ORIGINAL ARTICLE

Towards quantifying changes in forest cover in the *Araucaria* forest-grassland mosaic in southern Brazil

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Abstract

Quantitative estimates of past vegetation cover are needed both regionally so human-landscape interactions can be better understood, and globally to evaluate the effects of changing vegetation cover on the climate system. Models reducing the bias in the pollen representation of vegetation cover have been developed in the temperate regions of the northern hemisphere, while experience applying them in other parts of the world is limited. The *Araucaria* forest-grassland mosaic of southern Brazil is an area where open and forested plant communities exist naturally and have changed their cover over time due to changing climate and human activities. Therefore, this area is of particular interest for such studies. Modern pollen and vegetation comparisons were carried out in two protected areas: Vila Velha State Park in Paraná state and Aparados da Serra National Park in Rio Grande do Sul. Vegetation mapping and analysis focused on *Araucaria angustifolia* as the characteristic tree of this vegetation type. In the *Araucaria* forest-grassland mosaic open vegetation and woodland change at a scale of hundreds of metres. These changes are difficult to capture based on pollen proportions in surface samples. While the abundance of Poaceae pollen is not a good indicator of locally open conditions, several pollen taxa can be used as indicators of the local vegetation cover. Pollen vegetation ratios (R-values) compare well between the two study regions, indicating that pollen production of individual species within the large plant families of Poaceae and Asteraceae are similar within the overall region. *Araucaria angustifolia* pollen is underrepresented with regards to its vegetation cover, while Poaceae are among the highest pollen producers in the region. Diverse woodland species other than *A. angustifolia* were grouped as one forest taxon and as the species composition of woodlands differed between the two study areas, so did the estimated pollen productivity of this group. It would be rewarding in future investigations to estimate pollen productivity for groups of trees with the same pollen dispersal syndrome. The application of pollen dispersal models designed for closed canopy in the protected areas was challenging. Further model development is required to deal with pollen released at different levels in semi-open vegetation types.

Keywords Pollen productivity estimates · PPE · South America · Pollen vegetation relationship · *Araucaria angustifolia*

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Introduction

One of the main goals of pollen analysis is to reconstruct the vegetation cover of past landscapes. Pollen provides a biased representation of the vegetation resulting in the need to study the relationship between pollen and modern vegetation to reduce that bias. A simple but effective approach is to collect modern samples from different landscapes as modern analogues to interpret the fossil record, which can be matched statistically (e.g. Zanon et al. 2018). While this method has been utilized since the development of pollen analysis (e.g. Auer 1927), it still provides valuable insights where a numerical description of environmental parameters associated to surface samples is available (e.g. Davis et al.

2013). In Europe and North America, pollen vegetation comparisons were developed with the final goal of correcting the values in pollen diagrams directly. Davis (1963) introduced the R-value as the ratio of pollen to vegetation in the same vegetation plot. However, pollen coming from beyond the vegetation plot requires more sophisticated analytical approaches to the problem (Parsons and Prentice 1981). Andersen (1970) used absolute pollen deposition data obtained from pollen traps and compared it to the basal area of the trees in the vicinity of the traps, producing correction factors for the production of common European trees. In this case of pollen traps situated under the canopy, differential pollen transport is not important. However, the physical properties of different pollen types result in some pollen types staying airborne for longer, which will influence the pollen signal in most situations.

Mechanistic models of pollen transport can describe this differential dispersal of pollen types. Applied within the Extended R-value Model (ERV), the differential pollen production relative to a reference taxon can be evaluated (Prentice 1985; Sugita 1993). Motivated by the desire to reconstruct the deforestation of European landscapes with the introduction and intensification of agriculture (Roberts et al. 2018), these models and approaches were refined mainly in Europe (Gaillard et al. 2008). Recognizing the importance of vegetation feedback for explaining past climate change (Gaillard et al. 2010; Strandberg et al. 2014) motivated quantitative estimates of global vegetation cover change (Harrison et al. 2020). However, while pollen diagrams are becoming more readily available globally (Williams et al. 2018), estimates of relative pollen production for major plant groups are hitherto not available for most regions.

In South America, a large number of local and regional pollen surface sample studies have been conducted generally to assist in the qualitative interpretation of pollen diagrams (Marchant et al. 2009; Flantua et al. 2015). Little of that data is available and/or linked to environmental parameters allowing quantitative reconstructions (Montade et al. 2019). This shortcoming is represented by the small number of studies available from South America providing any kind of quantitative reconstruction based on pollen, as visible in the distribution of global pollen-based climate reconstructions by Bartlein et al. (2011). Quantitative estimates of past vegetation cover in South America have so far only been attempted for south-western Amazonia, reducing the landscape to two vegetation types: forest and non-forest (Whitney et al. 2019). This lack of quantitative vegetation reconstructions is partly due to the shortage of detailed information on the pollen representation of South American vegetation types (Whitney et al. 2019). To date, no study has been published for South America estimating relative pollen productivity following approaches developed in Europe and North America based on individual field studies (Bunting et al. 2013) or using available data (Dawson et al. 2016).

Pollen vegetation relationship studies indicating overrepresented and underrepresented taxa are available for specific vegetation types such as saltmarsh (Medeanic et al. 2016), coastal vegetation (Fontana 2005; Masciadri et al. 2013) and Cerrado (Ledru 2002). Studies explicitly estimating the pollen vegetation ratio using pollen traps and forest inventory data have been published for Barro Colorado Island, Panama (Bush and Rivera 1998; Haselhorst et al. 2020) as well as Noel Kempff Mercado National Park and Beni Basin in Bolivia (Gosling et al. 2005, 2009; Jones et al. 2011). Montade et al. (2016) published averaged pollen vegetation ratios for three isolated mountains in Ceará, north-eastern Brazil, based on a collection of surface soil samples and botanical surveys. Analysing the pollen composition of moss cushions collected in a private forest reserve compared to vegetation survey and long-term monitoring data, Cárdenas et al. (2019) provide ratios of average pollen versus vegetation proportions. Overall, quantitative pollen vegetation studies are indeed rare and have so far not developed beyond the R-value approach. These are generally based on averaging pollen and vegetation information, rarely calculating the ratio of values, making them comparable between sites. While these values are informative, general problems of the R-values need to be considered (Parsons and Prentice 1981).

Reconstructing changes in vegetation cover in South America is of interest in understanding the impact of pre-Columbian societies (McMichael et al. 2012) and climatically driven forest cover changes (Rodrigues et al. 2016). This is of particular interest in the *Araucaria* forest-grassland mosaic of southern Brazil, where pollen diagrams document a stepwise shift from open grasslands to dense forests during the Holocene (e.g. Behling et al. 2004). The area is part of the Atlantic Forest biome, a global biodiversity hotspot (Colombo and Joly 2010) and understanding its natural dynamics will contribute to securing its future survival. Before European arrival, this landscape was home to the southern Jê, who had semi-sedentary lifestyles and might have contributed to the afforestation as their diet included the seeds of *Araucaria* (Iriarte and Behling 2007). Several fossil pollen diagrams exist from the region, and their interpretation has so far been qualitative, relying on expert knowledge.

