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A quantitative study of modern pollen-vegetation relationships in southern Brazil’s *Araucaria* forest.

Macarena L. Cárdenas[a,b], Oliver J. Wilson[a]*, Lauri A. Schorn[c], Francis E. Mayle[a], José Iriarte[d]

[a] School of Archaeology, Geography and Environmental Science (SAGES), University of Reading, Whiteknights, P.O. Box 227, Reading RG6 6DW, Berkshire, United Kingdom

[b] Present address: Earthwatch Institute, Mayfield house, 256 Banbury Road, Oxford, OX2 7DE, United Kingdom

[c] Departamento e Engenharia Florestal, Universidade Regional de Blumenau, Brazil, 47-3221-6043, 47-99973-4820

[d] Department of Archaeology, University of Exeter, North Park Rd, Exeter, EX4 4QE, United Kingdom

* Corresponding author: o.j.wilson@reading.ac.uk

Abstract

Southern Brazil’s highland *Araucaria* forest is ancient, diverse and unique, but its future is under significant threat from 20th Century habitat loss and 21st Century climate change. Palaeoecological studies have revealed that it expanded rapidly over highland grasslands around 1,000 years ago, but whether this expansion was caused by human land use or climate change has been a topic of considerable debate. Discriminating between these potential drivers has so far not been possible with fossil pollen, however, as the palynological representation of floristic and structural differences in *Araucaria* forest remains poorly understood. Here, we address this shortcoming using modern pollen rain from moss polsters and vegetation surveys in forest areas with minimal current human disturbance. We show that forest plots with evident structural differences lack consistent differences in their floristic composition and cannot be reliably distinguished by their pollen spectra. We quantify pollen-vegetation relationships for 27 key tree genera of *Araucaria* forest, showing that, despite significant intra-taxon variability, 22 of these are under-represented or absent in the pollen record. These palynologically under-represented and silent taxa include many of the forest's most ecologically important tree species, with only *Araucaria, Lamanonia*, *Podocarpus*, *Myrsine* and *Clethra* being more abundant in the pollen rain than vegetation. Our results suggest that subtle structural changes in *Araucaria* forest, as well as moderate to significant floristic changes, may not be clearly distinguished in fossil pollen records – an important limitation when attempting to identify past human and climatic impacts on *Araucaria* forest via pollen analysis.

Key words: *Araucaria* forest, pollen, moss polsters, modern analogues, human impact

1. Introduction

1.1. Rationale

Disentangling the past effects of humans and climate on ecosystems requires a rigorous understanding of the vegetation changes that occurred, and how these are reflected in palaeoecological proxies. This is an important undertaking in Brazil's *Araucaria* forest (also known as Mixed Ombrophilous Forest), an ancient, highly diverse and threatened ecosystem in the country's southern highlands. Studies have charted changes in the distribution of *Araucaria* forest in relation to climatic variations since the late Pleistocene (Behling et al., 2004; Ledru et al., 2009), many finding rapid increases in its pollen abundance about 1,000 years ago which, in some sites, reached levels unprecedented for tens of thousands of years (Behling et al., 2004; Gu et al., 2017). This marked expansion ca. 1000 years ago was much more drastic than the steady expansion of *Araucaria* forest over the previous few millennia, and has been attributed by some authors to ancient human land use, rather than climate change, due to the coincident expansion of the local southern proto-Jê culture (Bitencourt and Krauspenhar, 2006; dos Reis et al., 2014; Lauterjung et al., 2018; Noelli, 2000; Robinson et al., 2018), whose economy, spiritual beliefs and living space were closely linked to the forest (De Souza et al., 2016a; Iriarte et al., 2016; Iriarte and Behling, 2007).

Understanding the extent to which *Araucaria* forest's late-Holocene expansion can be attributed to humans versus climate change will improve our understanding of the ecosystem's responses to prevailing climatic conditions – a particularly important endeavour in the face of continuing anthropogenic climate change. With regional temperatures forecast to become warmer, and precipitation more variable, as this century progresses (Chou et al., 2014), the cold- and humidity-dependent *Araucaria* forest is likely to contract (Bergamin, 2017; Wrege et al., 2009). Understanding how this iconic forest responded to past variations in climate – and how humans may have altered this response – may help conservationists anticipate and ameliorate the effects of modern climatic changes upon its distribution. This is especially important as *Araucaria* forest cover was much reduced by the 20th Century logging boom in the states of Paraná, Santa Catarina and Rio Grande do Sul (Carvalho and Nodari, 2010), with remnants now covering just 12.6% of the biogeographic region it previously dominated (Ribeiro et al., 2009).

The main proxy used for reconstructing past dynamics of vegetation on the southern Brazilian highlands is fossil pollen from lake/bog sediments, the informed and accurate interpretation of which requires appropriate characterisation and quantification of modern pollen-vegetation relationships. This is currently poor for Brazil's *Araucaria* forest. Existing pollen-vegetation studies (Behling et al., 2001; Garcia et al., 2004; Jeske-Pieruschka et al., 2010) are purely qualitative, identifying *Araucaria* forest's key indicator taxa but giving little insight into the degree to which the floristic composition or structure of these forests can be resolved palynologically. In this study, we address this shortcoming, presenting the first quantitative examination of the modern pollen-vegetation relationship of *Araucaria* forest and its constituent taxa.

1.2. Background

Araucaria forest is found at the southern and south-eastern reaches of the Atlantic Forest biome, a global biodiversity hotspot (Colombo and Joly, 2010; Myers et al., 2000). It occupies the biome's high-altitude and low-temperature extreme niches (Neves et al., 2017; Oliveira-Filho et al., 2014), mostly occuring above 500m altitude (Hueck, 1953; Lacerda, 2016) in areas with high annual rainfall and climatic conditions classified as Cfb – humid subtropical oceanic climate, with temperate summers and no dry season (Alvares et al., 2013) – under the Köppen system (Higuchi et al., 2012; Hueck, 1953). At more southerly latitudes in Brazil, some apparently natural stands of *Araucaria* forest can also be found at elevations below 500m (Behling et al., 2016).

Araucaria forest is home to over 1,500 species of plants, 6% of which are endemic to the Atlantic Forest biome (Neves et al., 2017), and is characterised by the dominance of the conifer *Araucaria angustifolia* in its canopy (Duarte et al., 2014; Leite and Klein, 1990; Meyer et al., 2013). This species has the third highest EDGE score (a metric which combines evolutionary distinctiveness and global endangerment) of all the world's gymnosperms (Forest et al., 2018), imperilled by logging and habitat loss which started in the late 19th Century and reduced the forests' area by 97% within three generations (Carvalho and Nodari, 2010; Thomas, 2013). Other important arboreal species include *Dicksonia sellowiana, Podocarpus sellowiana, Matayba elaeagnoides, Lithraea brasiliensis, Clethra scabra, Ocotea porosa*, and *Prunus myrtifolia* (Duarte et al., 2014; Meyer et al., 2013).

Araucaria forest is not floristically homogenous, however. Early studies differentiated eight types of *Araucaria* forest (Klein, 1978), and the ecosystem's mixture of tropical and temperate elements varies with longitude, altitude, temperature, river basin, and distance to other forest types (Duarte et al., 2014; Gonçalves and Souza, 2014; Higuchi et al., 2012; Klein, 1975; Oliveira-Filho et al., 2014; Sevegnani et al., 2016). At higher altitudes, under drier conditions and in areas of high fire frequencies and shallower soils, *Araucaria* forest forms mosaics with campos grasslands (Hueck, 1966; Müller et al., 2012; Oliveira-Filho et al., 2014), with other ecotones occurring with seasonally deciduous and dense ombrophilous forests at its western and eastern extents, respectively (Gonçalves and Souza, 2014; Oliveira-Filho et al., 2014).

Fossil pollen records from the eastern edge of southern Brazil's highland plateau show that the area was dominated by campos at the Last Glacial Maximum, with *Araucaria* forest likely confined to river valleys (Behling, 2002; Behling et al., 2004; Leonhardt and Lorscheitter, 2010). These forests subsequently expanded slightly 4,000-3,000 years ago, and then rapidly 1,500-900 years ago (Behling, 1997a, 1995; Behling et al., 2004; Iriarte and Behling, 2007; Jeske-Pieruschka and Behling, 2012; Leonhardt and Lorscheitter, 2010; Silva and Anand, 2011), in some places replacing grasslands within a century (Behling et al., 2004; Iriarte and Behling, 2007).

These changes have typically been attributed to climate change (Rodrigues et al., 2016a). However, recent speleothem data (Bernal et al., 2016) show that, although the initial *Araucaria* forest expansion at 4,000 yr BP does correlate with an increase in rainfall, no subsequent climate change accompanies the later, more significant forest expansion at 1,500-900 yr BP (Robinson et al., 2018). This has led several authors to invoke humans as the most likely cause for this most recent, rapid expansion of *Araucaria* forest (Bitencourt and Krauspenhar, 2006; dos Reis et al., 2014; Iriarte and Behling, 2007; Noelli, 2000), bolstered by evidence that, under natural conditions, expansion of forest patches into campos grassland can be extremely slow (less than 100m in 4,000 years (Silva and Anand, 2011)).

