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# Late Quaternary vegetation, biodiversity and fire dynamics on the southern Brazilian highland and their implication for conservation and management of modern *Araucaria* forest and grassland ecosystems

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Palaeoecological background information is needed for management and conservation of the highly diverse mosaic of *Araucaria* forest and Campos (grassland) in southern Brazil. Questions on the origin of *Araucaria* forest and grasslands; its development, dynamic and stability; its response to environmental change such as climate; and the role of human impact are essential. Further questions on its natural stage of vegetation or its alteration by pre- and post-Columbian anthropogenic activity are also important. To answer these questions, palaeoecological and palaeoenvironmental data based on pollen, charcoal and multivariate data analysis of radiocarbon dated sedimentary archives from southern Brazil are used to provide an insight into past vegetation changes, which allows us to improve our understanding of the modern vegetation and to develop conservation and management strategies for the strongly affected ecosystems in southern Brazil.

**Keywords:** Late Quaternary; *Araucaria* forest; Campos (grassland); palaeoecology; conservation; management

**Abbreviations:** AD, Anno Domini; cal yr BP, calibrated radiocarbon years before present; uncal yr BP, uncalibrated radiocarbon years before present

## 1. INTRODUCTION

Several Neotropical regions harbour the most biodiverse ecosystems on Earth, yet we know only little about why they are so biodiverse. We are especially ignorant of the role that history has played in the development of these hotspots of species richness including endemism (Churchill *et al.* 1995, Broecker 1997). This problem is particularly acute in the extra-Andean ranges of eastern Brazil, the so-called 'Mata Atlantica biodiversity hotspot', where rigorous palaeoecological work has only begun during the last few years.

In this paper, we present data from the southern Brazilian highland region, where a mosaic of Campos (grassland) and *Araucaria* forests is found. The presence of these mosaics under modern wet climatic conditions favourable for forest development has puzzled naturalists and ecologists for a long time. Lindman, travelling across southern Brazil in the late nineteenth century, observed that forests should be able to expand over these grasslands, and attributed their presence to the transitional situation between tropical forests to the north and temperate grasslands to the south (Lindman 1906). In addition, Rambo (1956*a*,*b*) and Klein (1975, 1984), hypothesized based primarily on plant geographical evidence, that the grasslands were the older vegetation type, with forest expansion being a more recent process after changes to the more humid climate conditions. Also Hueck (1966) raised the question of how the southern Brazilian grassland can exist under the present humid forest climatic conditions.

Understanding the origin of the grasslands is of prime importance to their conservation. If the grasslands are as a consequence of human-induced deforestation, vegetation management would probably be focused on re-establishment of forest vegetation. If, however, the grasslands have prevailed in the past due to different climatic regimes, it could be reasonable to conserve these 'natural' relicts and their high biodiversity.

Sustainable management and conservation of the modern mosaics of Campos and *Araucaria* forest depends, in part, therefore on the determination of historical reference conditions for the past human impact, e.g. fire magnitude and frequency, and the applied use of this information in developing long-term management and monitoring plans. In this study, we present the results from a palaeoecological study (fossil pollen and microfossil charcoal) of a sediment core

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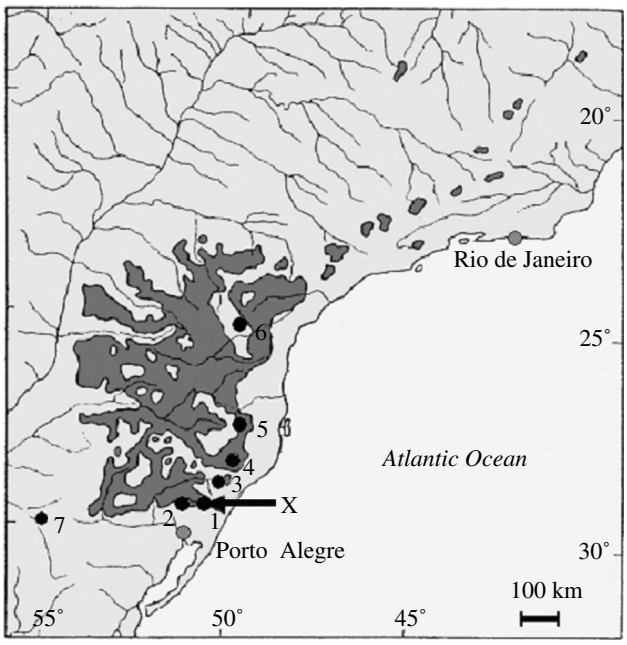


Figure 1. Map showing the distribution of *Araucaria* forest and Campos in southern Brazil (adapted after Hueck 1953, 1966) and the location of Cambará do Sul (X) and other sites mentioned in the text: (1) Aparados da Serra, (2) São Francisco de Paula, (3) Serra do Rio Rastro, (4) Morro da Igreja, (5) Serra da Boa Vista, (6) Serra Campos Gerais and (7) São Francisco de Assis.

sampled at Cambará do Sul on the southern Brazilian highland (Behling *et al.* 2004) to analyse past vegetation and fire dynamics. Special emphasis is placed on past plant diversity dynamics, in order to provide essential information for management and conservation of this biodiverse region. Important questions to be addressed include the following. How natural is the diverse mosaic of forest and grassland vegetation in southern Brazil? Was its development caused by pre-Columbian slash and burn activity, and deforestation of the post-Columbian settlers or rather a natural process of climate-driven forest expansion constrained by grassland fires? Are fires natural or of anthropogenic origin? What is the effect of climate change, fire and human impact on the overall biodiversity of the region through the time? How should we manage and conserve the modern species-rich forest and grassland ecosystems?

