heredity* 99(6): 580–591.
- Carnaval AC and Moritz C (2008) Historical climate modeling predicts patterns of current biodiversity in the Brazilian Atlantic Forest. *Journal of Biogeography* 35(7): 1187–1201.
- Cavalcante A, Soares JJ and Figueiredo MA (2000) Comparative phytosociology of tree sinusiae between contiguous forests in different stages of succession. *Revista Brasileira de Biologia* 60(4): 551–562.
- Cruz FW, Burns SJ, Jercinovic M et al. (2007) Evidence of rainfall variations in southern Brazil from trace element ratios (Mg/Ca and Sr/Ca) in a Late Pleistocene stalagmite. *Geochimica et Cosmochimica Acta* 71(9): 2250–2263.
- Cruz FW, Burns SJ, Karmann I et al. (2005) Insolation-driven changes in atmospheric circulation over the past 116,000 years in subtropical Brazil. *Nature* 434(7029): 63–66.
- Davis BAS, Zanon M, Collins P et al. (2013) The European Modern Pollen Database (EMPD) project. *Vegetation History and Archaeobotany* 22(6): 521–530.
- De’ath G (2013) mvpart: Multivariate partitioning (R package version 1.6–1). Available at: <http://ftp.auckland.ac.nz/software/CRAN/src/contrib/Descriptions/mvpart.html> (accessed 30 July 2018).
- Dufrêne M and Legendre P (1997) Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs* 67(3): 345–366.
- Flantua SGA, Hooghiemstra H, Grimm EC et al. (2015) Updated site compilation of the Latin American pollen database. *Review of Palaeobotany and Palynology* 223: 104–115.
- Flantua SGA, Hooghiemstra H, Vuille M et al. (2016) Climate variability and human impact in South America during the last 2000 years: Synthesis and perspectives from pollen records. *Climate of the Past* 12(2): 483–523.
- Garreaud RD, Vuille M, Compagnucci R et al. (2009) Present-day South American climate. *Palaeogeography, Palaeoclimatology, Palaeoecology* 281(3–4): 180–195.
- Grieser J, Giommes R and Bernardi M (2006) New_LocClim – The local climate estimator of FAO. *Geophysical Research Abstracts* 8: 08305.
- Hencker C, Assis AM and Lirio EJ (2012) Fitossociologia de um trecho de floresta estacional semidecidual no município de Itarana (ES). *Natureza on line* 10(4): 153–159.
- Hijmans RJ, Cameron SE, Parra JL et al. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25(15): 1965–1978.
- Hoorn C, Bogotá-A GR, Romero-Baez M et al. (2017) The Amazon at sea: Onset and stages of the Amazon River from a marine record, with special reference to Neogene plant turnover in the drainage basin. *Global and Planetary Change* 153: 51–65.
- Hueck K (1966) *Die Wälder Südamerikas*. Stuttgart: G Fischer.
- Izumi K and Lézine A-M (2016) Pollen-based biome reconstructions over the past 18,000 years and atmospheric CO₂ impacts on vegetation in equatorial mountains of Africa. *Quaternary Science Reviews* 152: 93–103.
- Jantz N, Homeier J, León-Yáñez S et al. (2013) Trapping pollen in the tropics – Comparing modern pollen rain spectra of different pollen traps and surface samples across Andean vegetation zones. *Review of Palaeobotany and Palynology* 193: 57–69.
- Jeske-Pieruschka V, Fidelis A, Bergamin RS et al. (2010) *Araucaria* forest dynamics in relation to fire frequency in southern Brazil based on fossil and modern pollen data. *Review of Palaeobotany and Palynology* 160(1): 53–65.
- Jolly D and Haxeltine A (1997) Effect of low glacial atmospheric CO₂ on tropical African montane vegetation. *Science* 276(5313): 786–788.

- Juggins PS (2015) rioja: Analysis of quaternary science data. Available at: <https://cran.r-project.org/web/packages/rioja/index.html> (accessed 24 January 2017).