Before European arrival, the indigenous people of the highlands, the southern Jê, had lifestyles that were at least semi-sedentary and practised a mixed economy that combined the cultivation of manioc (*Manihot esculenta*), maize (*Zea mays*), squash (*Cucurbita* sp.) and beans (*Phaseolus* sp.) with hunting, fishing, and gathering forest and riverine resources (Corteletti et al., 2015; De Souza et al., 2016b; Henry, 1964; Métraux, 1946; Noelli and De Souza, 2017). *Araucaria angustifolia* seeds, known as pinhão, have long been a critical food source for the southern Jê (Corteletti et al., 2015; Heineberg, 2014; Henry, 1964; Loponte et al., 2016; Métraux, 1946; Urban, 1985), with one group traditionally defining a year as “one period with no pine nuts” (Henry, 1964, p. 68). Ethnographic studies of extant southern Jê groups have also highlighted the importance of *Araucaria* forest – and *A. angustifolia* in particular – as a source of spiritual power and cultural identity (Fernandes and Piovezana, 2015; Haverroth, 1997; Hoffmann, 2011; Robinson et al., 2017; Silva, 2002).

Archaeological records show that the southern Jê flourished around 1,000 years ago (Iriarte et al., 2016, 2013; Noelli and De Souza, 2017; Robinson et al., 2018), as changes in domestic architecture appeared (De Souza et al., 2016b), combining with the arrival of funerary mound-and-enclosure complexes (De Souza et al., 2016a; Iriarte et al., 2016) to form highly structured ‘sacred landscapes’ (Iriarte et al., 2013) in the highlands. The temporal overlap of these changes with the most recent *Araucaria* forest expansion suggests that more available forest resources likely helped underpin the cultural changes (Iriarte and Behling, 2007), and there is some evidence that the southern Jê may in turn have helped expand the forest (dos Reis et al., 2014; Lauterjung et al., 2018; Robinson et al., 2018), though this has not yet been tested with fossil pollen data.

1.3. Aims

Quantitative studies of the relationships between present-day *Araucaria* forest and its constituent pollen assemblages are needed to improve the level of ecological detail that can be extracted from fossil pollen records, and thereby obtain a firmer basis for unravelling the relative roles of climate change versus human land use in driving this threatened forest's long-term dynamics over the past several millennia. We therefore conducted a study to quantitatively define the vegetation-pollen relationships of *Araucaria* forest taxa. Specifically, we analysed floristic inventories from vegetation plots, and collected their constituent pollen assemblages from moss polsters, to determine: 1. whether structurally different *Araucaria* forest patches can be differentiated by their pollen spectra, and 2. how the constituent species of these patches are represented in the modern pollen rain.

2. Methods

2.1. Study site

[Insert Figure 1 here]

Figure 1: Map of forest plot locations; numbers refer to plot codes (see Table 1 below). Plot colours: Cyan: riverine; Olive: slope; Black: rock outcrop; Purple: open understorey; Orange: closed understorey; Red: disturbed.

The Reserva Particular do Patrimonio Natural (RPPN) Emilio Einsfeld Filho (27°58'0.80"S, 50°49'20.03"W, 650-990 m a.s.l.), managed by the Florestal Gateados company, is located in the municipalities of Campo Belo do Sul and Capão Alto, southern Santa Catarina State, Brazil (Figure

1). RPPN Emilio Einsfeld Filho is located on the plateau of the Serra Catarinense, a gently undulating landscape. The reserve covers 6,329 hectares of native *Araucaria* forest patches within a wider matrix of campos grassland, with the largest density of forest along rivers, valleys and slopes. Forested areas have been protected from timber extraction since 1989 and cattle grazing since 1993 (Zeller, 2010).

The climate of the area corresponds to Cfb in the Köppen classification: humid subtropical with temperate summers and no dry season, but with occurrence of severe frosts (Alvares et al., 2013; Formento et al., 2004; Zeller, 2010). Between 2005 and 2009 the reserve's average annual temperature was 16^{o}C, with hottest months averaging 31^{o}C, coldest months averaging 6.5^{o}C and a lowest recorded temperature of -12^{o}C; in this period annual precipitation varied between 1300 and 2400 mm, with an average of 129 rainy days a year (Zeller, 2010).

2.2 Field sampling

2.2.1 Vegetation survey

The native *Araucaria* forest at RPPN Emilio Einsfeld Filho has been subject to ecological studies for the last 20 years, with permanent plots of 10 x 50 m installed to perform floristic inventories and study forest dynamics under distinct geographic conditions. Within each plot all trees with d.b.h. (diameter at breast height) ≥ 10 cm have been recorded (Formento et al., 2004; Maçaneiro et al., 2018). Percentage abundances were calculated based upon all recorded stems surveyed within each plot.

The sixteen plots used in this study are located within the oldest and least disturbed areas of forest and incorporate the widest available range of vegetation form and physical setting (Table 1). Data on canopy openness, slope, animal disturbance, geographical feature associations and topographic position were collected during botanical surveys in 2015, and the plots classified into six structural categories according to their dominant feature:

- slope: forest patches in areas with > 25% inclination
- rock outcrop: forest patches where rock outcrops cover > 20% of plot surface
- riverine: forest patch bounded by, or entirely within 50 m of, a water course (river or creek)
- open understorey: forest with closed canopy and scarce understorey
- closed understorey: forest with closed canopy and dense understorey
- naturally disturbed: forest patches with evidence of ground disturbance by wild boars

Plot ID	**Forest Plot category**	**Coordinates**	**Altitude (a.s.l.)**
114	Slope	28° 2'34.70"S, 50°45'21.40"W	780 m
118	Slope	28° 3'28.80"S, 50°45'45.80"W	924 m
117	Rock outcrop	28° 3'0.10"S, 50°45'16.50"W	856 m
110	Riverine	28° 1'17.30"S, 50°46'55.50"W	721 m
136	Riverine	28° 1'55.50"S, 50°45'59.00"W	740 m
151	Riverine	28° 3'22.50"S,	874 m

		50°45'29.60"W	
119	Open understorey	28° 3'16.80"S, 50°45'51.70"W	929 m
122	Open understorey	28° 2'59.00"S, 50°46'28.10"W	921 m
123	Open understorey	28° 3'4.10"S, 50°46'11.60"W	935 m
142	Open understorey	28° 3'42.60"S, 50°46'26.60"W	922 m
144	Open understorey	28° 3'24.30"S, 50°46'21.50"W	953 m
156	Disturbed	28° 4'29.00"S, 50°46'22.10"W	850 m
157	Disturbed	28° 4'11.80"S, 50°46'20.90"W	851 m
159	Disturbed	28° 4'21.60"S, 50°45'53.60"W	868 m
141	Closed understorey	28° 3'40.70"S, 50°46'14.90"W	931 m
149	Closed understorey	28° 3'53.50"S, 50°45'39.20"W	891 m

Table 1: The studied forest plots, their structural category, and the location and altitude of each transect’s starting point.

2.2.2 Modern pollen rain

Using moss polsters to study modern pollen rain has been widely used and recognized as a reliable technique (Atanassova, 2007; Caseldine, 1989; Hicks, 1977; López-Sáez et al., 2010; Pardoe, 2006; Pardoe et al., 2010; Tonkov et al., 2001). Moss polsters can collect several years’ pollen (Pardoe et al., 2010), occur naturally within the forest on different substrates and at varied heights (allowing for effective capture of pollen rain) and do not need to be installed and managed before analysis (Hicks, 1985). Moss polsters were gathered every 10 m along the 50 m length of each forest inventory plot surveyed. At each collection point, polsters were obtained from ground level (including rocks), chest height (1.20 m) and overhead (1.80 m). The samples for each point of collection were mixed to form one homogeneous sample for each plot (following Pardoe et al., 2010), placed in a labelled, sealed plastic bag, and stored at 4^{o}C to preserve the material.

2.3. Laboratory methods

Subsamples of 1 cm^3 were extracted from each homogenised sample for pollen processing. Each subsample was centrifuged, washed with distilled water, centrifuged again, then treated with 10% NaOH and put in a hot-water bath to deflocculate the organics. Afterwards, acetolysis was carried out in the samples to dissolve cellulose material (Faegri and Iversen, 1989).

Samples were mounted on slides in silicone oil and counted at 400× and 1000× magnification using a Leica DME binocular microscope. Samples were counted to a minimum of 300 terrestrial pollen grains. Aquatic taxa and spores were also counted as is standard practice, but were excluded from the total terrestrial pollen (TTP) sum; non-native species (e.g. pine from recent plantations surrounding the reserve) were also excluded from the TTP sum. For pollen determination, the reference collection of the Tropical Palaeoecology Research Group of the University of Reading was used, along with several pollen atlases – Colinvaux et al. (1999), Hooghiemstra (1984), Roubik and Moreno (1991), Behling (1993) – and the online Neotropical Pollen Key (Bush and Weng, 2007). Diagrams of vegetation and pollen abundance were made using C2 v.1.7.7 (Juggins, 2016).