This study aims to analyse the pollen vegetation relationship in the *Araucaria* region of southern Brazil to improve our ability to reconstruct local forest cover changes, both qualitatively and quantitatively. Going beyond the simple R-value approach, we aim to estimate relative pollen productivity for a few dominant pollen taxa with a special focus on *A. angustifolia*. We also investigate the general applicability of these values by selecting two study regions with contrasting climate.

Environmental setting and methods

Geography and climate

The two study regions are located in southern Brazil and differ in relation to their proximity to the Atlantic Ocean, resulting in differences in precipitation. Vila Velha State Park (25° 12′ S, 50° 02′ W) in Paraná state is situated more inland with a stronger seasonal climate. Aparados da Serra National Park (29° 10′ S, 50° 07′ W) in Rio Grande do Sul is located at the edge of the highland with a strong Atlantic influence (Fig. 1). The study areas are situated at an elevation of 850–960 m a.s.l. and ca. 900–1,000 m a.s.l. respectively. The climate in Vila Velha is characterized by a mean annual temperature of 17.4 °C and annual precipitation of 1,554 mm with more moisture availability during January and February. In Aparados da Serra the mean annual temperature is 14.8 °C with an annual precipitation of 1,807 mm, September and October being the wettest months (Alvares et al. 2013).

Vegetation

Vegetation in both parks is characterized by a mosaic of *Araucaria* forest and grassland. Species composition of forests and grasslands is different in the two parks. Vila Velha shows elements of the Cerrado vegetation biome. Open grassland areas are mainly related to shallow soils on the sandstone, while woodlands and semi-open areas dominated by large shrubs occupy the valleys and locations with deeper soils. Small groups of *A. angustifolia* trees occur in open areas, and the tree dominates some forest patches. However, the majority of the woodlands are dominated by taxa of the Myrtaceae, Fabaceae, Melastomataceae, Lauraceae and Asteraceae families; *A. angustifolia* is usually sub-dominant.

The grassland vegetation is also highly diverse, including Cyperaceae, *Dicksonia* sp., Poaceae and Asteraceae. The most abundant species are the grasses *Aristida jubata*, *Andropogon bicornis* and *Trachypogon canescens*. The most diverse plant family is the Asteraceae with 208 species, including 34 in the genus *Baccharis* (Cervi et al. 2007; Dalazoana et al. 2007; Mocochinski and Scheer 2008).

In contrast, in Aparados da Serra the forest patches are dominated by *A. angustifolia* in the emergent layer, usually accompanied by *Mimosa scabrella* and *Pictocarpa angustifolia* in the canopy layer and by arboreal elements such as *Lamanonia speciosa, Ilex microdonta, Podocarpus lambertii, Sapium glandulatum* and, *Myrsine* spp. in the understory. Small trees and shrubs from the families Melastomataceae (*Tibouchina, Leandra, Miconia cinerascens* and *Miconia sellowiana*) and Myrtaceae (*Myrceugenia euosma* and *Siphoneugena reitzii*) are common, the woody bamboo *Merostachys multiramea* is also present but less frequent (Rambo 1956; Baptista et al. 1979; MMA and IBAMA 2007).

A semi-open vegetation type is rare in Aparados da Serra. Here, the vast valleys are often filled with wetlands. Open vegetation patches are dominated by Poaceae, *Baccharis* spp. or *Eryngium* spp. Other important herbaceous taxa are *Polygala* spp., *Euphorbia* spp., *Cyperus* spp., *Bulbostylis* spp., *Rhynchospora* spp., *Sisyrinchium* spp., *Dicksonia sellowiana, Cyathea* spp., *Acaena eupatoria, Tradescantia* spp., *Desmodium* spp., *Oxalis* spp., and *Chaptalia* spp. In this park, the Asteraceae family is highly diverse, with 133 species, including 34 belonging to the genus *Baccharis* (Rambo 1956; Baptista et al. 1979; MMA and IBAMA 2007).

Pollen sampling and vegetation surveys

Vegetation surveys were carried out together with the collection of samples for pollen analysis in July 2018. Sites were selected to obtain a good representation of the different vegetation types and cover a gradient from fully open to fully forested situations. If possible, pollen samples were taken in small wet spots with mosses present. Here, the green parts of the mosses were sampled, assuming that these would contain at least 1 year of pollen deposition. Where no mosses were present, we sampled the soil litter. In all situations, several samples were collected from within about 1 m² and mixed. The centre point for the collection of the pollen sample was
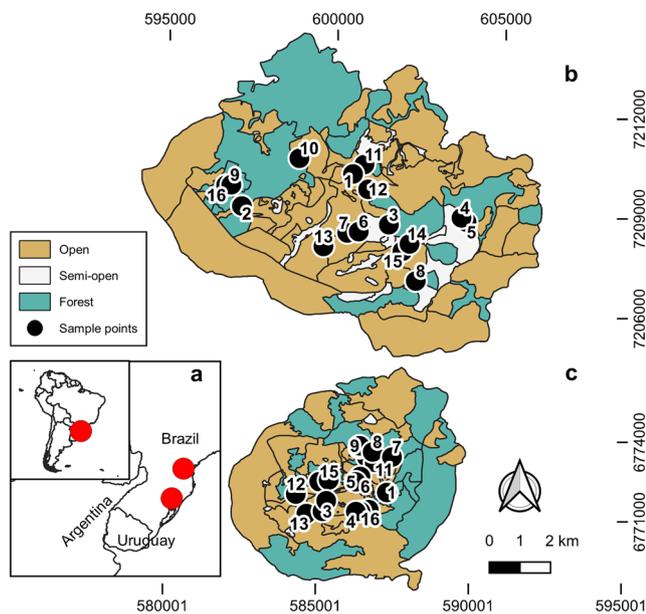
Fig. 1 **a** Location of the study area and distribution of the sampling sites in **b** Vila Velha State Park and **c** Aparados da Serra National Park

Table 1 Vegetation composition within 2,000 m radius, data given as percentage of area

Name	Vila Velha	Aparados da Serra
Araucaria angustifolia	12.39	12.92
Asteraceae	9.67	13.75
Baccharis	8.99	5.49
Cyperaceae	13.42	14.83
Poaceae	23.02	23.65
Forest taxa	25.96	18.75
Other taxa	6.55	10.60

respectively. The vegetation composition within 100 m around each surface sample was used in a cluster analysis and compared to the assignment samples in the field to one of three classes "open", "semi-open" and "forest". Results of this cluster analysis yielded two main groups in both regions (Fig. 2). The cluster "semi-open" vegetation is related to samples from the "open vegetation" in Vila Velha, and to "forest" in Aparados da Serra. In Vila Velha the cluster analysis is not fully separating sites from open and semi-open areas. One group collects all semi-open vegetation sites (3, 4, 8, 14), but includes sites 5 and 10 from open environments. Both sites 5 and 10 are situated near rock outcrops,