## 2. MODERN ENVIRONMENTAL SETTING

The vegetation on the southern Brazilian highland is composed of a mosaic of *Araucaria* forests and Campos (grassland). Data on the floristic composition of the southern highland are published by Hueck (1953, 1966), Klein (1978, 1979, 1984), Rambo (1953, 1956*b*), Por (1992), Boldrini (1997), Rosario (2001), Oliveira (2003) and Machado (2004). The distribution of subtropical *Araucaria* forest occurs between latitudes 24° and 30° S, mostly at elevations between 500 and 1400 m in southern Brazil and in isolated islands between 18° and 24° S between 1400 and 1800 m a.s.l. in southeastern Brazil (Hueck 1953, Rambo 1956*b*; figure 1). Important tree species are *Araucaria angustifolia*, *Ilex paraguariensis*, *Mimosa scabrella*, *Podocarpus lambertii*, *Myrcia* spp., *Myrceugenia* spp., *Eugenia* spp., *Myrciaria* spp., *Ocotea* spp. and *Nectandra* spp. The highly diverse Campos is characterized by non-arboreal species mainly in the families of Poaceae, Cyperaceae, Asteraceae, Apiaceae, Rubiaceae and Fabaceae. Under low grazing intensity, tall grasses dominate (*Andropogon* spp., *Aristida* spp., *Schizachyrium* spp.) mixed with shrubs such as *Baccharis* spp., *Vernonia* spp. (Asteraceae) and *Eryngium horridum* (Apiaceae).

Tropical Atlantic rainforest occurs in southern Brazil as a 100–200 km broad belt in the coastal lowlands near the border between the states of Santa Catarina and Rio Grande do Sul, and on the slopes of the southern Brazilian plateau (Serra Geral) at elevations up to 1000 m. Some rainforest species extend their range into the valleys of Serra Geral. The Atlantic rainforest is highly diverse in trees, shrubs, lianas, tree ferns and epiphytes. The dominant trees are from the families of Euphorbiaceae (*Alchornea*), Arecaceae (*Euterpe*), Myrtaceae, Moraceae, Bignoniaceae, Lauraceae and Sapotaceae (Hueck 1966, IBGE 1993). Dense cloud forest expands along the upper coastal mountains of the Serra Geral, composed of medium high trees and shrubs such as *Weinmannia humilis*, *Siphoneugena reitzii*, *Myrceugenia euosma*, *Drimys brasiliensis*, *Ilex microdonta*, *Berberis kleinii* and *Gunnera manicata*.

The modern vegetation is strongly affected by the logging of *A. angustifolia* forests and different agricultural land-use practices. During the last few decades large-scale afforestation of grassland by *Pinus* is seen on the highlands.

The study site, which is a bog located at 1040 m elevation in a small circular rocky basin of approximately 50 m in diameter, of the Cambará do Sul area is surrounded by a little disturbed *Araucaria* forest in the vicinity of the Aparados da Serra National Park. The bog is in a forest reserve and the surrounding forest today has little impact by logging and cattle.

The climate of southern Brazil is influenced by the South Atlantic anticyclone, a semi-permanent high-pressure system which transports moist tropical air masses over the continent from easterly and north-easterly directions during the whole year. Disturbances are related to polar cold fronts, which when meeting the tropical air masses produce strong rainfall in southern Brazil (Nimer 1989; Hastenrath 1991). Higher rainfall in southern Brazil is also related to El Niño events (Ratisbona 1976; Martin *et al.* 1993). The climate of the southern highland region is defined as warm temperate (subtropical) and humid without marked dry periods (Nimer 1989). The southern highlands form an orographic barrier for southeasterly to north-easterly winds. As a consequence, the rainfall is high with an average annual rainfall of over 2000 mm. The mean annual temperature is 14.5°C. The lowest recorded temperature during the last 100 years is −6.5°C (Nimer 1989).

## 3. PALAEOECOLOGICAL RECORDS OF SOUTHERN BRAZIL

### (a) *Past vegetation and climate dynamics*

Several palaeoecological studies from the Campos and *Araucaria* forest regions of the southern Brazilian

highlands have been carried out in the last decade (figure 1). Data from the states of Paraná (Serra Campos Gerais: Behling 1997), Santa Catarina (Serra do Rio Rastro, Morro da Igreja, Serra da Boa Vista: Behling 1993, 1995) and Rio Grande do Sul (Aparados da Serra: Roth & Lorscheitter 1993; São Francisco de Paula: Behling *et al.* 2001; Cambará do Sul: Behling *et al.* 2004) have demonstrated that extensive areas of Campos vegetation existed on the highlands through Glacial, Early and Mid Holocene times. The dominance of Campos vegetation was attributed to cold and dry glacial, and warm and dry Early Holocene climates. A dry season lasting probably approximately three months per year was the characteristic for the Early and Mid Holocene period (Behling 1997, 2002). Initial expansion of *Araucaria* forests started by migration from the gallery forests on the highland along the rivers *ca* 3210 calibrated (cal) year (yr) before present (BP), which indicates a turn to somewhat wetter climates.

A marked expansion of *Araucaria* forests started on the highlands, replacing Campos vegetation in Santa Catarina State *ca* 930 cal yr BP ago, and in Paraná State (Serra Campos Gerais) *ca* 1400 cal yr BP ago, reflecting a very humid climate without a marked seasonal dry period. Pollen data are also available from the lowland Campos (grassland) region near the city São Francisco de Assis in the western Rio Grande do Sul State (Behling *et al.* 2005). The region was naturally covered by Campos throughout the recorded Glacial and Holocene periods under the cold and relatively dry, and warm and dry conditions, respectively. Initial expansion of gallery forest after 5170 cal yr BP indicates a change to wetter climatic conditions. Maximum extent of gallery forest after 1550 cal yr BP reflects the wettest recorded period.

In this paper, new detailed high resolution data are presented from a sequence from the Cambará do Sul that spans the last 42 840 uncalibrated (uncal) years (figure 2). For a more complete palaeoenvironmental data and reconstruction, including records of selected single pollen and spore taxa, see also Behling *et al.* (2004). The pollen record from this site indicates the dominance of a diverse Campos vegetation between 42 840 uncal and 11 500 cal yr BP. The highland region of northwestern Rio Grande de Sul State was probably almost treeless. The evidence of a few single pollen grains representing *Araucaria* forest and Atlantic rainforest vegetation in the Late Pleistocene sediments were probably wind transported over some distance from forest refugia in deep and protected valleys in the highlands or from 6 to 7 km distant slopes of the Serra Geral mountains, or from the lowland vegetation of the coastal region, respectively. The widespread treeless Campos vegetation suggests a cold and dry climate with repeated frosts events and minimum austral winter temperatures below $-10^{\circ}$C, which do not permit the growth of *Araucaria* on the highlands. Mean annual temperature depression was probably similar to the southeastern Brazilian highland, which was in the range of 5–7°C between *ca* 26 000 and 17 000 uncal years ago, during the Last Glacial Maximum (LGM) period (Behling & Lichte 1997). During the LGM, the driest period recorded, pollen of *Eryngium*-type was abundant indicating drier conditions, and the shallow lake was not permanent indicating a seasonally dry climate. Based on the Cambará do Sul record, it is suggested that seasonal climatic conditions developed after 26 900 uncal years ago. Seasonal climate with a long annual dry period since the LGM period prevailed until the Late Holocene.