2.4. Data analysis

2.4.1 Vegetation data processing

Analysis of each plot's floristic inventory data used percentage abundance (relative to the total number of individual trees counted) and relative coverage value (RCV). RCV (expressed as a percentage) indicates the importance of a species within a forest plot, taking into account its individuals' density and dominance.

$$RCVi = \frac{(RDoi + RDeni)}{\sum(RDo + RDen)} * 100$$

RCVi: Relative Coverage Value for species i (%)

RDoi: Relative dominance for species i (basal area (m²) per hectare)

RDeni: Relative density for species i (number of individuals per hectare)

RDo: Relative dominance for all species (m² / ha)

RDen: Relative density for all species (n / ha)

2.4.2 Statistical analysis of vegetation and pollen data

To investigate the extent to which structural differences between plots are reflected in their vegetation composition and pollen rain, we conducted cluster and Detrended Correspondence Analysis (DCA) multivariate analyses using PAST (Hammer et al., 2001) v.3.19 (2018). Raw floristic inventory and pollen data were normalised using natural logarithm before running the analyses. Only taxa with abundance ≥ 2% in two or more plots were considered for cluster and multivariate analysis.

Cluster analysis was run with hierarchical clustering using the Unweighted Pair Group Method (UPGM) algorithm, which iteratively joins clusters based on the average distance between all members of the groups (Kent and Coker, 1992; Legendre et al., 2012). The measure of similarity or distance measurements between samples (forest plots) was calculated using Bray-Curtis index of dissimilarity (Kent and Coker, 1992). The DCA uses the same algorithm as Decorana (Hill and Gauch, 1980), with modifications according to Oksanen and Minchin (1997). The DCA method was preferred as it allows the identification of the ecological variances amongst the forest plots (Correa-Metrio et al., 2014).

To enable direct comparisons between taxa in the vegetation and pollen rain, which were mostly identified at different taxonomic levels, the vegetation-pollen analysis was performed at genus level, with congeneric species combined for the analysis (Burn et al., 2010).

To quantify the vegetation-pollen relationships of taxa in this study area, we calculated mean p/v (pollen/vegetation) values (Burn et al., 2010; Gosling et al., 2009; Montade et al., 2016), which are analogous to R values (Davis, 1963). We calculate the p/v value for taxon *i* as:

$$p/v_i = \frac{Pollen\ abundance\ (\%)\ averaged\ over\ all\ plots_{\ i}}{Vegetation\ abundance\ (\%)\ averaged\ over\ all\ plots_{\ i}}$$

Although more complex measures of pollen production exist (e.g. Parsons and Prentice, 1981; Sugita, 2007a, 2007b), p/v values provide a straightforward and intuitive index of the relationship between vegetation and pollen abundance and continue to be foundational for vegetation reconstruction (Mrotzek et al., 2017).

To complement this metric and show the variability in pollen-vegetation relationships between plots, we also calculated a pollen-vegetation abundance differential for taxon *i*:

$$Abundance\ differential_i = Pollen\ abundance\ (\%)_i - Vegetation\ abundance\ (\%)_i$$

Plots where a taxon was absent from both the pollen rain and vegetation survey were not included in calculations of mean differentials. p/v values and abundance differentials could not be calculated for herbaceous taxa as these were not included in the vegetation survey. Data were plotted using R v.3.4.2 (R Core Team, 2017) and PAST (Hammer et al., 2001) v.3.19 (2018).

3. Results

3.1. Vegetation

Across the 16 forest plots, 54 tree species with d.b.h. ≥ 10 cm were recorded, of which 33 had relative abundances of 2% or higher in at least two plots; the relative (percentage) abundance of these species within each plot is shown in Figure 2. The most consistently present species were *Lithraea brasiliensis* (15 plots), *Cinnamodendron dinisii* (13 plots), *Myrsine coriacea, Ocotea pulchella* and *Araucaria angustifolia* (12 plots), undifferentiated *Eugenia* sp. (11 plots), and *Calyptranthes* cf. *concinna, Ilex theezans, Pera glabrata, Podocarpus lambertii* and *Zanthoxylum kleinii* (10 plots).

The taxa with the highest average abundance in the vegetation were *L. brasiliensis* (9.1%), *Cinnamodendron dinisii* (7.7%), *A. angustifolia* (7.3%), undifferentiated *Eugenia* sp. (6.7%), *O. pulchella* (5.7%), and *Calyptranthes* cf. *concinna* (5.0%). Of the common taxa, *L. brasiliensis* had the highest maximum abundance (34.2%), followed by *Eugenia* sp. (26.4%), *A. angustifolia* (26.1%), *E. uniflora* (25.7%) and *Cinnamodendron dinisii* (24.1%). Two less common species with high maximum abundances were *Matayba elaeagnoides* (found in three plots, max. 35.6%) and *Nectandra megapotamica* (three plots, max. 28.6%).

Generally, tree species that were more abundant also had higher relative coverage values (RCVs;

Figure 3): the taxa with the highest RCVs averaged across all plots were *L. brasiliensis* (10.3%), *A. angustifolia* (10.0%), *O. pulchella* (7.8%), *C. dinisii* (6.1%), *Styrax leprosus* (5.3%) and undifferentiated *Eugenia* sp. (5.2%). Some species were found in few plots, but had high RCVs where they were present: the less frequent species with the highest RCVs averaged across the plots in which they were found were *M. elaeagnoides* (15.6%, four plots), *Luehea divaricata* (9.2%, three plots), *N. megapotamica* (9.0%, three plots), *Vernonanthura discolor* (7.4%, five plots), *Sebastiania commersoniana* (7.0%, six plots), *Prunus myrtifolia* (5.7%, six plots), *Piptocarpha angustifolia* (5.2%, two plots), *Myrceugenia* sp. (5.1%, five plots) and *Myrsine umbellata* (5.0%, two plots).

3.2. Pollen

170 pollen and spore types were found in the 16 forest plots. Of these, 118 could be identified to family level, 95 of which could be refined to genus, one to species (*Ilex theezans*). We also assign species names to *Araucaria angustifolia* and *Podocarpus lambertii* because no other species of these genera occur in our study area. The plots' pollen spectra are summarised in Figure 4, where abundant and important taxa are shown.

Eight pollen types were found in all 16 plots: *A. angustifolia*, Asteraceae (others total), *Eugenia* type, 'cf *Lithraea* a (Anacardiaceae)', *Myrsine*, Poaceae, *P. lambertii*, and Pteridophyta. Additionally, Araceae pollen was found in 15 plots, and *Lithraea, Vernonanthura*-type and *Calyptranthes*-type in 14; *Sebastiania* and undifferentiated Myrtaceae pollen was found in 12 plots, and *Clethra*, *I. theezans* and *Pteris* each in 10 plots. Additionally, *Alchornea* pollen and *Cyathea*-type spores were found at very low levels (average abundance 0.27% and 0.2% respectively) in 11 plots, with *Senecio*-type (average 0.35%) and *Mimosa scabrella*-type (average 0.25%) present in 10 plots.

Myrsine pollen was the most abundant across all plots (averaging 19.5%), followed by *A. angustifolia* (16.6%), Pteridophyta (13.2%), *Podocarpus lambertii* (7.9%) and Poaceae (5.2%).

Eugenia-type, ‘cf *Lithraea* a (Anacardiaceae)’, Asteraceae (others total), *Lamanonia*, *I. theezans, Calyptranthes*-type, *Vernonanthura*-type and *Clethra* pollen all had average abundances between 1% and 5%.

[Insert Figure 2 here]

Figure 2: Relative abundance (%) of selected tree species in the vegetation survey. Species included in the cluster analysis and DCA are indicated with an asterisk.

[Insert Figure 3 here]

Figure 3: Relative Coverage Values (RCVs, %) of selected tree species in the vegetation survey. ‘Ave. (all)’ = sum of RCVs/total number of plots; ‘Ave. (present)’ = sum of RCVs/number of plots in which taxon was present.

[Insert Figure 4 here]

Figure 4: Relative abundance (%) of selected pollen types. Taxa included in the cluster analysis and DCA are indicated with an asterisk

3.3. Plot differentiation

33 taxa from the vegetation survey and 15 pollen types met the 2% abundance threshold for inclusion in the plot differentiation analysis (see section 2.4.2); these are identified with asterisks in the summary diagrams (Figures 2 and 4).

[Insert Figure 5 here]

Figure 5: Cluster analyses (left; a, c) and DCAs (right; b, d) of plots by vegetation (top; a, b) and pollen (bottom; c, d) taxa found in ≥2 plots at ≥2% abundance. In the DCAs, convex hulls are delimited for structural categories containing three or more plots. Plot types are identified by colour and two-letter code (op: open; cl: closed; ri: riverine; di: disturbed; ro: rock; sl: slope; see

Table 1).

In the cluster analysis of vegetation data (Figure 5a), similarity scores range from ~0.25 to > 0.75. Two plot groupings that are somewhat structurally consistent can be highlighted. One such cluster contains three of the five open-understorey plots (P119, P122 and P123) with the lone slope plot P118 (similarity score > 0.65); the other is the pairing of riverine plots P136 and P110 which, despite having similarity scores < 0.6 relative to each other, are together highly dissimilar to all other plots.

In the DCA of vegetation data (Figure 5b), most variation is explained on axis 1 (eigenvalue 0.3781), with values ranging from -196 (*Cyathea* sp.) to 365 (*Nectandra megapotamica*). The majority of sample plots are clustered between 0 and 143 on axis 1, with the riverine plots P136 (202) and P110 (255) more distinguished. The values on axis 2 (eigenvalue 0.1268) range from -337 (*Sapium glandulosum*) to 388 (*Myrsine umbellata*); sample plots are all clustered between 0 and 140 on this axis.