- Ledru M-P (1993) Late quaternary environmental and climatic changes in central Brazil. *Quaternary Research* 39(1): 90–98.
- Ledru M-P, Braga PIS, Soubiès F et al. (1996) The last 50,000 years in the Neotropics (southern Brazil): Evolution of vegetation and climate. *Palaeogeography, Palaeoclimatology, Palaeoecology* 123(1): 239–257.
- Ledru M-P, Montade V, Blanchard G et al. (2016) Long-term spatial changes in the distribution of the Brazilian Atlantic Forest. *Biotropica* 48(2): 159–169.
- Ledru M-P, Mourguiart P and Riccomini C (2009) Related changes in biodiversity, insolation and climate in the Atlantic rainforest since the last interglacial. *Palaeogeography, Palaeoclimatology, Palaeoecology* 271(1–2): 140–152.
- Marchant R, Almeida L, Behling H et al. (2002a) Distribution and ecology of parent taxa of pollen lodged within the Latin American Pollen Database. *Review of Palaeobotany and Palynology* 121(1): 1–75.
- Marchant R, Behling H, Berrio J-C et al. (2002b) Pollen-based biome reconstructions for Colombia at 3000, 6000, 9000, 12 000, 15 000 and 18 000 14C yr ago: Late quaternary tropical vegetation dynamics. *Journal of Quaternary Science* 17(2): 113–129.
- Marchant R, Harrison SP, Hooghiemstra H et al. (2009) Pollen-based biome reconstructions for Latin America at 0, 6000 and 18 000 radiocarbon years. *Climate of the Past* 5(1): 369–461.
- Markgraf V, Webb RS, Anderson KH et al. (2002) Modern pollen/climate calibration for southern South America. *Palaeogeography, Palaeoclimatology, Palaeoecology* 181(4): 375–397.
- Mauri A, Davis BAS, Collins PM et al. (2015) The climate of Europe during the Holocene: A gridded pollen-based reconstruction and its multi-proxy evaluation. *Quaternary Science Reviews* 112: 109–127.
- Mayle FE and Iriarte J (2014) Integrated palaeoecology and archaeology – A powerful approach for understanding pre-Columbian Amazonia. *Journal of Archaeological Science* 51: 54–64.
- Montade V, Diogo IJS, Bremond L et al. (2016) Pollen-based characterization of montane forest types in north-eastern Brazil. *Review of Palaeobotany and Palynology* 234: 147–158.
- Montade V, Peyron O, Favier C et al. (2019) A pollen–climate calibration from western Patagonia for palaeoclimatic reconstructions. *Journal of Quaternary Science* 34(1): 76–86.
- Morellato LPC and Haddad CFB (2000) Introduction: The Brazilian Atlantic Forest. *Biotropica* 32(4b): 786–792.
- Neves DM, Dexter KG, Pennington RT et al. (2017) Dissecting a biodiversity hotspot: The importance of environmentally marginal habitats in the Atlantic Forest Domain of South America. *Diversity and Distributions* 23(8): 898–909.
- Oksanen J, Blanchet FG, Friendly M et al. (2018) Vegan: Community ecology package. Available at: <https://cran.r-project.org/web/packages/vegan/index.html> (accessed 7 February 2018).
- Oliveira MA, Grillo AS and Tabarelli M (2004) Forest edge in the Brazilian Atlantic Forest: Drastic changes in tree species assemblages. *Oryx* 38(4): 389–394.
- Oliveira-Filho AT and Fontes MAL (2000) Patterns of floristic differentiation among Atlantic Forests in southeastern Brazil and the influence of climate. *Biotropica* 32(4b): 793–810.
- Oliveira-Filho AT and Scolforo JRS (2008) *Inventário Florestal de Minas Gerais: Espécies Arbóreas Da Flora Nativa*. 1st Edition. Lavras, Brazil: Editora Ufla.
