

New insights into vegetation, climate and fire history of southern Brazil revealed by a 40,000 year environmental record from the State Park Serra do Tabuleiro

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Abstract The present study reveals palaeoenvironmental changes in the coastal southern Brazilian highlands during the last 39720 B.P., by the means of pollen, charcoal and multivariate data analyses. The isolated mountain range of Serra do Tabuleiro corresponds to the southern distribution limit of many tropical plant species and is therefore sensitive to climate change. Palaeoenvironmental reconstructions from the Ciama 2 core at 860 m a.s.l. indicate that Campos (subtropical grassland) covered extensive areas on the highlands throughout the recorded glacial period, thus suggesting cold and dry climatic conditions. The initial development of the Atlantic rainforest occurred after the glacial period, whereas plant diversity began to increase at the beginning of the Holocene due to climate change towards warmer and wetter conditions. At about 10400 cal. B.P., the Atlantic rainforest started to move over the slopes and Campos retracted. Multivariate data analysis showed a change of vegetation dynamics after 11200 cal. B.P. with the initial development of the Atlantic rainforest continuing until the mid-Holocene. Major vegetation changes, including the further expansion of the Atlantic rainforest and the

initial development of the *Araucaria* forest in the higher regions of the Serra do Tabuleiro, occurred during the late Holocene after about 3600 cal. B.P. These changes reflect higher precipitation levels without an annual dry season. Multivariate data analysis reveals a clearly directional change of vegetation dynamics corresponding to the progressive expansion of the Atlantic rainforest from 3850 to 1600 cal. B.P. A second directional change of vegetation dynamics occurred from 320 to 160 cal. B.P. (A.D. 1630 to 1790) with a further development of the Atlantic rainforest and the partial replacement of Campos by *Araucaria* forest and Atlantic rainforest. Thereafter, an ecosystem disturbance, which resulted in forest opening, took place. Palaeofires probably did not occur during glacial times, whereas fire events, which were probably caused by Amerindians, were common in the Serra do Tabuleiro region from ca. 10400 until 3600 cal. B.P.

Keywords Late Quaternary · Campos · Atlantic rainforest · *Araucaria* forest · Southern Brazilian climate · Fire history · Serra do Tabuleiro

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Introduction

Previous palaeoenvironmental studies conducted in southern Brazil have been considerably improving the understanding of vegetation dynamics in relation to climate changes during the late Quaternary. For the southern Brazilian highlands, Campos seems to be the predominant vegetation type during glacial times when colder and drier climate conditions prevailed (Behling 1998, 2002; Roth and Lorscheitter 1993; Ledru et al. 1998; Behling et al. 2004; Leonhardt and Lorscheitter 2010). The initial *Araucaria* forest expansion occurred about 2850 B.P. in

Serra dos Campos Gerais (Behling 1997) and after 2000 B.P. in Serra do Araçatuba (Behling 2007), both in Paraná state (Fig. 1c). For the highlands of Santa Catarina state, Behling (1995) proposed a first *Araucaria* forest expansion at about 3460 B.P. in Serra da Boa Vista and at about 2390 B.P. in Serra do Rio do Rastro. In Rio Grande do Sul, located further south than Santa Catarina, the initial *Araucaria* forest expansion is documented for about 3950 B.P. in Cambará do Sul (Behling et al. 2004) and after 4000 B.P. in the São Francisco de Paula region (Leonhardt and Lorscheitter 2010; Jeske-Pieruschka and Behling 2012). A marked *Araucaria* forest expansion is reported since about 1400 cal. B.P. in the state of Paraná (Behling 1997, 2007) and for the last 1,000 years for the highlands of the state of Santa Catarina and Rio Grande do Sul (Behling 1995; Behling et al. 2001, 2004). Although the early expansion of *Araucaria* forests occurred at different times, all interpretations suggest that *Araucaria* forest initially expanded by migrating out of gallery forests along rivers and wet areas after the mid-Holocene, when climate changed to more humid conditions. The vegetation history of the Atlantic rainforest in Volta Velha, southern Brazil is reported by Behling and Negrelle (2001). The authors documented an initial Atlantic rainforest development after 12300 B.P. as part of a successional sequence and the appearance of a dense forest after the marine regression at about 6100 B.P. for the Santa Catarina lowlands. Furthermore, Lorscheitter (2003) indicates fossil evidence of Atlantic rainforest taxa at the beginning of the Holocene at about 10000–8000 B.P. along the coastal plain and valleys of Rio Grande do Sul. More recently, Leal and Lorscheitter (2007) propose the occurrence of some Atlantic rainforest species in Serra Velha on the lower slopes of the Serra Geral, Rio Grande do Sul since 8800 B.P. However, with the exception of Behling et al. (2004), who reported environmental changes over a time frame of 42840 B.P. for the Cambará do Sul site, no other record which reaches back as far as to the pre-last glacial maximum (LGM) period is available for the entire region of southern Brazil. Thus, our study, covering the last 39720 B.P. of vegetation, climate and fire history in Santa Catarina state, located about 175 km to the north from Cambará do Sul site, contributes to a better understanding of palaeoenvironmental changes and human activities in a very sensitive climatic region of South America.