During the Early and Mid Holocene (11 500–4320 cal yr BP), Campos vegetation still dominated the landscape. *Araucaria* forest taxa increased slightly, but were still rare, indicating that populations migrated into the study region, probably along small streams. Atlantic rainforest taxa became more common, suggesting an expansion on the Serra Geral coastal slopes closer to the study site. Widespread Campos vegetation coupled with the rare occurrence of *Araucaria* forest taxa suggest a dry climate. Changes in the composition of the Campos vegetation document a change to a warm and dry climate. Annual precipitation must have been lower than 1400 mm and the climate was seasonal, with a dry season lasting approximately three months. The climatic conditions did not favour the expansion of *Araucaria* forest taxa in the study area during the Early and Mid Holocene.

During the initial Late Holocene period (4320–1100 cal yr BP), *Araucaria* forests expanded in the region, forming a net of gallery forests along the streams, while regionally grassland vegetation dominated. *Araucaria* forests included populations of *Myrsine*, and less frequently individuals of arboreal such as *M. scabrella*, Myrtaceae, *Podocarpus* and *Ilex*. The tree fern *Dicksonia sellowiana* was common in the gallery forests. The Atlantic rainforest taxa and probably also cloud forest species were well established on the upper coastal slopes, located approximately 6–10 km distance to the study site since the Late Holocene. During the second period in the Late Holocene (1100–430 cal yr BP), a remarkable strong expansion of *Araucaria* forest taxa took place, primarily *A. angustifolia* and *M. scabrella*, within 100 years replacing the Campos vegetation. During the uppermost Late Holocene period (430 cal yr BP–modern) still *Araucaria* forests kept expanding, reducing the Campos area in the study region. The expansion of *Araucaria* forests, including tree ferns, since 4320 cal yr BP and especially after 1100 cal yr BP is apparently related to a change to a wetter climate, with higher rainfall rates and a shorter annual dry season, or no marked dry season.

### (b) *Past fire dynamics and human impact*

So far only a few charcoal records are available from southern Brazil. The Serra Campos Gerais record in the Paraná State and the São Francisco de Assis record in the Rio Grande do Sul State (figure 1) indicate that fires were quite rare during the Glacial periods (Behling 1997; Behling *et al.* 2004). A marked increase in fire frequency is found in both the records at the beginning of the Holocene period.

In the Cambará do Sul record, the relatively low amount of carbonized particles (figure 2, data, calculated as accumulation rate (particles $cm^{-2}$ per yr), also documents that natural grassland fires were rare during the glacial periods (between 42 840 uncal and