Fig. 2 Pollen diagrams for **a** Vila Velha with 16 sampling points and **b** Aparados da Serra with 18 sampling points. Dendrogram based on vegetation data
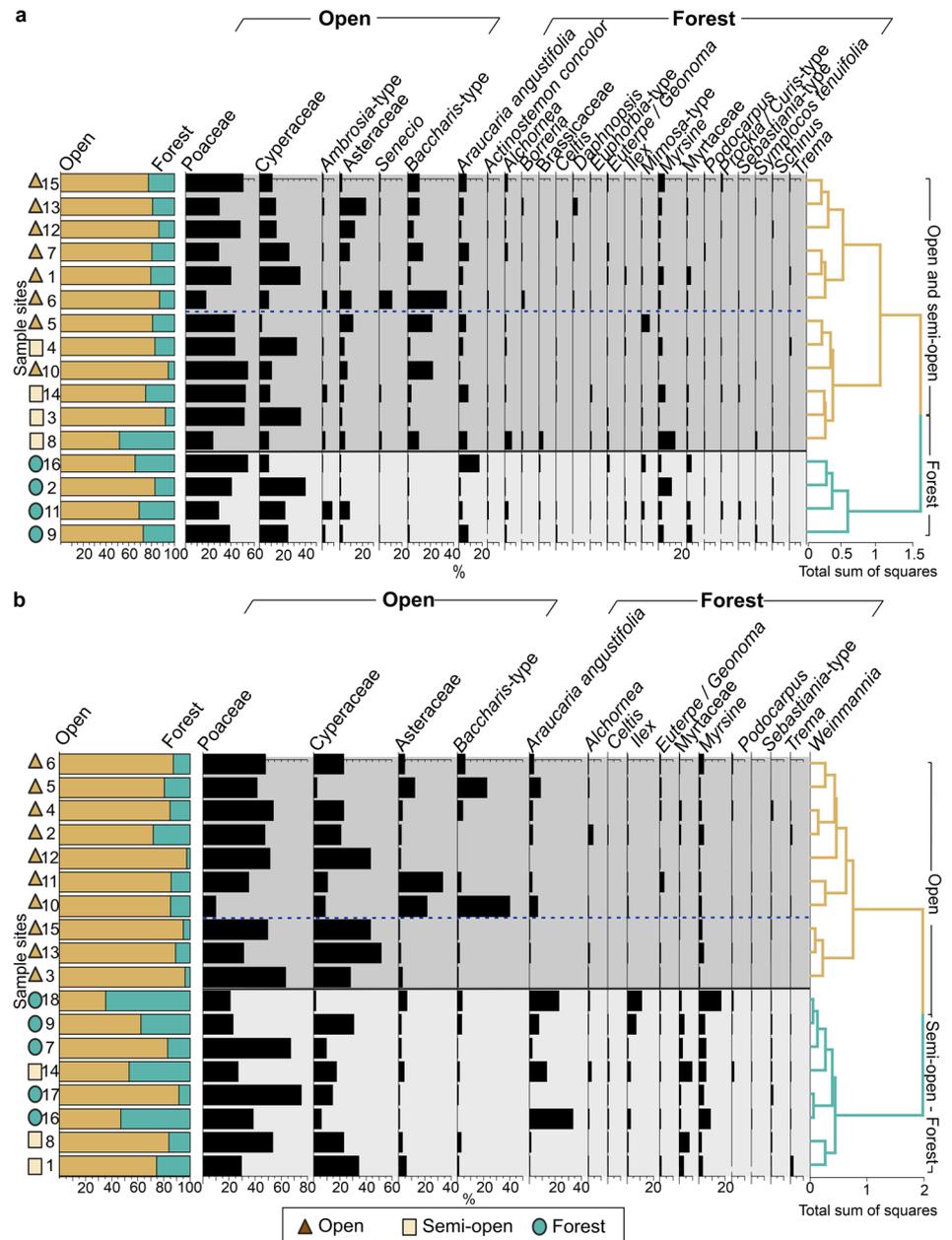
which reduces the overall vegetation cover and might be the reason for the assignment of the samples to this group.

Pollen analysis of the 34 surface samples yielded a total of 75 different pollen and spore taxa (ESM Table 2). In Vila Velha (Fig. 2) the most abundant pollen type is Poaceae (average 40, min 18, max 55%), followed by Cyperaceae (19, min 2, max 40%). The proportion of *A. angustifolia* pollen varies between 0 and 18%, with an average of 5%. All other tree pollen taxa are combined in the forest group (average 16, min 4, max 42%), with *Myrsine, Mimosa* and *Alchornea* as the most abundant. *Baccharis*-type (average 9, min 1, max 34%) is the most abundant Asteraceae pollen, and as plants of the genus were mapped in the field, it is considered separately. *Ambrosia*-type and *Senecio* are most of the remaining Asteraceae pollen (average 11, min 1, max 27%), which are grouped under Asteraceae p.p. in further analyses.

Pollen percentages from both areas are compared to the results of the cluster analysis of the 100 m radius vegetation data (Fig. 2). For Vila Velha, pollen proportions of tree versus herbaceous pollen types do not show a clear difference between sites from the three environments. However, forest sites have higher pollen percentages of *A. angustifolia* and Myrtaceae and lower proportions of *Baccharis*-type. Pollen and vegetation data show better correspondence for the samples from Aparados da Serra. The open vegetation group contains a cluster of three sites (3, 13, 15), which are wetlands within large open areas, and their pollen content reflects this in the dominance of Poaceae and Cyperaceae.

We used the indicator species analysis (IndVal) to identify the pollen taxa that are characteristic for the vegetation groups identified by the cluster analysis (Table 2). In Villa Velha, higher pollen proportions of *Baccharis*-type are a strong indication (IndVal 0.94) that the sample is from open semi-open vegetation, while the occurrence of *Schinus* pollen indicates forest (IndVal 0.72). In Aparados da Serra the open vegetation is not well indicated by a particular pollen type, while tree pollen proportions of Myrtaceae (0.91), *A. angustifolia* (0.79), *Ilex* (0.78), *Celtis* (0.79), *Myrsine* (0.74) and *Trema* (0.78) are robust indicator taxa for forest plots.

Pollen vegetation relationships

Multivariate data analysis

Principal component analysis of the vegetation data (Fig. 3a, c) separated forested from open vegetation sites. Semi-open sites have different affinities in the two study areas and plot near open sites in Vila Velha and forest sites in Aparados da Serra. In Vila Velha, forest plots are characterized by *A. angustifolia*, which separates these plots from semi-open plots. As mentioned before, plot 5 and 10 differ from other open plots because they are situated near and within rock outcrops and exposed soil, changing the proportion of the mapped vegetation in comparison to the overall open character of these sites. Apart from these two samples, the PCA separates semi-open from open plots. In Aparados da Serra (Fig. 3c), the vectors for *A. angustifolia* and forest are not strongly separated, indicating similar tree composition in forest and semi-open plots.