In the pollen cluster analysis (Figure 5c), plots' similarity scores range from ~0.5 to > 0.85. Two small clusters dominated by open understorey forest plots were found: P122 and P123 (both open; similarity > 0.7), and P144 and P119 (both open) with the rocky forest plot P117 (similarity > 0.7). These two groupings are quite dissimilar from each other, however, and the cluster that contains them both also contains seven non-open plots, and excludes the final open plot (P142).

In the DCA of pollen spectra (Figure 5d) axis 1 (eigenvalue 0.2454) ranges from -72 (*Pteris*) to 305 (*Lamanonia*), with 15 of the plots clustered between 0 and 119; P151 is located at 184. The forest plots are less well distinguished on axis 2 (eigenvalue 0.07194), sitting between values of 0 and 110 on an axis that ranges from -233 (Myrtaceae others total) and 426 (*Clethra* total).

3.4. Vegetation-pollen relationships.

We examined the vegetation-pollen relationships of 27 arboreal genera. Four of these

(*Myrceugenia, Nectandra, Ocotea* and *Piptocarpha*) were present in the vegetation but with no identifiable pollen produced or preserved (p/v = 0), and one (*Clethra*) was frequent in the pollen record without being recorded in the vegetation survey (giving it a mathematically infinite p/v value). Four other genera had higher average abundances for pollen than vegetation (p/v > 1), and 18 were more abundant in the vegetation than pollen (p/v < 1) – see Figure 6.

Of the taxa found in both pollen and vegetation datasets, the most over-represented genus is *Lamanonia*, followed by *Podocarpus*, *Myrsine* and *Araucaria*. In plot P151 *Lamanonia* was not recorded in the vegetation but its pollen made up 20.3% of the total; with this data point excluded from the average calculations, *Lamanonia*'s p/v value is 1.25. The most under-represented genera found in the pollen rain are *Cinnamodendron*, *Allophylus*, *Prunus*, *Styrax*, *Luehea* and *Zanthoxylum* (p/v < 0.05); *Casearia*, *Matayba*, *Pera* and *Lithraea* also have p/v scores < 0.1. *Calyptranthes, Campomanesia, Eugenia, Sapium, Sebastiania* and *Xylosma* all have p/v values between 0.1 and 0.5. The pollen type 'cf *Lithraea* a (Anacardiaceae)' was three times more common than pollen that could be confidently identified to the *Lithraea* genus; assigning these grains to *Lithraea* changes the genus's p/v score from 0.09 to 0.39.

[Insert Figure 6 here]

Figure 6: p/v values of key genera of *Araucaria* forest in this study. *Clethra* has an infinitely high p/v value; faint sections in the bars of *Lamanonia* and *Lithraea* reflect alternate calculations of their p/v values (see section 3.4).

Between-plot variability in vegetation-pollen relationships is not well demonstrated by p/v values, as their calculation requires a taxon to be present in both vegetation and pollen records for a plot. The only taxon for which this occurs in all plots is *Eugenia*, whose plot-specific p/v scores varied between 0.04 (P141) and 2.26 (P122), with 14 plots having p/v values < 1. This variability is more evident with pollen-vegetation abundance differentials (Table 3 and Figure 7). *Myrsine, Araucaria* and *Podocarpus* had the most positive mean values (all above +5%); *Nectandra, Eugenia, Lithraea, Cinnamodendron, Styrax*, *Ocotea,* and *Matayba* had the most negative mean values (all below -5%). *Lithraea*'s mean differential changes to -5.52% if 'cf *Lithraea* (Anacardiaceae)' pollen is included in the calculation.

Genus	**Mean**	**Min**	**Max**	**Range (Max-Min)**
Allophylus	-4.13	-8.57	0.20	8.77
Araucaria	+9.36	-9.48	20.63	30.11
Calyptranthes	-3.44	-17.06	1.09	18.15
Campomanesia	-2.08	-5.71	0.81	6.52
Casearia	-4.17	-13.84	0.45	14.29
Cinnamodendron	-8.08	-24.14	0.44	24.57
Clethra	+1.76	0.37	6.68	6.31
Eugenia	-8.47	-25.92	7.17	33.09
Ilex	-1.07	-8.73	2.93	11.66
Lamanonia	+2.69	-1.16	20.32	21.49
Lithraea	-8.25	-32.56	0.26	32.82
Luehea	-4.89	-8.89	0.18	9.07
Matayba	-6.29	-34.14	0.36	34.50
Myrceugenia	-4.61	-9.09	-1.75	7.34

Myrsine	+13.88	-3.05	55.75	58.80
Nectandra	-11.73	-28.57	-2.17	26.40
Ocotea	-7.25	-16.36	-1.75	14.61
Pera	-4.83	-21.04	1.21	22.25
Piptocarpha	-3.02	-4.29	-1.75	2.53
Podocarpus	+5.78	-5.73	19.24	24.97
Prunus	-3.21	-6.82	0.23	7.04
Sapium	-1.27	-5.05	0.44	5.49
Sebastiania	-4.35	-25.85	0.55	26.40
Styrax	-7.52	-22.86	0.45	23.31
Vernonanthura	-0.38	-4.89	1.83	6.72
Xylosma	-2.16	-7.02	1.49	8.51
Zanthoxylum	-4.76	-12.73	0.20	12.93

Table 3: Pollen-vegetation abundance differential values (%) for key genera of *Araucaria* forest in this study.

Myrsine had the most extreme positive values: +55.75% (P114, slope), +41.25% (P157, disturbed), +30.70% (P141, closed understorey), +26.38% (P142, open understorey) and +20.48% (P159, disturbed). Values above +20% also occurred twice for *Araucaria* (+20.63% in P151, riverine, and +20.30% in P159, disturbed) and once for *Lamanonia* (+20.32% in P151, riverine). Similarly negative values (below -20%) were more evenly spread among taxa, with two cases in *Styrax* (-22.86% in P122, open understorey, and -20.00% in P141, closed understorey) and one each in *Matayba* (-

34.14% in P136, riverine), *Lithraea* (-32.56% in P114, slope), *Nectandra* (-28.57% in P110, riverine), *Eugenia* (-25.92% in P156, disturbed), *Sebastiania* (-25.85% in P151, riverine), *Cinnamodendron* (-24.14% in P159, disturbed), and *Pera* (-21.04% in P119, open understorey).

[Insert Figure 7 here]

Figure 7: Pollen-vegetation abundance differentials (square-root transformed) for selected genera. Positive values denote plots where a taxon's pollen was more abundant than its vegetation; negative values reflect vegetation being more abundant than pollen. Blank cells denote plots where a taxon was absent from both pollen and vegetation data.

The genus with the greatest difference between maximum and minimum abundance differentials is *Myrsine*, with wide variation (> 30%) also found in *Matayba, Eugenia*, *Lithraea* and *Araucaria*; *Nectandra*, *Sebastiania*, *Podocarpus*, *Cinnamodendron*, *Styrax* and *Lamanonia* had differences between 20 and 30%. Most genera had both positive and negative abundance differentials, with the exceptions being *Clethra* (all positive) and *Myrceugenia, Nectandra, Ocotea and Piptocarpha* (all negative). However, few taxa (*Araucaria, Eugenia, Ilex, Myrsine, Podocarpus*) had differentials > 2% in both positive and negative directions.

4. Discussion

4.1. Detecting structural differences in *Araucaria* forest

The vegetation of the studied forest area is characteristic of *Araucaria* forest, containing 19 of its 30 most important tree species (Schorn et al., 2012). Three of the predominant species in this study (*A. angustifolia, O. pulchella*, *P. lambertii*), as well as others found at lower levels (*Matayba elaeagnoides, Lamanonia ternata*), are key indicator species (Gonçalves and Souza, 2014). *Lithraea brasiliensis*, the most common, abundant and dominant species in our sample plots, is the fifth most important tree across Santa Catarina's *Araucaria* forest, especially significant below 1200 m a.s.l (Meyer et al., 2013; Schorn et al., 2012).

The floristic composition of the plots is somewhat variable, with no pair of plots having a similarity score above 0.8 (Figure 5a), but this variability in composition does not generally reflect the structural differences between the plots. This can be seen in the cluster analysis (Figure 5a): three of the open understorey plots (P119, P122, P123) are clustered together along with the slope plot P118, but the remaining two open plots (P142 and P144) are far removed; the cluster that would include all five open plots would have 14 members. Similarly, the disturbed plots P157 and P159 are closely paired, but the cluster that would also include the third disturbed plot (P156) would encompass nine plots in total. The riverine plots P110 and P136 are distinct from the rest of the plots but cannot be grouped with the third member of the riverine group (P151) without including all sampled plots in the cluster.