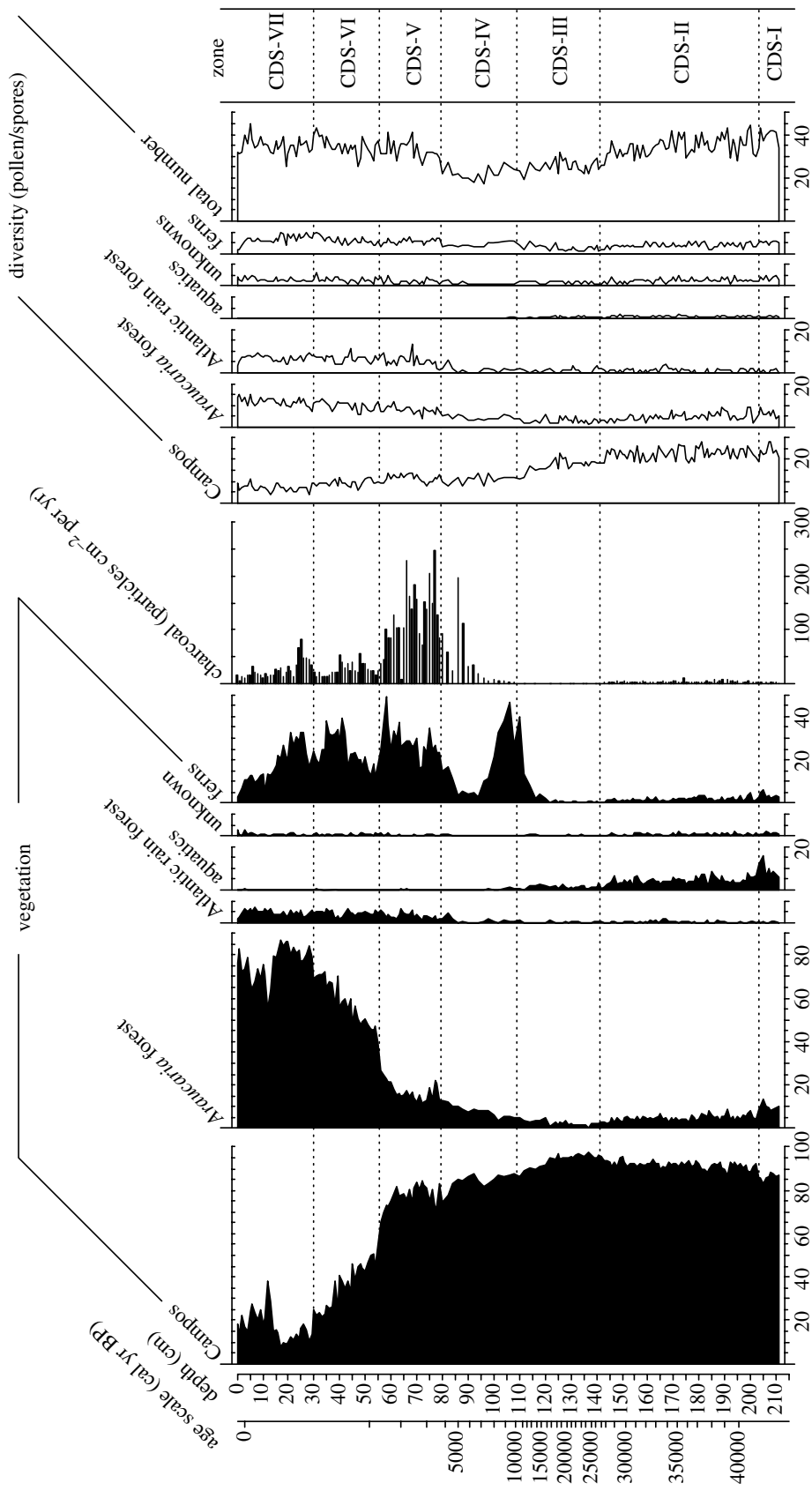


Figure 2. Summary pollen percentage diagram for the Cambará do Sul, including the age scale (cal yr BP) records of ecological groups, influx of carbonized particles, records of pollen and spore richness, its total number and pollen zones.

11 500 cal yr BP). Fire became frequent for the first time at *ca* 7400 cal yr BP, but not with the beginning of the Holocene as in the above mentioned records. This is probably in response to the onset of occupation by Amerindians (Dillehay *et al.* 1992), who may have used fire for hunting, coupled with seasonal climatic conditions leading to accumulation of flammable biomass. The different timing of the marked increase in fire frequency, which suggests an earlier occupation than on the southernmost highland region, is a good indication that frequent fires during the Holocene period are not natural, but of anthropogenic origin. Fire was facilitated by the presence of Poaceae species; it is likely that the presence of tall grasses during this period led to the accumulation of large amounts of highly flammable biomass in the growing season (Pillar & Quadros 1997). The abundance of Poaceae and the decrease of some other Campos taxa suggest that frequent fires may also have been a driving factor changing the floristic composition of the Campos (Bond & Wilgen 1996).

At *ca* 1100 cal yr BP, carbonized particles became less frequent in the sediments of the Cambará do Sul. The expansion of *Araucaria* forests reduced the area of Campos near the peat bog and fires became rare there, during the entire Late Holocene period since 1100 years ago. The somewhat higher accumulation rates of carbonized particles indicate that fire were still frequent in the wider region. Frequent fires at the end of the Holocene are also documented from other records, where present-day vegetation is still a mosaic of grassland and forest (Behling 1997, Behling *et al.* 2005, in press).

Besides the impact of early anthropogenic fires, the Cambará do Sul pollen data show an increase in Poaceae pollen (13.5 cm core depth) and then Cyperaceae pollen (9.5 cm) at *ca* 170 cal yr BP (AD 1780) and 100 cal yr BP (AD 1850), respectively. This indicates a post-Columbian disturbance of the *Araucaria* forest, probably by cattle within the forest. Cattle were introduced in the highland Campos in the first decade of the eighteenth century by the Jesuits from the Missions of the east side of the Uruguay river (Porto 1954). The village of the Cambará do Sul (7 km distance to the study site) was founded in 1864. The first farmers had free-range cattle likely entering into the forest somewhat earlier. First *Pinus* pollen grains (11 cm core depth) have been found at *ca* 130 cal yr BP, AD 1820. This coincides with the first German settlements in the lower slopes of the Serra Geral in Rio Grande do Sul, around AD 1825, which may have introduced the exotic taxa. A decrease in *A. angustifolia* pollen was detected between 30 and 15 cal yr BP (AD 1920 and AD 1935), signalling the start of intense selective logging. An enormous reduction of *A. angustifolia* (decrease of pollen from 41 to 2%, starting at 3.5 cm core depth) begins at *ca* 10 cal yr BP, AD 1940, with intensified selective logging of *Araucaria* trees during the last 50–60 years, but still not in the area surrounding the peat bog. Owing to the cattle in the forest and the logging of the *Araucaria* trees, other tree species, especially *M. scabrella*, and Myrtaceae, *Lamanonia speciosa* and *Ilex* became more frequent in the present secondary vegetation. Also *D. sellowiana* was removed from the *Araucaria* forest during the last 50–60 years. Tree fern trunks are used for orchid and other ornamental plant cultivation.

### (c) *Past biodiversity dynamics*

The number of different pollen and spore taxa counted on the pollen slides have been calculated and shown in figure 2. A total number of 300 pollen grains were counted for each subsample. The taxa were grouped into the same vegetation groups as shown on the left side of the pollen summary diagram. Also included in figure 2 are the total number of different pollen and fern types. The pollen and spore richness (see also figure 4) can be used as an indicator of past plant-diversity dynamics in the surroundings of the study site Cambará do Sul.

The data, prepared for this paper, show that the richness of the different pollen and spore types is relatively high between 42 840 and 27 000 years ago, especially due to the high number of different Campos pollen. During the drier LGM and Late Glacial period (27 000–11 500 years ago), which is drier than the previous periods, the number of different taxa, especially by Campos pollen, decreases markedly. Even during the dry and warm Early Holocene, the number decreases slightly (11 500–4320 cal years ago), especially by the onset of frequent fires at *ca* 7400 cal yr BP. However, the possible consequences for the grassland diversity of the large mammal extinctions that had occurred by *ca* 8000 uncal yr BP (Kern 1997) remain uncertain. One possibility is that the removal of large herbivores from the grasslands may have led to the dominance of tall grasses and, therefore, decrease of the grassland diversity by local extinctions of short grasses and forbs. Fires *per se* may not have caused the diversity decrease. On the contrary, with extinction of large mammals and in the absence of more frequent human induced fires, tall grasses would have dominated completely and probably the diversity decrease would be more pronounced.

During the Late Holocene period (4320–1100 cal yr BP), *Araucaria* forests and also some taxa of the Atlantic rainforest expanded into the region, indicating a change of the wetter climatic conditions. Since this period, the diversity of pollen and spore taxa is high again, but now due to the occurrence of different forest taxa in the study region rather than due to Campos taxa. Fires became frequent after 7400 years ago, but became locally less frequent due to the expansion of the *Araucaria* forest during the last 1100 years. There was no significant increase in diversity during these two Late Holocene periods, except during the end of this zone where the highest diversity of the record is observed before a decrease is found at the end of the record. The slightly higher increase is due to the opening of the forest by the free-range cattle during the post-Columbian times after AD 1780. New taxa could move into the forest since that time. The decrease of pollen and spore richness in the uppermost four subsamples occurred by the strong deforestation of *Araucaria* trees and the formation of secondary forests during the last decades.