The PCA of the pollen data (Fig. 3b, d) does not yield a clear separation of open, semi-open and forested sites, particularly for Vila Velha (Fig. 3b). Five of the open sites (5, 6, 7, 10, 13) with high pollen percentages of *Baccharis*-type and other Asteraceae are separated from semi-open and forested plots. Three open sites (1, 12, 15) instead appear inseparable from semi-open and forested plots because all are characterized by high values of Poaceae and Cyperaceae. In sample 1, for example, Poaceae and Cyperaceae sum up to ~75%, while pollen from the Asteraceae family is rare. Sample 15 comes from open vegetation; however, semi-open vegetation occurs only 100 m from the site. Pollen composition in sample 15 is similar to sample 14 from a site in this nearby semi-open vegetation.

Also, in Aparados da Serra (Fig. 3d), pollen composition does not separate open, semi-open and forested sites. The first axis represents the variance in the pollen proportions of Poaceae versus the forest elements, generally separating open versus forested sites. However, a sample from the forested site 17 and the semi-open site 8 are also high in

Table 2 Results of the Indicator Species Analysis (IndVal)

Taxon	Landscape unit	Vila Velha			Aparados da Serra		
		IndVal	pvalue	freq	IndVal	pvalue	freq
Baccharis-type	Open and semi-open	0.94	0.002*	16	0.66	0.323	15
Araucaria angustifolia	Forest	0.64	0.237	15	0.79	0.086*	17
Celtis		0.28	0.695	7	0.79	0.004*	8
Ilex		0.51	0.304	10	0.78	0.06*	15
Myrsine		0.59	0.656	16	0.74	0.007*	18
Myrtaceae		0.58	0.267	12	0.91	0.001*	14
Trema		0.41	0.447	9	0.68	0.036*	16
Schinus		0.72	0.034*	10	0.16	0.918	6

*Indicates significant p-values, i.e. $p < 0.05$

Fig. 3 PCA biplots of pollen assemblages and vegetation for Vila Velha (**a**, **b**) and Aparados da Serra (**c**, **d**) respectively
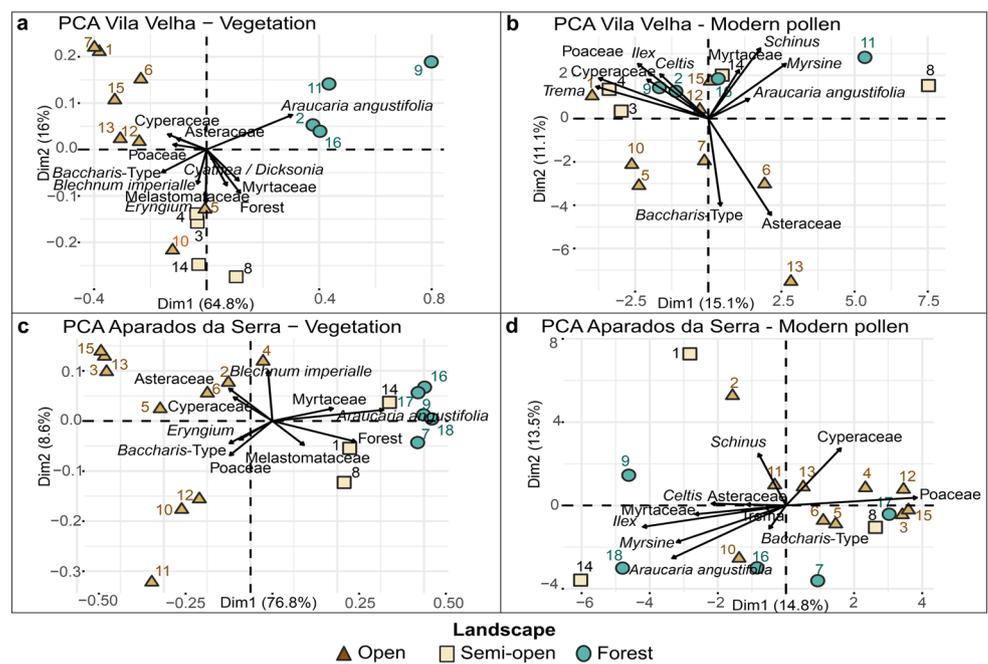
Poaceae pollen and plot with the open grassland samples. Sample 17 has been taken in a small forest opening with grasses that may have contributed to its high Poaceae pollen proportion. Sample 8 is situated at the forest edge and was therefore classified as semi-open, while the local abundance of grasses may explain the position in the PCA. This comparison of the pollen and vegetation composition in the PCA analysis indicates that the pollen composition at each site is strongly influenced by the vegetation beyond the 100 m radius used here for comparison.

Representation factors (R-values)

A visual comparison of the average pollen proportions over all study sites with the average vegetation proportions in the 100 m radius of the sampling points (Fig. 4a–d) shows that Poaceae is the most overrepresented and *A. angustifolia* the most underrepresented taxon. Striking are the similarities in average R-values between the two regions, also when using the vegetation cover in an overall 2 km buffer around all sites (Fig. 5). The R-values for the six different taxa follow the same trend in both study regions except for an under-representation of Asteraceae p.p. in Aparados da Serra, while this taxon has a near one to one average pollen to average vegetation proportion in Vila Velha. In both regions, the pollen of *A. angustifolia* is strongly under-represented; *Baccharis* and the forest group are under-represented. Pollen from Cyperaceae and Poaceae are over-represented.
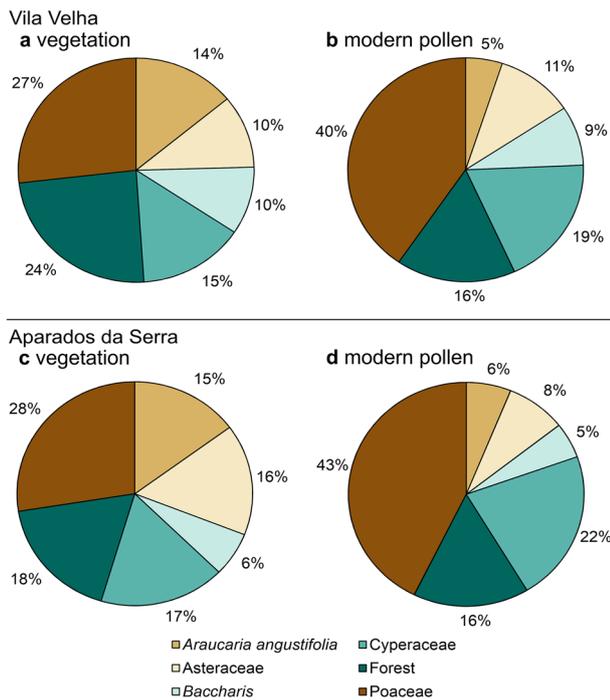
Vegetation and pollen proportions at individual sites show a large scatter. The site-based ratios follow the same pattern as the ratio based on averages (Table 3). The scatter

of values around the mean is generally higher in Aparados da Serra, particularly for Asteraceae p.p. and *A. angustifolia*.
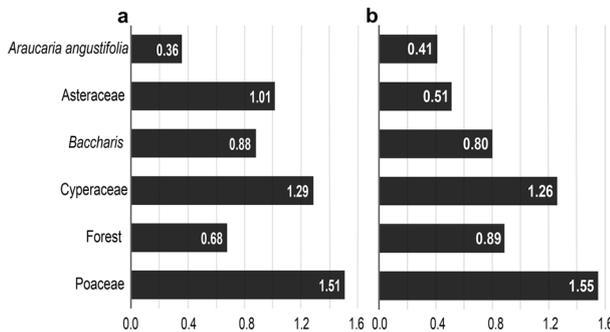
ERV analysis

Relative pollen productivity is expressed in relation to a reference taxon, which needs to occur in all pollen and vegetation samples. Poaceae fulfils this criterion in many study regions and is therefore commonly used as a reference taxon (Broström et al. 2008). However, as presented above, high proportions of Poaceae occur in samples of all vegetation types. The samples from Aparados da Serra do not contain a gradient of Poaceae pollen percentages long enough for successful ERV calculations. This situation led to spuriously high PPEs in some analyses. Thus, we have selected Cyperaceae as an alternative reference taxon, which is also present in all vegetation plots while showing a stronger gradient in the vegetation and pollen data.