This pattern is further shown in the DCA (Figure 5b), of which only axis 1 has an eigenvalue > 0.3 (0.3781), which would be suggestive of ecological relevance (Peterson and Gale, 1991; Rezende et al., 2015). Here again P110 and P136 are the only plots that are clearly distinguished by their vegetation. Their floristic difference to the other studied plots may partly result from their location at the northern end of the studied area, > 1.5 km from the other plots. Their regeneration stage could also be an explanatory factor: these plots have the highest RCVs for *Matayba elaeagnoides*, as well as the highest recorded abundances of the pioneer *Nectandra megapotamica*, two of the three highest abundances of *Allophylus edulis*, and the presence of *Sebastiania commersoniana*, all of which are important taxa in regenerating *Araucaria* forest patches (Meyer et al., 2013; Schorn et al., 2012).

The most common and abundant tree pollen in our study sites came from *Araucaria angustifolia*, Myrtaceae (mainly *Eugenia*), Anacardiaceae cf *Lithraea*, *Myrsine* and *Podocarpus*, with *Lithraea*, *Vernonanthura*-type, *Sebastiania*, *Ilex* and *Clethra* found in the majority of plots at generally low abundances (Figure 4). Pteridophyte spores were both common and abundant, and Poaceae was the most prevalent herbaceous pollen taxon, with Asteraceae and Araceae pollen also common but less abundant. The sum of all herbaceous pollen varies from 5-20%, averaging 10% – similar to the 5-15% found by Garcia et al. (2004) in a study of *Araucaria* forest peat deposits in Sao Paulo state, but lower than the 24-60% found by Jeske-Pieruschka et al. (2010) in a forest patch surrounded by campos grassland. The herbaceous pollen counts in the latter were likely increased by influx from the grasslands surrounding the forest, and as a result of disturbance from grazing in the studied forest patch (Jeske-Pieruschka et al., 2010).

The plots are less well differentiated by pollen than by their vegetation, as shown by their generally higher cluster similarity scores (Figure 5c). As with the vegetation there are some potential pairings of open understorey plots (P122 and P123; P119 and P144 with the rocky plot P117), but these are quite distinct from each other – the cluster that would encompass all five open plots would only exclude the riverine plot P151. No potential groupings in the pollen cluster analysis mirror clusters of the plots' vegetation (Figure 5a,c), and there are no consistent groupings of structurally similar plots. This is also seen in the DCA (Figure 5d), where the eigenvalue for axis 1 (0.2454) may indicate the separation is not ecologically relevant (Peterson and Gale, 1991; Rezende et al., 2015). Here, as in the cluster analysis, the only plot that is clearly distinguished is P151, due in large part to its exceptionally high abundance of *Lamanonia* pollen.

These results show that the notable structural differences between the different forest plot categories are not echoed in the composition of their woody taxa. Since there are no consistent floristic differences between plot types, it is unsurprising that these structural differences cannot be detected by their pollen signals – especially as pollen's sensitivity is affected by relatively coarse taxonomic resolution and differential pollen production and preservation between taxa.

4.2. Vegetation-pollen relationships

The pollen records of the studied forest plots did not consistently reflect large variations in a taxon's abundance in the vegetation (Figure 6 & 7). *L. brasiliensis*, for example, makes up 2.9% of the vegetation in P110 and 34.1% in P114 (Figure 2), but *Lithraea* pollen is equally abundant in each plot (1.6%) (Figure 4); its abundance in the vegetation is intermediate in P117 (10.9%) and P118 (12.3%) but its pollen makes up just 0.9% and 1.0% of those plot totals, respectively. This variability in vegetation-pollen relationships can also be illustrated with *Myrsine*: its pollen made up more than half of all counted grains (55.8%) in P114, despite no individuals from the genus being recorded in the vegetation survey; it was also significantly over-represented in P157 (pollen abundance 43.4%, vegetation abundance 2.2%), but proportionately represented in P119 (17.3% of the pollen; 17.0% of the vegetation) and under-represented in P118 (5.7% of the pollen, 8.8% of the vegetation).

However, general patterns of over- or under-representation of each taxon in the pollen record could be determined – only *Araucaria, Eugenia, Ilex, Myrsine* and *Podocarpus* had both positive and negative abundance differentials above 2% (Table 3). The majority (22 of 27) of the arboreal genera examined were under-represented in the pollen record (p/v values <1; Figure 6), with four (*Myrceugenia, Nectandra, Ocotea* and *Piptocarpha*) being palynologically silent. These under-represented taxa include many of the most abundant tree species in the plots, as well as some of the most ecologically important taxa in *Araucaria* forest (*Lithraea, Matayba, Cinnamodendron, Ocotea, Prunus* and *Nectandra*) (Sevegnani et al., 2013). The highest p/v value among these key genera is *Lithraea*'s 0.09 (i.e. less than one tenth as abundant in the pollen record as in the vegetation), and no pollen which could be reliably identified as *Ocotea* or *Nectandra* was counted at all.

Under-representation in the pollen record is common in the Neotropics (Bush, 1995; Bush and Rivera, 1998; Gosling et al., 2009; Haselhorst et al., 2013). This is partly due to the relative rarity of anemophilous plants – generally the most over-represented taxa – in tropical forests, although entomophilous plants are less under-represented in tropical pollen spectra than in temperate regions (Bush, 1995; Viera et al., 2012; Whitehead, 1983). Our results fit this general pattern: of the under-represented taxa in our study, *Nectandra* and *Ocotea* are pollinated by thrips (Thysanoptera) (Danieli-Silva and Varassin, 2013; Souza and Moscheta, 2000), and *Lithraea, Ilex, Matayba, Prunus, Eugenia* and *Cinnamodendron* depend on bees and other small insects (de Deus et al., 2014; Hermes and Köhler, 2006; Imperatriz-Fonseca et al., 1989; Montalva et al., 2011; Tomlinson, 1974; Wilms et al., 1997). Additionally, *Ocotea* pollen is fragile, with a thin exine that means it preserves poorly (Behling, 1993). By contrast, the over-represented taxa *Araucaria* (Bittencourt and Sebbenn, 2008, 2007) and *Podocarpus* (Midgley, 1989; Negash, 2003; Wilson and Owens, 1999) are anemophilous, as are South American members of *Myrsine* (Albuquerque et al., 2013; Otegui and Cocucci, 1999), and therefore produce abundant pollen.

Lamanonia was over-represented in the pollen record (p/v 5.44; 1.25 when excluding P151) despite being insect-pollinated (de Deus et al., 2014; Hermes and Köhler, 2006; Wilms et al., 1997). Its relative abundance of pollen in this study may be explained by its mass-flowering habit (Hermes and Köhler, 2006), so it is possible that *Lamanonia*'s pollen-vegetation relationship varies significantly year-on-year. *Clethra* is another entomophilous taxon (Freitas and Sazima, 2006) with over-represented pollen in this study: its pollen was found in 10 of the 16 plots at an average abundance of 1.10% (0.37-4.58%), but no individuals were recorded in the vegetation (Figure 2) despite *C. scabra* being the third most important tree species in *Araucaria* forest (Schorn et al., 2012). Given *Clethra* pollen is not adapted for long-distance travel, it is unlikely to have originated outside the plots; potentially, individuals from this genus were present but too small to be included in the survey (i.e. d.b.h. < 10 cm), making it difficult to make a true assessment of the taxon's pollen-vegetation relationship.

4.3. Implications for palaeoecology

Our findings have important implications for the interpretation of fossil pollen records. Many of the key taxa used to reconstruct past *Araucaria* forest dynamics were identified palynologically in this study, but two were largely missing. Pollen from *Mimosa scabrella* and *Weinmannia* is commonly cited as evidence of *Araucaria* forest (Behling, 1997a, 1995; Behling et al., 2004; Leonhardt and Lorscheitter, 2010) but *M. scabrella* pollen was not abundant (present in 10 of the 16 plots, maximum abundance 0.89%) and *Weinmannia* pollen was absent; neither species was recorded in the vegetation survey. *M. scabrella* is a species which is especially encouraged by anthropogenic forest disturbance, so its absence here may be connected to the relatively long time since the last anthropogenic disturbance of our studied plots. Moreover, both taxa (especially *Weinmannia*) are much more floristically important at elevations above 1,200 m a.s.l. (Sevegnani et al., 2013) so their absence here is unsurprising, and highlights the biases of existing palaeoecological studies towards high-altitude regions along the eastern edge of the highland plateau (Behling, 2007, 1997a, 1995; Behling et al., 2004; Jeske-Pieruschka et al., 2013; Leonhardt and Lorscheitter, 2010; Scherer and Lorscheitter, 2014).

The geographical bias of existing studies can further be seen in the classifications proposed by Rodrigues et al. (2016b) for distinguishing woodland types in southern Brazil based on pollen spectra. Although our sites (721-953 m a.s.l.) have vegetation which is most similar to that in the ‘low Poaceae subtropical forest’ (LPSF) category (Behling et al., 2004; Behling and de Oliveira, 2018; Jeske-Pieruschka et al., 2013; Jeske-Pieruschka and Behling, 2012), they are excluded from this group due to their absence of *Weinmannia* pollen. Instead, our plots would likely be included in the disparate ‘low Poaceae subtropical-tropical’ (LPST) group, along with two sites in Santa Catarina’s coastal tropical forest (9-10 m a.s.l.) (Behling, 1997b, 1995), one in northern Argentina at the westernmost limit of *Araucaria* forest taxa (604 m a.s.l.) (Gessert et al., 2011), and another at low altitude in south-central Rio Grande do Sul (176 m a.s.l.) (Santa Mônica, unpublished, cited in Rodrigues et al., 2016b) . The significant altitudinal, geographical and floristic differences between these sites suggests LPST may not be a true grouping, and that the classification of southern Brazil’s forests by their pollen spectra will improve as more westerly plateau sites, with different assemblages of *Araucaria* forest, are studied.