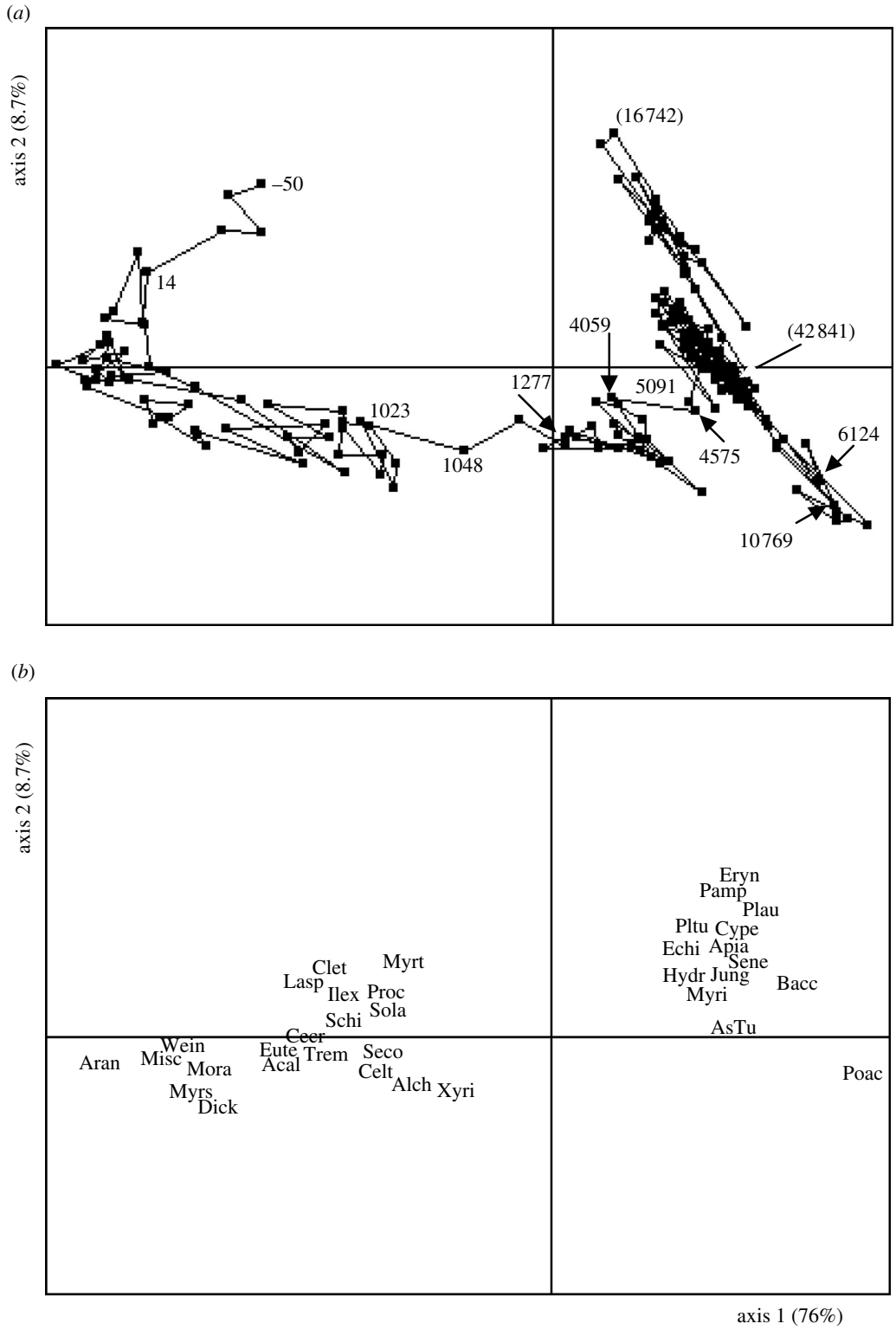


Figure 3. Ordination diagrams of pollen taxa described from sediment core from Cambará do Sul, Brazil. (*a* and *b*) The diagrams map the complete vegetation trajectory over 42 840 uncal yr BP. Dates after 11 540 are cal yr BP (1950); uncalibrated dates are in parenthesis. Ordination method is principal coordinates analysis based on Euclidean distances between sampling units, using percentages of pollen taxa of 138 in diagrams.

### (**d**) *Analysis of vegetation and plant diversity dynamics*

Between 42 840 and 26 900 years ago, vegetation dynamics was characterized by small random changes in the pollen composition, which is indicative of rather stable climate and plant communities (figure 3). This was followed by a sharp change, beginning around 27 000 years ago, to a new phase during the LGM period, when changes were undirectional in short time-scales, but strikingly directional in the long-term towards Campos characterized by more *Eryngium* and less Poaceae and Myrtaceae species. This pattern supports the idea that the vegetation dynamics is a convolution of alternating determinism, during directional phases, and chaos, during random phases (Anand and Orlóci 1997; Anand 2000, Orlóci *et al.* 2002*a*). During 42 840–27 000 cal yr BP, pollen compositional changes between adjacent time points

occurred with higher velocity than during the LGM period. This corroborates evidence from the other pollen profiles indicating that compositional changes of vegetation tend to slow down during cooler climate periods (Orlóci 2000; Orlóci *et al*. 2002*a*,*b*).

The rate of vegetation change increased sharply during the Late Holocene. The undirectional phase that characterized the vegetation trajectory after the initial expansion of *Araucaria* forest taxa, until around 1740 cal yr BP, coincides with an interval of highly stable pollen composition including the presence of Campos taxa. This situation could be similar to the present-day *Araucaria* forest patches occurring in a matrix dominated by Campos grassland.

The increase in Araucaria forest taxa occurred rapidly between 1740 and 1000 cal yr BP, as depicted clearly by the directional phase in the vegetation dynamics during this period. The cause of this change is primarily related to the climate, but could as well be the consequence of the reduction of the Campos vegetation which then tended not to burn as frequently.