In addition to two different reference taxa, PPEs were estimated using two different pollen dispersal models (GPM and LSM) implemented in two different programs (ERV. Analysis.v 2.5.3-D) and ERV Analysis in R-R). ERV results were evaluated considering the vegetation data in circles of different radii from the sampling point. Here we represent the results for the maximum distance of 100 m (Fig. 6). Ideally, the accuracy of ERV calculations should improve with more rings added in the analysis, i.e. a larger vegetation sampling area. However, in both study regions, the distance between modelled and empiric pollen values is lowest with the 50–100 m rings (Fig. 7), indicating that the ERV model performs best with only rings up to 100 m radius included

Fig. 4 Percentages of pollen and vegetation cover within 100 m radius in Vila Velha (**a**, **b**) and Aparados da Serra (**c**, **d**)

Fig. 5 Mean representation factor (R-values) for the six major taxa as averaged pollen proportions over all sites in one region versus averaged vegetation within 2,000 m of the sample site in **a** Vila Velha and **b** Aparados da Serra

in the analysis. This observation may indicate that vegetation composition has not been adequately described for rings beyond 100 m radius. Hence, the 100 m radius represents a good compromise of the higher data accuracy of the field-based vegetation survey and the representation of adjacent woodlands. Results are therefore discussed for this distance. Complete results, including spurious values, are presented in ESM Table 3.

The results of the ERV analysis differ consistently for the dispersal models regardless of the reference taxon. The difference is most pronounced for *A. angustifolia*, the taxon

with the largest pollen grains and hence the highest fall speed (Table 4). For both study areas, pollen productivity of *A. angustifolia* is as high, or higher than pollen productivity of the reference taxon Poaceae or Cyperaceae when calculated with the GPM. In calculations with the LSM, pollen productivity of *A. angustifolia* is much lower. Still, LSM-PPEs of *A. angustifolia* are higher in Aparados da Serra than in Vila Velha. For the other taxa, differences in GPM- and LSM-PPEs are smaller. For the remaining taxa, both models result in different PPEs between regions, which, at least in the case of *Baccharis*-type and the forest taxon, can be explained by different species involved and agree with the regional differences in R-values.

Scatter plots (Fig. 8) of modelled against empiric pollen data indicate for Vila Velha good correspondence between pollen and vegetation abundances for *Baccharis*-type, and poor correspondence for the forest taxon and Poaceae. In Aparados da Serra *A. angustifolia* and the forest taxon show the best relationship between the variance in vegetation and pollen proportions.

Discussion

Representation of openness in the pollen spectra from the *Araucaria* forest-grassland mosaic

The *Araucaria*-grassland mosaic in southern Brazil is characterized by well-defined forest edges, clearly separating open and semi-open vegetation from woodlands. Despite that, it appears challenging to separate these two vegetation types in pollen data using ordination and classification techniques. These difficulties may be due to Poaceae and *A. angustifolia* pollen showing only a weak local signal, corresponding to the vegetation in a 100 m radius. In the case of Poaceae, this could be caused by species of the family frequently growing within the forest and dominating the surrounding grasslands. Both at Vila Velha and Aparados da Serra, the woodlands contained bamboo of the genus *Merostachys* and *Chusquea*.

The other effect obscuring the local separation of the two vegetation types is the different height at which the pollen is released, often described as the "edge effect" of woodlands leading to a spread of tree pollen over a larger area away from the forest (Bunting et al. 2013). *Araucaria* trees often raise their branches over the canopy of other trees so that perhaps a larger proportion of its pollen is transported above the canopy (Rempe 1937). In Aparados da Serra, the pollen of several trees growing below the canopy of *Araucaria* was found more frequently within or close to woodlands and was therefore identified as good indicators for forested sites. *Schinus* is the only tree taxon in Vila Velha consistently more abundant in samples from woodlands, while in

Table 3 Site-based representation factor (p/v values) for the six major taxa in this study in Vila Velha and Aparados da Serra

Location, site No	*A. angustifolia*	Asteraceae	*Baccharis*	Cyperaceae	Forest	Poaceae
Vila Velha						
1	0.28	0.11	0.28	2.31	0.71	1.47
2	0.05	0.19	0.13	3.93	0.49	2.51
3	0.00	0.18	0.17	2.00	0.42	1.58
4	0.30	0.52	0.18	2.20	0.57	1.53
5	0.45	1.67	1.91	0.12	0.55	1.53
6	0.45	2.01	2.80	0.43	0.71	0.51
7	1.67	0.91	1.08	1.41	0.73	0.82
8	0.63	1.10	0.82	0.56	1.57	0.87
9	0.25	1.01	0.39	2.62	0.60	2.60
10	0.04	0.86	3.09	1.05	0.13	3.35
11	0.23	1.52	0.04	1.40	1.10	1.06
12	0.25	1.47	0.48	0.90	0.51	1.64
13	0.51	2.08	0.87	0.77	1.02	0.86
14	0.92	0.97	0.21	0.59	0.78	1.76
15	0.77	0.55	0.76	0.68	0.76	1.66
16	0.56	0.36	0.09	0.83	0.52	3.55
Mean	0.46	0.97	0.83	1.36	0.70	1.71
Aparados da Serra						
1	0.04	0.83	0.31	2.87	0.78	1.34
2	0.26	0.14	0.00	0.97	2.86	1.55
3	0.00	0.18	0.16	1.40	0.30	2.23
4	0.22	0.18	0.69	1.16	0.98	1.83
5	0.50	0.91	3.47	0.14	0.69	1.48
6	0.19	0.70	0.96	1.48	0.51	1.78
7	0.13	0.61	0.06	0.81	0.46	3.00
8	0.09	0.42	0.39	1.60	0.61	2.10
9	0.43	0.38	0.44	1.97	1.51	0.89
10	0.35	2.07	5.98	0.61	0.40	0.37
11	0.11	3.17	0.48	0.78	0.49	1.42
12	0.04	0.10	0.00	1.92	0.29	1.58
13	0.09	0.23	0.27	2.67	0.67	1.13
14	1.01	0.39	0.21	0.88	2.92	0.90
15	0.05	0.05	0.12	2.05	0.45	1.61
16	2.88	0.12	0.00	0.30	1.30	1.34
17	0.03	0.06	0.13	0.83	0.41	2.76
18	1.29	0.72	0.47	0.09	2.12	0.80
Mean	0.56	0.60	0.74	1.20	1.00	1.55

Vila Velha *Baccharis*-type pollen was a reliable indicator of open vegetation. The different land use activities can explain the lack of abundant *Baccharis*-type pollen in Aparados da Serra, where *Baccharis* shrubs are suppressed by grazing and frequent fires (Rambo 1956).