- Overbeck GE, Müller SC, Fidelis A et al. (2007) Brazil's neglected biome: The south Brazilian Campos. *Perspectives in Plant Ecology, Evolution and Systematics* 9(2): 101–116.
- Peyron O, Combourieu-Nebout N, Brayshaw D et al. (2017) Precipitation changes in the Mediterranean basin during the Holocene from terrestrial and marine pollen records: A model–data comparison. *Climate of the Past* 13(3): 249–265.
- Prentice C, Guiot J, Huntley B et al. (1996) Reconstructing biomes from palaeoecological data: A general method and its application to European pollen data at 0 and 6 ka. *Climate Dynamics* 12(3): 185–194.
- Prentice IC and Harrison SP (2009) Ecosystem effects of CO₂ concentration: Evidence from past climates. *Climate of the Past* 5(3): 297–307.
- Rezende CL, Scarano FR, Assad ED et al. (2018) From hotspot to hopespot: An opportunity for the Brazilian Atlantic Forest. *Perspectives in Ecology and Conservation* 16: 208–214.
- Ribeiro MC, Metzger JP, Martensen AC et al. (2009) The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation* 142(6): 1141–1153.
- Roberts DW (2016) labdsv: Ordination and multivariate analysis for ecology. Available at: <https://CRAN.R-project.org/package=labdsv> (accessed 30 July 2018).
- Rodrigues JM, Behling H and Giesecke T (2016a) Differentiating vegetation types from eastern South American ecosystems based on modern and subfossil pollen samples: Evaluating modern analogues. *Vegetation History and Archaeobotany* 25(4): 387–403.
- Rodrigues JM, Behling H and Giesecke T (2016b) Holocene dynamics of vegetation change in southern and southeastern Brazil is consistent with climate forcing. *Quaternary Science Reviews* 146: 54–65.
- Safford HD (1999a) Brazilian Páramos I. An introduction to the physical environment and vegetation of the Campos de altitude. *Journal of Biogeography* 26(4): 693–712.
- Safford HD (1999b) Brazilian Páramos II. Macro- and mesoclimate of the campos de altitude and affinities with high mountain climates of the tropical Andes and Costa Rica. *Journal of Biogeography* 26(4): 713–737.
- Safford HD (2007) Brazilian Páramos IV. Phytogeography of the campos de altitude. *Journal of Biogeography* 34(10): 1701–1722.
- Schäbitz F, Wille M, Francois J-P et al. (2013) Reconstruction of palaeoprecipitation based on pollen transfer functions – The record of the last 16 ka from Laguna Potrok Aike, southern Patagonia. *Quaternary Science Reviews* 71: 175–190.
- Scheer MB and Mocoichinski AY (2016) Upper montane grassland structure within six subranges of Serra do Mar, Southern Brazil. *Hoehnea* 43(3): 401–435.
- Tonello MS, Mancini MV and Seppä H (2009) Quantitative reconstruction of Holocene precipitation changes in southern Patagonia. *Quaternary Research* 72(3): 410–420.
- Whitmore J, Gajewski K, Sawada M et al. (2005) Modern pollen data from North America and Greenland for multi-scale paleoenvironmental applications. *Quaternary Science Reviews* 24(16): 1828–1848.
- Williams JW, Grimm EC, Blois JL et al. (2018) The Neotoma Paleocology Database, a multiproxy, international, community-curated data resource. *Quaternary Research* 89(1): 156–177.
- Wilmshurst JM and McGlone MS (2005) Origin of pollen and spores in surface lake sediments: Comparison of modern palynomorph assemblages in moss cushions, surface soils and surface lake sediments. *Review of Palaeobotany and Palynology* 136(1): 1–15.
- Zanon M, Davis BAS, Marquer L et al. (2018) European Forest cover during the past 12,000 years: A palynological reconstruction based on modern analogs and remote sensing. *Frontiers in Plant Science* 9: 253.