An old question in ecology is whether diversity is related to community stability (see McCann 2001 for a review). By defining the community stability either as resistance to change or resilience, provided a long enough time-step is considered, more stable communities will tend to change less over time than the unstable communities. Therefore, we can use velocity of compositional change, calculated on the basis of palaeopollen data (Orlóci *et al*. 2002*a*,*b*), as a surrogate for community instability. The correlation of velocity and diversity may offer insights on the long-term association between diversity and community instability. For the Cambará do Sul data (figure 4), in the Early Holocene, only, correlations were highly negative, indicating that during this period when communities had higher diversity they changed more slowly, but during other periods, correlations had several positive peaks indicating that they changed faster. It is interesting to note that diversity was in general lower during the Early Holocene. What are the most probable cause–effect relationships behind these correlations? A hypothesis is that, on the one hand, under certain conditions producing low community diversity, a slightly higher diversity would enhance the community stability. On the other hand, during periods in which diversity is in general higher, community instability would enhance diversity even more. Both the trends seem to be present in the long-term vegetation dynamics depicted by the Cambará do Sul pollen record.

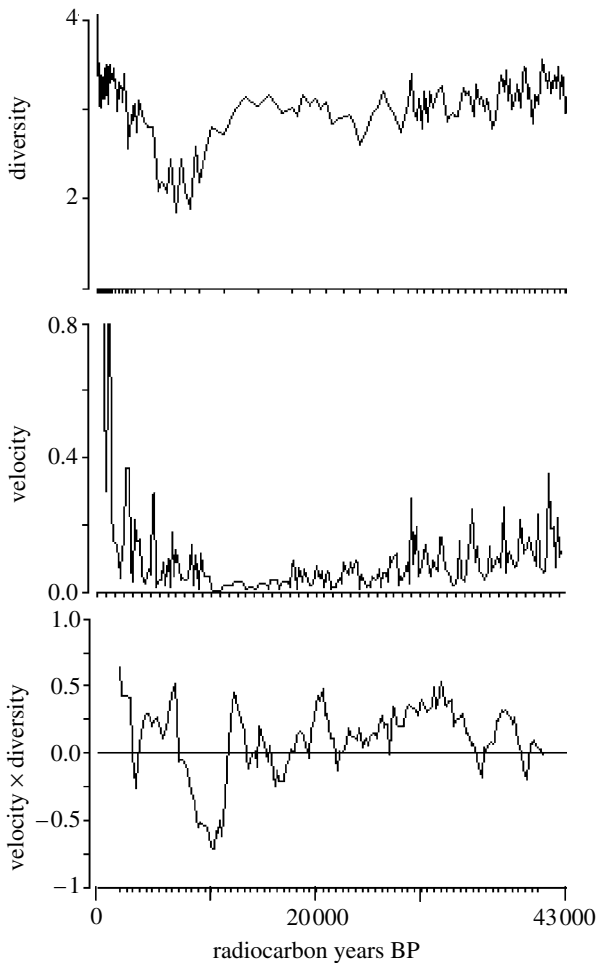


Figure 4. Diversity (Shannon) and velocity of compositional change in a pollen described sediment core from Cambará do Sul, Brazil, using percentages of 138 pollen taxa counts over 42 840 uncal yr BP. Velocity is based on Euclidean distances between adjacent sampling units. Interpolated data for equal time steps (200 years) used for sliding-window correlations (4000 years). Data are from Behling *et al*. 2004.

## 4. DISCUSSION AND CONCLUSIONS FOR CONSERVATION AND MANAGEMENT

The palaeoecological and palaeoenvironmental background information from the southern Brazilian highland provide important implications for conservation and management regarding dynamics of vegetation, biodiversity, fire and human impact including land use. Several pollen records document that the highly diverse patches of the Campos vegetation are natural remnants of a Large Glacial and Early–Mid Holocene area, and not former forest areas. This suggests that the Campos should be protected and not be subjected to afforestation as is at the moment the case, where areas of original grassland are being replaced by exotic pine forests.

The Campos area became markedly reduced by the expansion of *Araucaria* forest, especially during the last *ca* 1100 years, probably due to climatic change to wetter conditions. Natural expansion of *Araucaria* forest, which today in general is not possible due to human activities, would contract the area of the Campos. There is evidence that by excluding grazing and fire, present-day *Araucaria* forest tends to expand over the grassland (Oliveira & Pillar 2004; Duarte & Pillar in press).

The relatively late and strong expansion of *Araucaria* forests has implications for the modern vegetation. Could it imply that small, natural forest patches found within the grassland matrix would be less species diverse than nearby larger, continuous forest and thus, older areas of *Araucaria* forests found in valleys along the rivers would have higher species diversity? If yes, it would indicate that *Araucaria* forests in valleys along the rivers should deserve special attention for conservation. The results also show that *Araucaria* forest needs wet conditions with no marked dry seasons. Future climatic changes, such as drier conditions and longer dry periods, will markedly affect the forests growing on the southern highlands.

The so far available charcoal records indicate that natural (ignited by lightning) fires were rare in the Campos vegetation. The increase of fire frequency over the past 7400 years is probably owing to the occupation of the southern highland by Amerindians, in the Early Holocene or later as in the Cambará do Sul area. It has to be considered that anthropogenic fires played an important role during the Holocene and have certainly changed the floristic composition of the Campos, and some plants and present-day plant communities may have adapted to the fires (Overbeck *et al.* 2005). Further, the increase in charcoal coincided with a reduction in the diversity in the Campos, but whether this could be seen as a causal relationship is not clear; climate change and mammal extinctions are important factors that may have affected diversity. The palaeorecord shows that the later expansion of *Araucaria* forest was possible (or may have been facilitated) despite the high fire frequency and that fire in the surroundings of the study site Cambará do Sul became absent due to the expansion of the forest.