The above mentioned weak local pollen signal of Poaceae and *A. angustifolia* has been observed in other studies from southern Brazil. For instance, a pollen vegetation comparison in the *Araucaria*-grassland mosaic in Santa Catarina State (Cárdenas et al. 2019) revealed no correspondence between pollen proportions and local site characteristics, including open and closed vegetation. Jeske-Pieruschka et al. (2010) only indicated small differences in pollen composition inside and outside the woodland in a study of 18 surface samples crossing an *Araucaria* dominated forest patch in Rio Grande do Sul State.

While grasses are the most abundant taxon in open vegetation types of South America and make up nearly one-third of the plant cover in the two study areas, they also act as high pollen producers, being the most abundant pollen

Fig. 6 PPEs results of six major taxa in Vila Velha at 50–100 m radius (**a**) and 1,500–2,000 m radius (**b**) and Aparados da Serra at 50–100 m radius (**c**) and 1,500–2,000 m radius (**d**). *Spurious values resulting from the analysis are not shown in this graphic
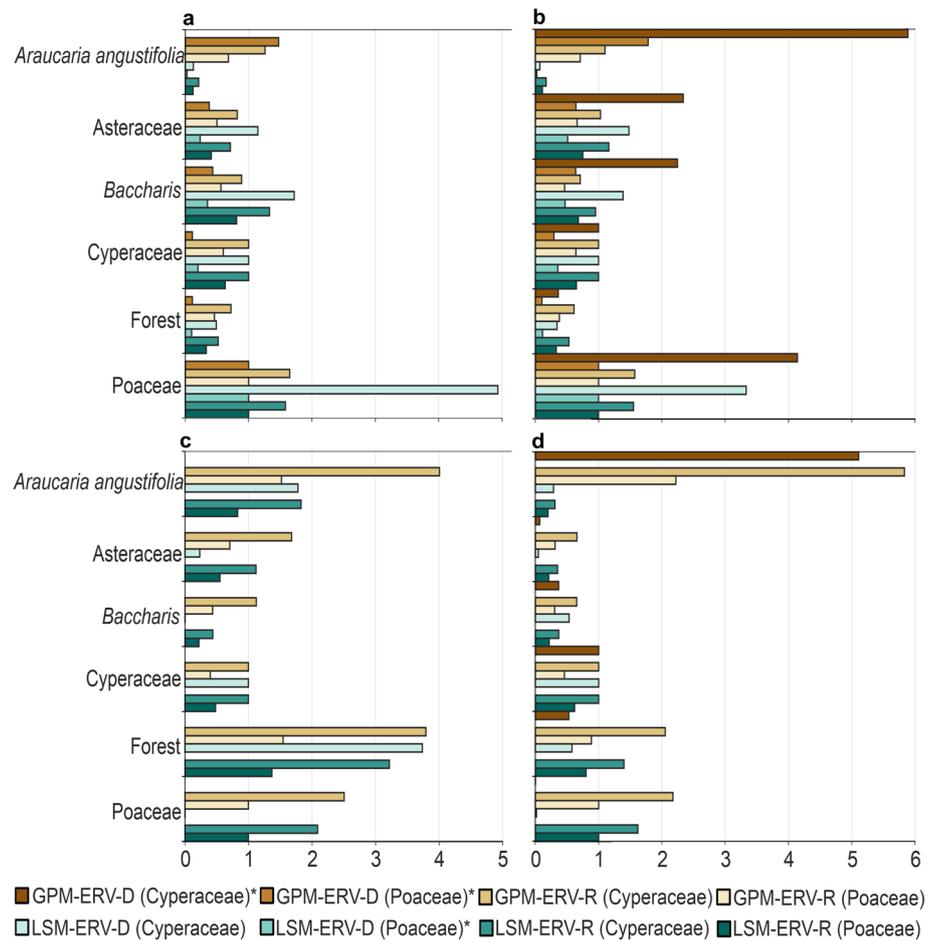
Fig. 7 Chord distances between modelled and empiric pollen values within 2,000 m for **a** Vila Velha and **b** Aparados da Serra
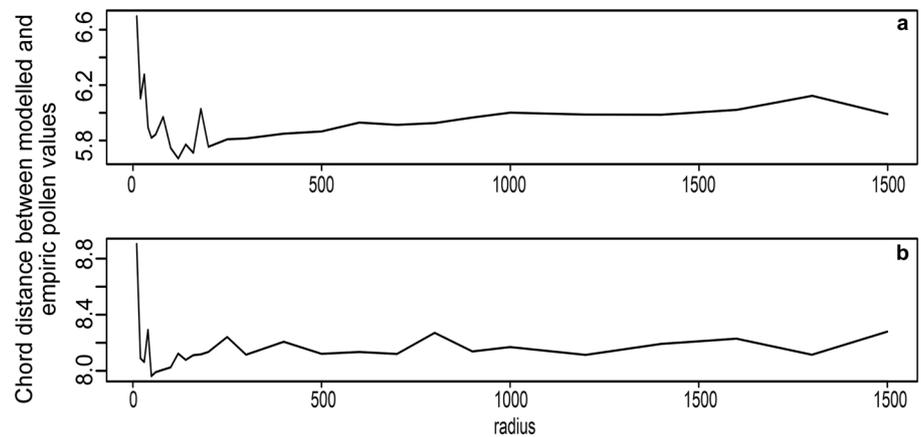
type in the air. This high regional deposition of Poaceae pollen results in the pollen type also being abundant in surface samples from woodland patches with low grass cover. In the Neotropics, Bush (2002) observed that Poaceae pollen is dominant where trees with high pollen production are lacking. Nevertheless, Poaceae pollen provides an important measure to separate different ecosystems at the landscape scale (Rodrigues et al. 2016) and was an indicator taxon for

Araucaria forest and high elevation grassland in an analysis of 196 surface samples from eastern Brazil (Montade et al. 2016). In a surface sample study from southern South America, Paez et al. (2001) observed that Poaceae pollen is abundant in samples from *A. araucana* populations, the second species in the genus with similar pollen morphology to *A. angustifolia*.