Most of the taxa widely used in palaeoecological studies were here found to be over-represented in the pollen record (*Araucaria, Myrsine, Podocarpus, Lamanonia*) or under-represented but very abundant in the vegetation (Myrtaceae, such as *Eugenia* and *Calyptranthes* which are rarely distinguished to genus in fossil pollen). Fossil *Lithraea* pollen is quite often identified (Behling, 2007; Behling et al., 2016, 2005; Gessert et al., 2011) or grouped with *Schinus* (Behling, 1997b, 1997a; Behling et al., 2004; Jeske-Pieruschka et al., 2010) but rarely treated as important (but see Behling, 1997a; Gessert et al., 2011); given the floristic importance of *L. brasiliensis* (Meyer et al., 2013; Schorn et al., 2012) and its under-representation in the pollen rain (p/v 0.09-0.39, pollen 8.25% less abundant than vegetation on average), the presence and dynamics of *Lithraea* pollen may warrant more detailed examination in future studies. *Lithraea* is one of several key *Araucaria* forest taxa we have shown to be either significantly under-represented (*Matayba, Cinnamodendron, Prunus*) or absent (*Ocotea, Nectandra*) in the pollen record, even when quite abundant in the vegetation. This suggests that some significant changes in past forest composition may not be reflected in fossil pollen, highlighting a potentially important limitation of pollen as a palaeoecological proxy for determining this ecosystem’s responses to past millennial-scale human land use and climate changes.

The importance of fossil pollen’s limited sensitivity to compositional changes in *Araucaria* forest is reinforced when considering that structural differences between plots were not clearly reflected in their pollen signals. Although the plots had notably different structural characteristics to one another, this was only weakly echoed in the floristic composition of their arboreal component, and even less so in their pollen spectra, which were more similar to each other than the vegetation. This implies that pollen records may not clearly detect structural changes in *Araucaria* forest, especially when these are not accompanied by significant or long-term alterations in floristic composition. Further investigations of the sensitivity of pollen rain to larger-scale changes in composition and structure of *Araucaria* forest might involve integration with the state-wide plot network of the Santa Catarina forest floristic inventory (Vibrans et al., 2010) or palynological examination of forest fragments with relatively intense present human land use, such as caívas, faxinais or ervais (Fichino et al., 2017; Mello and Peroni, 2015; Reis et al., 2018). Such research would aid the interpretation of fossil pollen records which do show significant changes with climatic changes and human land use (e.g. Behling et al., 2004), permitting shifts in pollen composition to be more accurately related to changes in the vegetation.

The difficulty of detecting structural and compositional changes in *Araucaria* forest with pollen records has implications for the reconstruction of past human impacts on the forest. Before European arrival, the indigenous southern Jê people lived in semi-subterranean dwellings in the forest, practising swidden cultivation and exploiting *Araucaria angustifolia* nuts and Myrtaceae fruits (Corteletti, 2012; Corteletti et al., 2015; dos Reis et al., 2014; Iriarte and Behling, 2007). It has been suggested that their lifestyles helped to spread *Araucaria* forest more quickly than natural drivers, such as climate change, and even beyond the forest's natural limits (Bitencourt and Krauspenhar, 2006; Iriarte and Behling, 2007; Lauterjung et al., 2018; Noelli, 2000; Robinson et al., 2018), but our findings raise the question of whether, and how, more subtle impacts within the forest – especially structural and compositional changes – would be represented in fossil pollen sedimentary archives. There is significant ongoing debate over the extent to which pre-Columbian peoples altered the floristic composition of Amazonian forests (Barlow et al., 2012; Levis et al., 2018, 2017; McMichael et al., 2017; Shepard and Ramirez, 2011) and the limitations of fossil pollen analysis in identifying such impacts are well known (e.g. Carson et al., 2016), with recent simulations showing that pollen sites in tropical forest-grassland mosaics (like those between *Araucaria* forest and campos grasslands) may be insensitive to large changes in forest cover (Whitney et al., 2019). The forest plots in our study have been free of human disturbance for several decades, so their present condition is unlikely to mirror the full range of southern Jê land use. Nevertheless, our findings highlight potential limitations of pollen analysis as a tool for investigating and reconstructing the role of the southern Jê in shaping the *Araucaria* forest's floristic composition and structure – the absence of evidence of human impacts may not equate to evidence of their absence.

5. Conclusions

In this study, the pollen rain from 16 structurally different *Araucaria* forest plots has been characterised and compared with floristic inventory data, and 27 tree genera have had their vegetation-pollen relationships quantified.

Our results show that the structurally different plots do not exhibit consistent differences in the floristic composition of their tree taxa. Correspondingly, their structural differences cannot be clearly detected in their pollen rain, with pollen spectra more similar than vegetation between plots.

On average, the most abundant tree species in the plots are *Lithraea brasiliensis*, *Cinnamodendron dinisii*, *Araucaria angustifolia*, *Eugenia* sp., *Ocotea pulchella* and *Calyptranthes* cf. *concinna,* representing the typical composition of *Araucaria* forest at this altitude. As well as these*, Styrax leprosus* has a high average relative coverage value (RCV) across all plots, and species including *Matayba elaeagnoides*, *Nectandra megapotamica*, *Vernonanthura discolor*, *Prunus myrtifolia*, *Piptocarpha angustifolia*, *Myrceugenia* sp. and *Myrsine umbellata* have high RCVs in the (relatively few) plots in which they occur. The modern pollen rain of *Araucaria* forest in our study area (720-920m a.s.l.) is characterised by *Myrsine* (19.5%), *A. angustifolia* (16.6%), Pteridophyta (13.2%), *Podocarpus lambertii* (7.9%) and Poaceae (5.2%), along with *Eugenia*-type, Anacardiaceae cf. *Lithraea*, Asteraceae (others), *Lamanonia*, *Ilex theezans, Calyptranthes*-type, *Vernonanthura*-type and *Clethra* at lower abundance.

Vegetation-pollen relationships vary between plots but general patterns of over- or under-representation could be identified for the majority of taxa. *Araucaria, Lamanonia*, *Podocarpus*, and *Myrsine* are over-represented in the pollen record (average p/v >1), and *Clethra* pollen was frequently identified but the genus is absent from the vegetation survey. All of the other 22 genera analysed are under-represented, with *Myrceugenia, Nectandra, Ocotea* and *Piptocarpha* palynologically silent.

The palynological under-representation of ecologically key *Araucaria* forest taxa and the lack of clear differentiation of structural differences in the forest's pollen spectra have important implications for the interpretation of fossil pollen records, highlighting the challenges of resolving past human impacts and ecological changes within *Araucaria* forest using this proxy. This quantitative analysis of vegetation-pollen relationships for key *Araucaria* forest taxa is a key tool for interpreting fossil pollen records and understanding past vegetation dynamics on the highlands of southern Brazil.

Author contributions

MLC and FEM conceived the study; MLC collected moss polsters; MLC and LAS collected vegetation survey data; MLC performed pollen analysis and counting; MLC and OJW analysed the data and interpreted the results; OJW, MLC and FEM drafted the manuscript; all authors commented on the manuscript before submission.

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Figures

Figure 1: Map of forest plot locations; numbers refer to plot codes (see Table 1 below). Plot colours: Cyan: riverine; Olive: slope; Black: rock outcrop; Purple: open understorey; Orange: closed understorey; Red: disturbed.