The consequences of the fire and grazing suppression at present in conservation areas with mosaics of forest and grassland in the south Brazilian highland should be carefully considered. The evidence indicates that with suppression of fire and grazing an active process of forest expansion, which had been halted by human disturbances, is re-established. If this management is maintained, in a few decades the grassland in conservation areas will shrink and eventually disappear. The other side of the coin is that the forest areas will increase. We believe Campos grasslands deserve conservation and it is not the case that these ecosystems do not belong to the present-day climate and depend on human disturbances, thus they should be condemned to extinction. Furthermore, fire and grazing suppression produce large accumulation of flammable biomass, increasing the risk of catastrophic, uncontrolled fires with unpredictable consequences on the biodiversity. Grassland fire, by legislation is prohibited in farms for management purposes, but in this case grazing by cattle maintains the grassland.

The introduction of cattle during the post-Columbian settlement and free-range cattle opened out the *Araucaria* forest. This favoured the migration of new species and changed the floristic composition. Limited free-range cattle may have a little effect on the stability of forests, but the present-day browsing and trampling levels by cattle in the forests prevent forest regeneration and risk its conservation. An urgent new management plan is necessary to protect the *Araucaria* forests. Data show that the selective logging of *A. angustifolia* trees and the tree fern *D. sellowiana*, as well as the strong deforestation of *Araucaria* forest during the twentieth century changed the forest markedly and the secondary forest developed. This implies that 'natural-like' *Araucaria* forests may be the secondary forests. Adequate and detailed studies are necessary to identify little disturbed 'virgin' forests which should then be protected. The protection of *A. angustifolia* since the 1980s was an important step, because forests have been regenerating more effectively since that time.

Changes in the presence of different pollen and spore types in the Cambará do Sul record suggest that dry climatic conditions reduce the plant diversity and wet conditions allow a higher diversity. The use of a limited number of cattle for Campos management might be a good alternative rather than the use of frequent fire with its negative effects such as soil degradation, air pollution and the impact of uncontrolled fires. Large mammals which have lived in the grasslands of southern Brazil until the beginning of the Holocene might be an important factor to maintain the high diversity of the Campos, similar to modern cattle.

Further, the free-range cattle during the post-Columbian times changed the *Araucaria* forest and increased the plant diversity slightly, but high numbers of cattle in the forest will have a negative effect. Data indicate that strong deforestation of the *Araucaria* forest and the formation of the secondary forests decreases the plant diversity.

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## REFERENCES

Anand, M. 2000 The fundamentals of vegetation change—complexity rules. *Acta Biotheoretica* **48**, 1–14. (doi:10.1023/A:1002630726523)

Anand, M. & Orlóci, L. 1997 Chaotic dynamics in a multispecies community. *Environ. Ecol. Stat.* **4**, 337–344. (doi:10.1023/A:1018595016851)

Behling, H. 1993 Untersuchungen zur spätpleistozänen und holozänen Vegetations- und Klimageschichte der tropischen Küstenwälder und der Araukarienwälder in Santa Catarina (Südbrasilien). *Dissertationes Botanicae* **206**, p. 149, J. Cramer, Berlin, Stuttgart, Germany.

Behling, H. 1995 Investigations into the Late Pleistocene and Holocene history of vegetation and climate in Santa Catarina (S Brazil). *Veg. Hist. Archaeobot.* **4**, 127–152. (doi:10.1007/BF00203932)

Behling, H. 1997 Late Quaternary vegetation, climate and fire history in the *Araucaria* forest and campos region from Serra Campos Gerais (Paraná), S Brazil. *Rev. Palaeobot. Palynol.* **97**, 109–121. (doi:10.1016/S0034-6667(96)00065-6)

Behling, H. 2002 South and Southeast Brazilian grasslands during Late Quaternary times: a synthesis. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **177**, 19–27. (doi:10.1016/S0031-0182(01)00349-2)

Behling, H. & Lichte, M. 1997 Evidence of dry and cold climatic conditions at glacial times in tropical Southeastern Brazil. *Quatern. Res.* **48**, 348–358. (doi:10.1006/qres.1997.1932)

Behling, H., Bauermann, S. G. & Neves, P. C. 2001 Holocene environmental changes from the São Francisco de Paula region, southern Brazil. *J. South Am. Earth Sci.* **14**, 631–639. (doi:10.1016/S0895-9811(01)00040-2)

Behling, H., Pillar, V., Orlóci, L. & Bauermann, S. G. 2004 Late Quaternary *Araucaria* forest, grassland (Campos), fire and climate dynamics, studied by high resolution pollen, charcoal and multivariate analysis of the Cambará do Sul core in southern Brazil. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **203**, 277–297. (doi:10.1016/S0031-0182(03)00687-4)

Behling, H., Pillar, V. & Bauermann, S. G. 2005 Late Quaternary grassland (Campos), gallery forest, fire and climate dynamics, studied by pollen, charcoal and multivariate analysis of the São Francisco de Assis core in

western Rio Grande do Sul (southern Brazil). *Rev. Palaeobot. Palynol.* **133**, 235–248. (doi:10.1016/j.revpalbo.2004.10.004)

Behling, H., Pillar, V., Müller, S. & Overbeck, G. In press. Late Holocene fire history in a forest–grassland mosaic in southern Brazil: natural and anthropogenic fire and implications for conservation. *J. Appl. Vegetat. Sci*.

Boldrini, I. I. 1997 Campos do Rio Grande do Sul: Caracterização Fisionômica e Problemática Ocupacional. *Boletin Instituto Biociencias/UFRGS* **56**, 1–39.

Bond, W. J. & van Wilgen, B. W. 1996 *Fire and Plants*. London, UK: Chapman & Hall.

Broecker, W. 1997 Future directions of paleoecological research. *Quatern. Sci. Rev.* **16**, 821–825. (doi:10.1016/S0277-3791(97)00050-4)

Churchill, S. P., Balslev, H., Forero, E. & Luteyn, J. L. (eds) 1995 *Biodiversity and conservation of neotropical montane forests*. New York, NY: The New York Botanical Garden.

Dillehay, D. T., Calderón, G. A., Politis, G. & Beltrão, M.C. de 1992 Earliest hunters and gatherers of South America. *J. World Prehist.* **6**, 145–204. (doi:10.1007/BF00975549)

Duarte, L., da S., Dos Santos, M. M. G., Hartz, S. M. & Pillar, V. D. In press. The role of nurse plants on *Araucaria* forest expansion over grassland in South Brazil. *Austral Ecol.*

Hastenrath, S. 1991 *Climate dynamics of the tropics*, p. 488. Dordrecht, The Netherlands; Boston, MA; London, UK: Kluwer Academic Publishers.