Table 4 Estimation of fall speed of common taxa in the study area

Name	Taxa included	Fall speed (m/s)
A. angustifolia	*Araucaria angustifolia*	0.140
Asteraceae	*Alternanthera*, Amaranthaceae, *Ambrosia*-type, Asteraceae, Cichorioideae, *Pfaffia gnaphalioides*, *Senecio*, *Solanum*, *Valeriana stenophylla*, *Vernonia*, *Xyris*	0.015
Baccharis	*Baccharis*-type	0.016
Cyperaceae	Cyperaceae	0.027
Poaceae	Poaceae	0.020
Forest	*Actinostemon concolor*, *Acalypha*, *Alchornea*, *Celtis*, Euphorbiaceae, *Ilex*, *Matayba*, *Myrsine*, Myrtaceae, Mimosaceae, Moraceae, *Ranunculus bonariensis*, *Rhamnus*-type, *Sebastiania*-type	0.020

Fig. 8 Scatter plots of true pollen and modelled pollen proportions within 100 m radius from 16 samples in Vila Velha and 18 samples in Aparados da Serra for the six taxa selected in this study
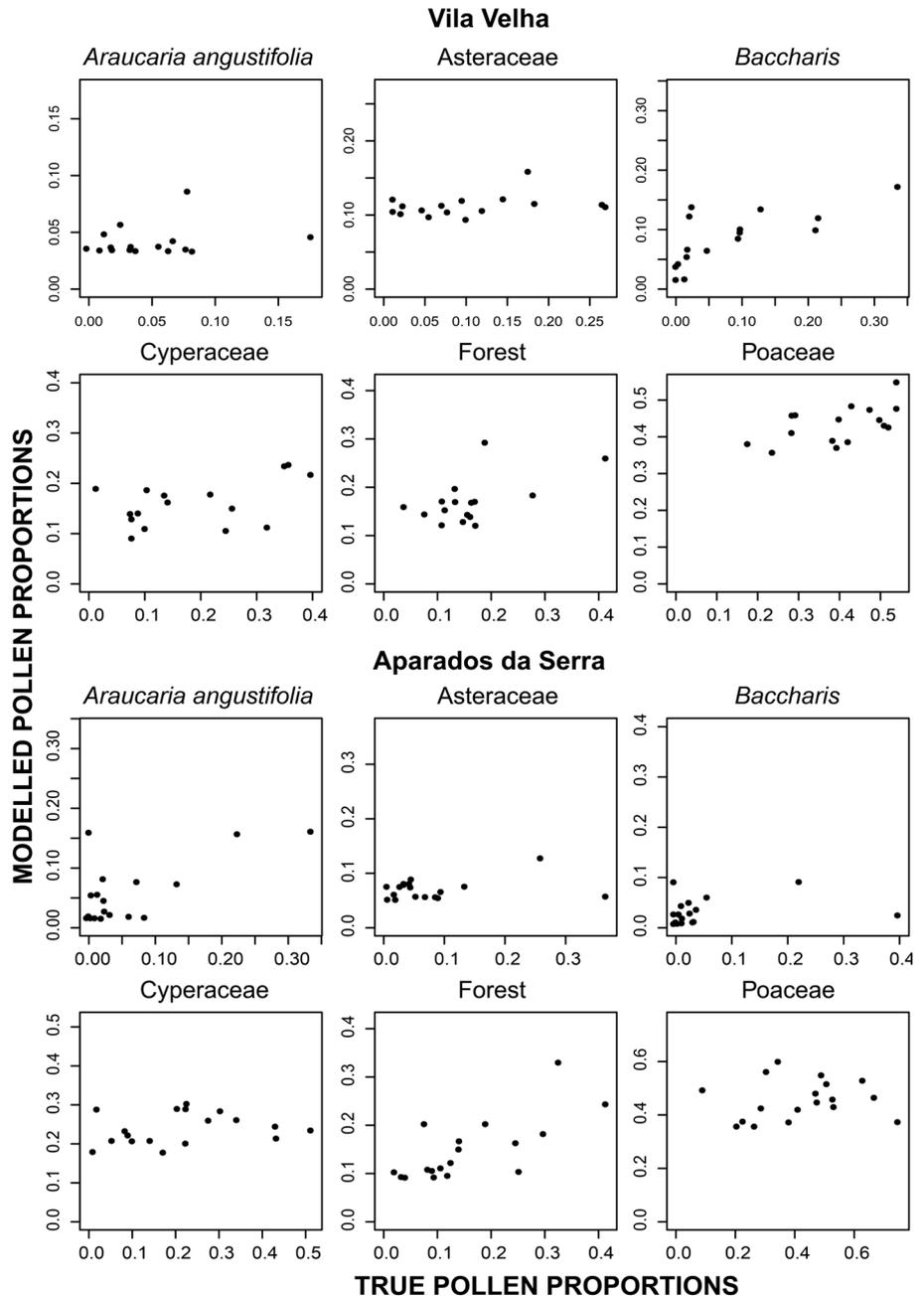
Representation of pollen taxa and pollen productivity

Campos vegetation is characterized by high abundances of Asteraceae, particularly *Baccharis*, Cyperaceae and the dominating Poaceae. Both Poaceae and Cyperaceae have R-values of above one, i.e. they are over-represented in pollen records. Plants with such high pollen representation are generally anemophilous, with numerous exposed anthers, small pollen grains (30–40 μm), and high pollen production (Davis 1984; Hjelle 1997). Also, conifers are usually over-represented in the pollen record as they are wind-pollinated, as is *A. angustifolia*. However, the tree is dioecious with rather large (60 μm), non-saccate pollen grains resulting in the highest estimated fall speed among the taxa investigated here.

Pollen trapping in *A. angustifolia* stands of north-eastern Argentina yielded pollen deposition values between 3,000 and 14,000 grains cm^{-1} $year^{-1}$ in a situation directly below flowering trees (Simón et al. 2018). These values are similar to the average pollen influx measured in *A. angustifolia* dominated forest in the province Santa Catarina, Southern Brazil (Behling 1997) and compare to pollen deposition of trees in the genus *Pinus* in Europe (Abraham et al. 2020). A gene flow study of an isolated group of 11 *Araucaria* trees documents that the large pollen type is well dispersed and most trees in that group were fertilized by pollen travelling around 2 km from the nearest more extensive woodland (Bittencourt and Sebbenn 2007). In the study presented here, it was not feasible to identify all trees in the woodland. Although species of the genus *Mimosa*, *Myrsine*, *Clethra* and Myrtaceae family were also recorded, their abundance in the small areas mapped was often too low for reliable comparisons to their equally low pollen percentages. The combined forest taxa group yielded higher R-values compared to *A. angustifolia*. This result may be due to these trees producing more pollen than *A. angustifolia*.

The different R-values for the forest group between Vila Velha and Aparados da Serra are likely due to differences in forest composition, with higher abundances of pollen from Myrtaceae, *Ilex* and *Myrsine* in Aparados da Serra in the pollen samples. Cárdenas et al. (2019) indeed estimate higher R-values for several tree taxa, including *Clethra*, *Myrsine* and *Podocarpus*, compared to *A. angustifolia*. Also, taxa including the Myrtaceae family, identified as low pollen producers, revealed high R-values in other studies (Gosling et al. 2009; Cárdenas et al. 2019). These differences indicate that pollen production and dispersion differ substantially among species of this family. Moreover, many forest trees are palynologically silent (Gosling et al. 2009; Cárdenas et al. 2019), which hampers drawing any further conclusion from the forest group taxon.