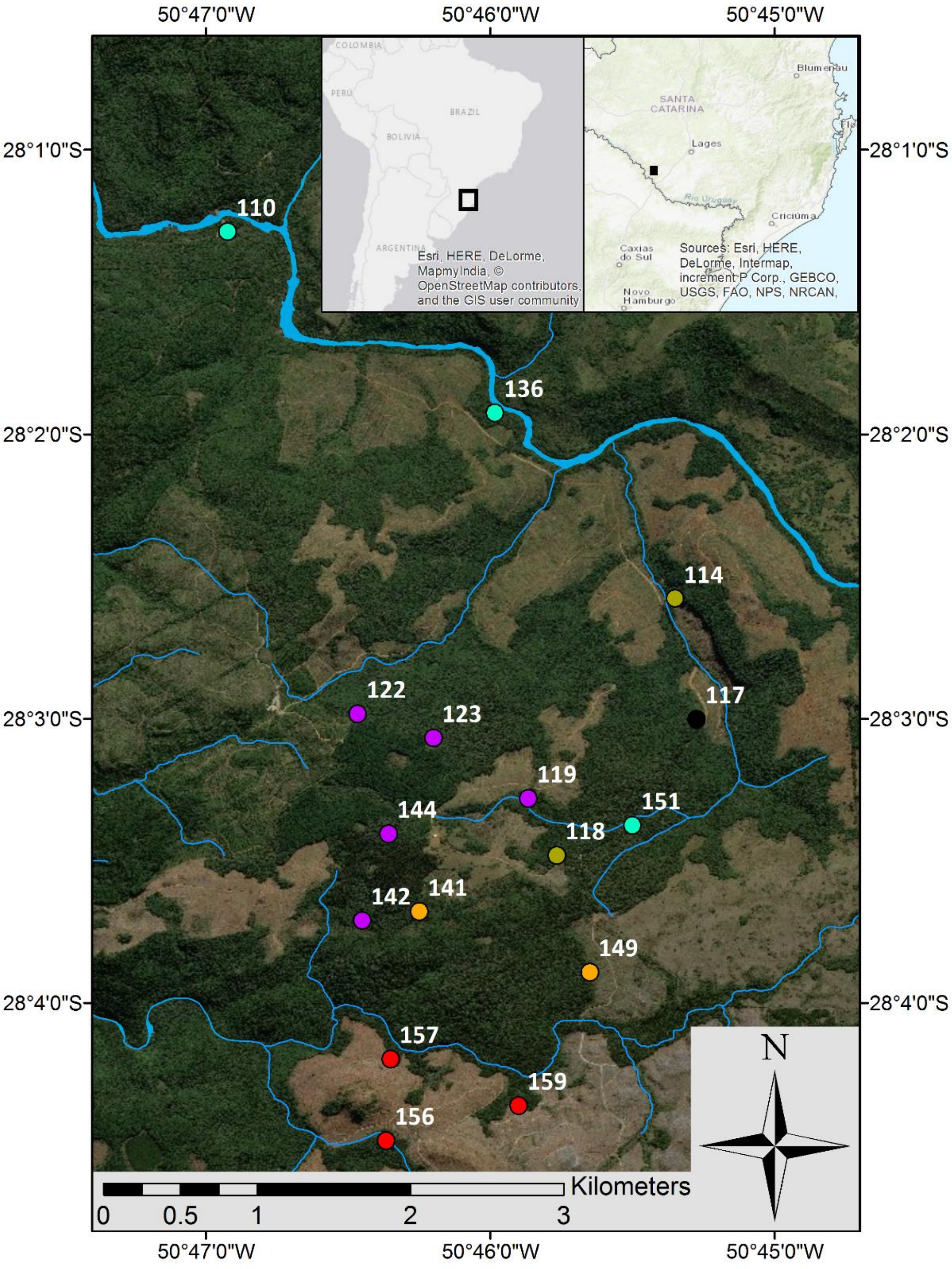

Figure 2: Relative abundance (%) of selected tree species in the vegetation survey. Species included in the cluster analysis and DCA are indicated with an asterisk.

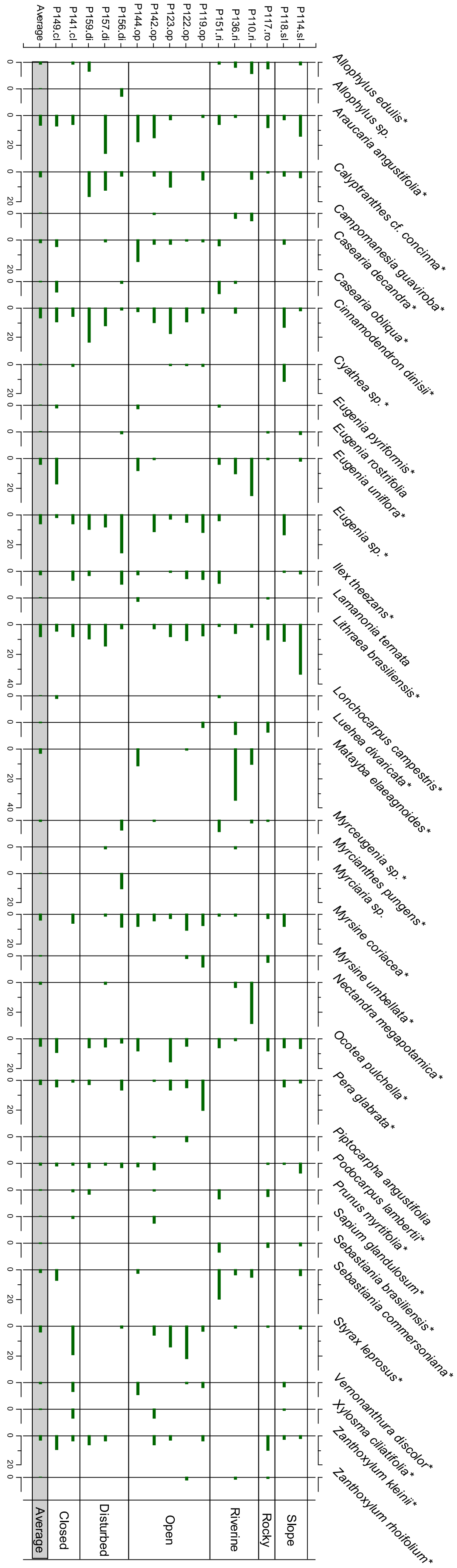

Figure 3: Relative Coverage Values (RCVs, %) of selected tree species in the vegetation survey. 'Ave. (all)' = sum of RCVs/total number of plots; 'Ave. (present)' = sum of RCVs/number of plots in which taxon was present.

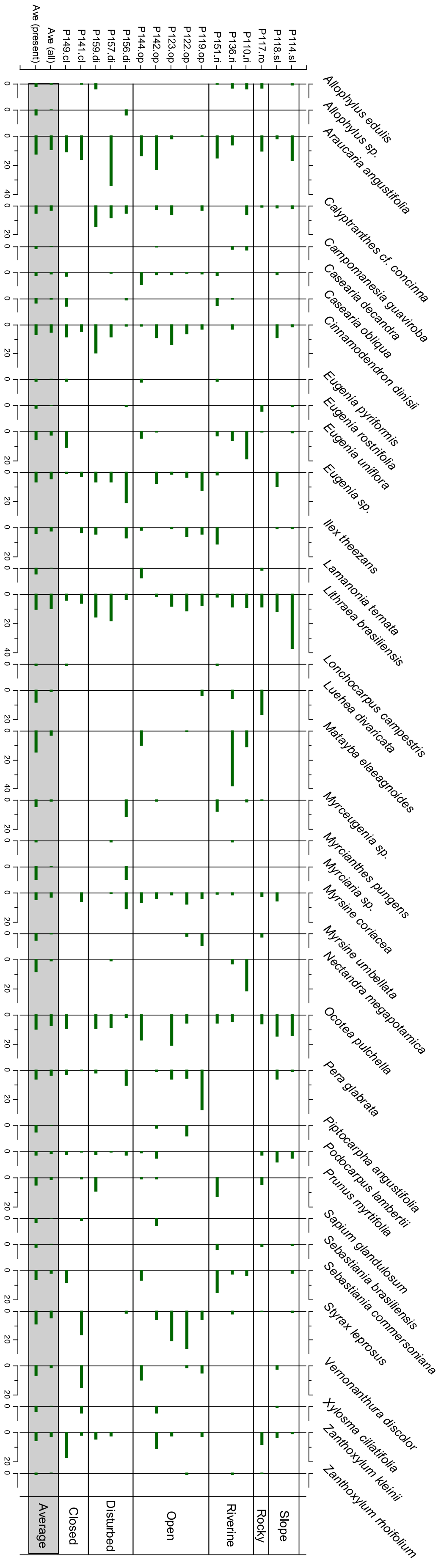

Figure 4: Relative abundance (%) of selected pollen types. Taxa included in the cluster analysis and DCA are indicated with an asterisk

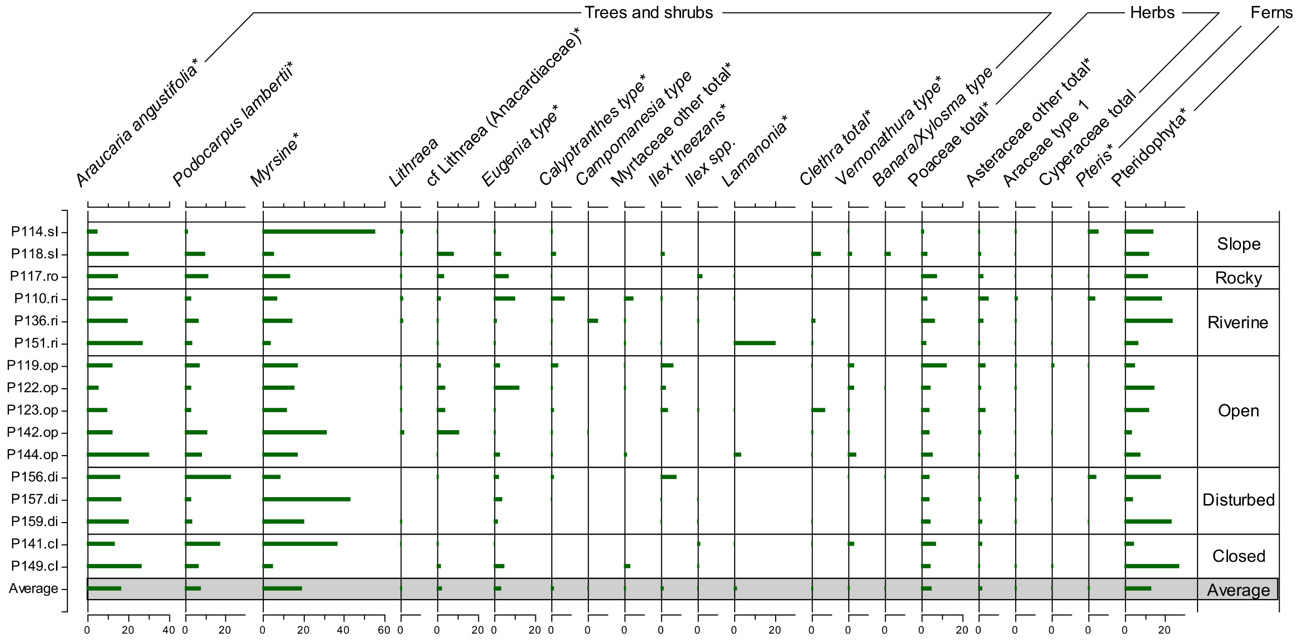

Figure 5: Cluster analyses (left; a, c) and DCAs (right; b, d) of plots by vegetation (top; a, b) and pollen (bottom; c, d) taxa found in ≥2 plots at ≥2% abundance. In the DCAs, convex hulls are delimited for structural categories containing three or more plots. Plot types are identified by colour and two-letter code (op: open; cl: closed; ri: riverine; di: disturbed; ro: rock; sl: slope; see Table 1).