Hueck, K. 1953 Distribuição e habitat natural do Pinheiro do Paraná (*Araucaria angustifolia*). *Bolet. Fac. Filos. Ciênc. Univ. São Paulo, Bot.* **10**, 1–24.

Hueck, K. 1966 *Die Wälder Südamerikas*, p. 422. Stuttgart, Germany: Fischer.

IBGE 1993 Mapa de Vegetação do Brasil, Rio de Janeiro.

Kern, A. 1997 In *Arqueologia Pré-histórica do RS* (eds A. Kern, A. Jacobus, P. M. Ribeiro, S. Copé, P. I. Schmitz, G. Naue & I. B. Becker), pp. 89–102, 2nd edn. Porto Alegre, Brazil: Mercado Aberto 355.

Klein, R. M. 1975 Southern Brazilian phytogeographic features and the probable influence of upper Quaternary climatic changes in the floristic distribution. *Boletim Paranaense de Geociências* **33**, 67–88.

Klein, R. M. 1978 Mapa fitogeográfico do estado de Santa Catarina. In *Flora Ilustrada Catarinense* (ed. P. R. Reitz), p. 24. Itjai, SC: HBR.

Klein, R. M. 1979 Ecologia da flora e vegetação do Vale Itajai. *Sellowia* **31**, 1–164.

Klein, R. M. 1984 Aspectos dinâmicos da vegetação do sul do Brasil. *Sellowia* **36**, 5–54.

Lindman, C. A. M. 1906 *A Vegetação no Rio Grande do Sul*. São Paulo/Belo Horizonte, Brazil: EDUSP/Itatiaia.

Machado, R. E. 2004 *Padrões vegetacionais em capões de Floresta com Araucária no Planalto Nordeste do Rio Grande do Sul, Brasil. Programa de Pós-Graduação em Ecologia* (M.Sc. dissertation), Instituto de Biociências, UFRGS, Porto Alegre. Available at http://ecoqua.ecologia.ufrgs.br/arquivos/Reprints&Manuscripts/Theses&Dissertations/MachadoRafaelE_2004_MScDissert.pdf.

Martin, L., Fournier, M., Mourguiart, P., Siefeddine, A. & Turcq, B. 1993 Southern Oscillation signal in South American palaeoclimatic data of the last 7000 years. *Quatern. Res.* **39**, 338–346. (doi:10.1006/qres.1993.1040)

McCann, K. S. 2000 The diversity–stability debate. *Nature* **405**, 228–233. (doi:10.1038/35012234)

Nimer, E. 1989 *Climatologia do Brasil*. Rio de Janeiro: Fundação Instituto Brasileiro de Geografia e Estatística.

Oliveira, J. M. 2003 *Padrões e processos espaço-temporais em ecótonos de Campos e Floresta com Araucária, em São Francisco de Paula, RS*. Programa de Pós-Graduação em Ecologia (M.Sc. dissertation), Instituto de Biociências, UFRGS, Porto Alegre. Available at http://ecoqua.ecologia.ufrgs.br/arquivos/Reprints&Manuscripts/Theses&Dissertations/OliveiraJulianoM_2003_MScDissert.pdf.

Oliveira, J. M. & Pillar, V. D. 2004 Vegetation dynamics on mosaics of Campos and *Araucaria* forest between 1974 and 1999 in Southern Brazil. *Commun. Ecol.* **5**, 197–202. (doi:10.1556/ComEc.5.2004.2.8)

Orlóci, L., 2000 From Order to Causes. A personal view, concerning the principles of syndynamics. Published at the web address: http://mywebpage.netscape.com/lorloci/koa.

Orloci, L., Pillar, V. D., Anand, M. & Behling, H. 2002*a* Some interesting characteristics of the vegetation process. *Commun. Ecol.* **3**, 125–146. (doi:10.1556/ComEc.3.2002.2.1)

Orloci, L., Anand, M. & Pillar, V. D. 2002*b* Biodiversity analysis: issues, concepts, techniques. *Commun. Ecol.* **3**, 217–236. (doi:10.1556/ComEc.3.2002.2.8)

Overbeck, G., Müller, S. C., Pillar, V. D. & Pfadenhauer, J. 2005 Fine-scale post-fire dynamics in southern Brazilian subtropical grassland. *J. Veg. Sci.* **16**, 655–664. (doi:10.1658/1100-9233(2005)016[0655:FPDISB]2.0.CO;2)

Pillar, V. D. & Quadros, F.L.F. de 1997 Grassland-forest boundaries in Southern Brazil. *Coenoses* **12**, 119–126.

Por, F. D. 1992 *Sooretama the Atlantic rain forest of Brazil*, p. 130. The Hague, The Netherlands: SPB Academic Publishing bv.

Porto, A. 1954 *História das Missões Orientais do Uruguai*, 2nd edn. Porto Alegre, Brazil: Livraria Selbach.

Rambo, B. 1956*a* *A fisionomia do Rio Grande do Sul*. Porto Alegre, Brazil: Livraria Selbach.

Rambo, B. 1956*b* A flora fanerogâmica dos aparados riograndenses. *Sellowia* **7**, 235–298.

Rambo, B. 1953 História da flora do planalto riograndense. *Anais Botânicos do Herbário "Barbosa Rodriges"* **5**, 185–232.

Ratisbona, L. R. 1976 In *The Climate of Brazil*, vol. 12 (ed. W. Schwerdtfeger) *Climates of Central and South America*, p. 532. Amsterdam, The Netherlands: Elsevier.

Rosario, D. A. P. 2001 *Padrões florísticos e tipos funcionais em Floresta com Araucária e suas relações com o solo*. Dissertação de Mestrado, Programa de Pós-Graduação em Ecologia, UFRGS. p137. Available at http://ecoqua.ecologia.ufrgs.br/arquivos/Reprints&Manuscripts/Theses&Dissertations/RosarioDenise_2001_DissertMSc.pdf.

Roth, L. & Lorscheitter, M. L. 1993 Palynology of a bog in Parque Nacional de Aparados da Serra, East Plateau of Rio Grande do Sul, Brazil. *Q. South Am. Antarct. Peninsula* **8**, 39–69.