Gosling et al. (2009) also report small R-values for Poaceae, which may be partially due to the available vegetation data coming mainly from tree inventories. As discussed above, pollen productivity of Poaceae may indeed be low compared to the trees present in a particular study region (Bush 2002). The calculation of R-values does not account for pollen dispersal. Hence, the difference in R-values between taxa may relate to differences in pollen productivity or pollen dispersal. PPE calculation does account for pollen dispersion by distance weighting plant abundances. As long as a suitable dispersal model is applied in the calculations, PPEs quantify differences in pollen productivity between taxa. Only *A. angustifolia* represents a single species in vegetation and pollen data, while even the genus *Baccharis* combines species with different life forms present in different abundances in the two study areas.

The choice and parameterization of the pollen dispersal model is the most important factor influencing the resulting pollen productivity estimates (Theuerkauf et al. 2013). The decrease in pollen contribution of a given plant with distance from the point of reference may be described by simple particle dispersal models such as GPMs (Bunting et al. 2013). For several regions, LSMs (Kuparinen et al. 2007) have shown to describe pollen deposition more realistically than GPMs (Theuerkauf et al. 2013; Mariani et al. 2016). In this study, dispersal model selection strongly affected *A. angustifolia*, with GPM-PPEs being much higher than the LSM-PPEs. This difference is due to the large difference in fall speed. The fall speed of pollen has a significant influence on the predicted dispersal pattern in the GPM but not as strong in the LSM (Fig. 9). The GPM model predicts that most *A. angustifolia* pollen would be deposited within metres of the parent tree, which is clearly not observed in the field. Because the GPM underestimated the dispersal distances of *A. angustifolia* pollen, the resulting PPEs are unrealistically high. Both models assume horizontally homogeneous canopies, which is violated in the current study where groups of *A. angustifolia* in the open grassland are more similar to smokestacks with respect to their pollen release. In this parkland situation with pollen being released at different heights and with edge effects occurring at forest margins, also the chosen LSM model may not be fully suited.

Nevertheless, the estimate of a pollen productivity for *A. angustifolia* of 0.8 relative to Poaceae for Aparados da Sierra based on the LSM model may be realistic considering that about half of the trees are female therefore non-pollen-producing. The *A. angustifolia* PPE of 0.1 in Villa Velha instead appears too low. For this study area, the scatterplots do not show the expected 1:1 relationship between modelled and empiric pollen values (Fig. 8). This pattern indicates that the relationship between abundances of *A. angustifolia* in the vegetation and pollen deposition is not that close.

Fig. 9 Proportion of pollen remaining airborne until 1,000 m distance from a pollen source, calculated with the GPM (brown) and LSM (green) and for three different fall speeds of pollen (0.02, 0.03, 0.14 m s^{-1}). The highest fall speed represents pollen of *Araucaria angustifolia*
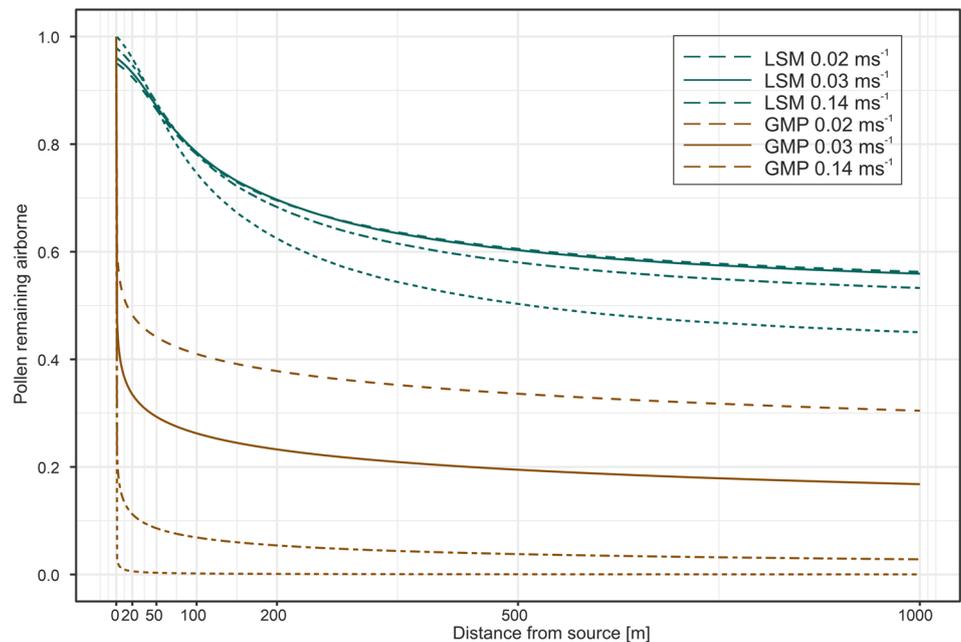
For example, pollen deposition is highest in site 16 (17.7%), although *A. angustifolia* is only intermediately abundant within 100 m distance from that site. The poor pollen vegetation relationship for *A. angustifolia* in Vila Velha may relate to the location of this area near the distribution limit of the tree. Near this limit, the growth and pollen production of trees may be more variable and influenced by local site conditions. Also, the age of a tree determines its pollen production (Matthias et al. 2012). Differences in age-structure may hence cause biases in the pollen vegetation relationship.

Similarly, pollen production will be related to the ratio of male versus female trees, which may differ between sites. Regardless, the inadequacy of the dispersal models considering the different release height of pollen is likely the major problem in this mosaic landscape. Developing dispersal models incorporating the effect of release height might improve pollen vegetation relationships in these landscapes.

Conclusions

The application of procedures designed in high latitude vegetation types of the northern hemisphere to estimate pollen productivity in the low latitudes of South America is challenging but possible. This study shows that it is possible for the *Araucaria* forest-grassland mosaic of southern Brazil, while documenting several problems for this particular vegetation type. Poaceae is the most overrepresented taxon in the *Araucaria* forest-grassland mosaic of southern Brazil. Grasses occur in all vegetation types with different cover abundance, while their pollen proportion in surface samples is not providing clear differences between forest and

open areas. Locally open vegetation types can be detected by *Baccharis*-type pollen indicating open conditions and *Araucaria* and *Celtis* pollen indicating woodland.

Similarities in R-values and PPEs between regions document that pollen production of individual species within the large plant families of Poaceae and Asteraceae is similar, allowing the application of resulting PPEs on the broader region. Conversely the forest group consisting of trees from different families showed a different behaviour between the study areas. Here it seems necessary to develop PPEs for at least groups of trees with similar pollen dispersal syndromes. The dioecious nature of *A. angustifolia* hampers estimating pollen productivity of this iconic tree. The obtained productivity of 0.8 with respect to Poaceae is lower than the pollen productivity of the general forest, resulting in the tree being underrepresented by its pollen even though it is wind-pollinated.

The application of pollen dispersal models designed for closed canopies in the natural parkland situation with pollen released at different levels may explain some difficulties in estimating PPEs. Further model development needs to include the effect of pollen release at different heights.

The insights and obtained PPEs for 6 major pollen taxa are now available for exploring the increasing number of pollen diagrams from the region and perhaps refining previous interpretations.

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