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 diverse 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 (1956a,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
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) and the location of Cambara 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.

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 Cambara 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 northeasterly 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 northeasterly 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
Catarina State 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, 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 trend 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 do 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°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 & Licht 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 (4320–11000 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 selowiana 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 Cambara 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.
Fire became frequent for the first time at ca 7400 cal yr BP, 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 Cambara 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 Cambara 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 Cambara 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 Cambara 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.
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 Orlo´ci 1997; Anand 2000, Orlo´ci et al. 2002a). During 42 840–27 000 cal yr BP, pollen compositional changes between adjacent time points

Figure 3. Ordination diagrams of pollen taxa described from sediment core from Cambara 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.
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. 2002a,b).

The rate of vegetation change increased sharply during the Late Holocene. The unidirectional 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. 2002a,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.

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.

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.

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 palaeo-record 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 marked 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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