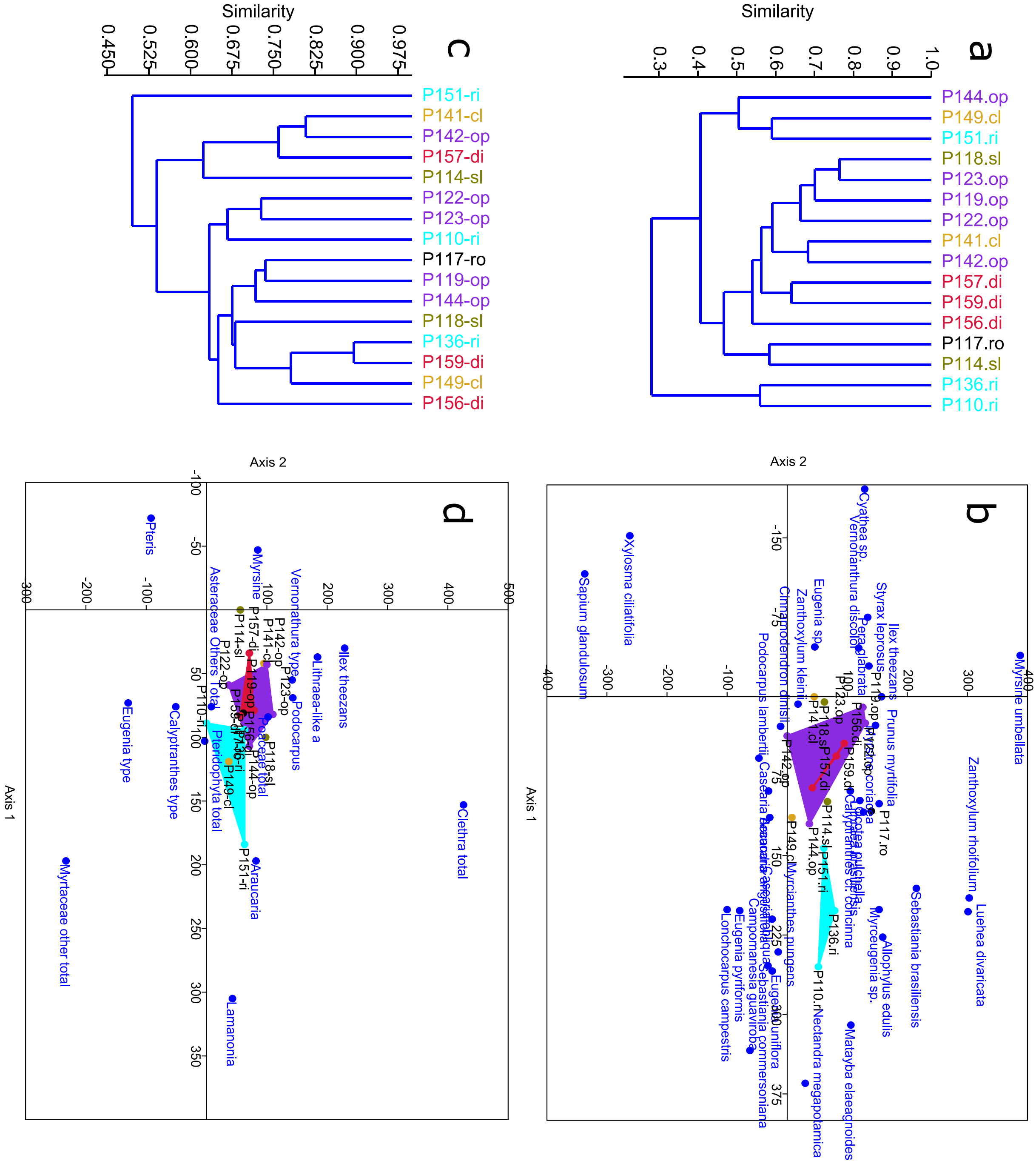

Figure 6: p/v values of key genera of *Araucaria* forest in this study. *Clethra* has an infinitely high p/v value; faint sections in the bars of *Lamanonia* and *Lithraea* reflect alternate calculations of their p/v values (see section 3.4).

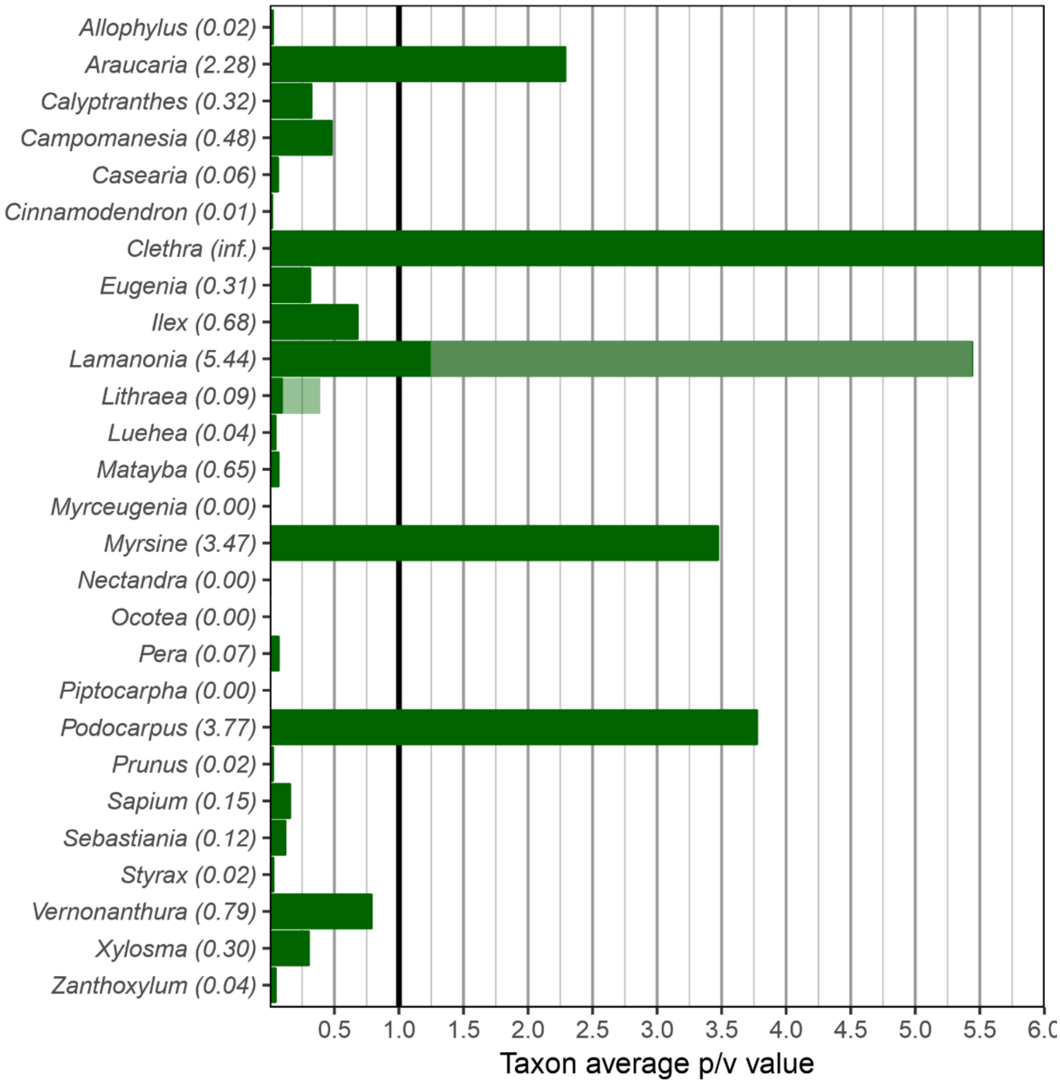

Figure 7: Pollen-vegetation abundance differentials (square-root transformed) for selected genera. Positive values denote plots where a taxon's pollen was more abundant than its vegetation; negative values reflect vegetation being more abundant than pollen. Blank cells denote plots where a taxon was absent from both pollen and vegetation data.