Here we present new palaeoecological data from a peat core of the Serra do Tabuleiro coastal mountain range. This region is covered by Campos (subtropical grassland) with some patches of *Araucaria* forest on the highlands and Atlantic rainforest growing in the lowlands and on the slopes. The Atlantic rainforest ecosystem is described as a hotspot of biological diversity (e.g. Myers et al. 2000; Tabarelli et al. 2005) and is known to be highly vulnerable

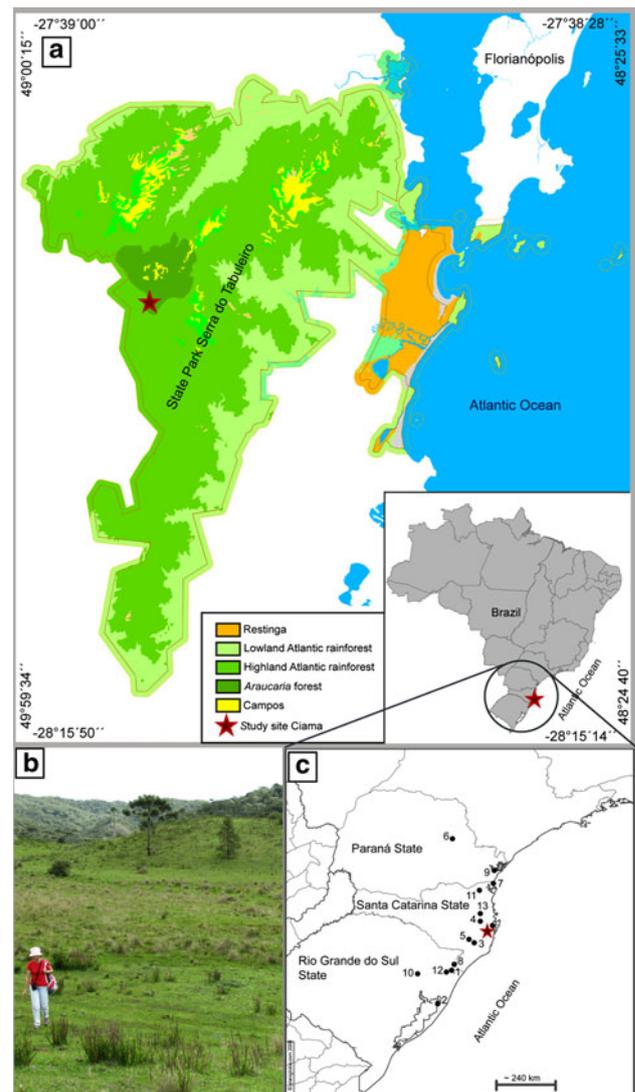


Fig. 1 a Map of the study area, showing the vegetation types of the State Park Serra do Tabuleiro. b View of the Ciama area with the peat bog surrounded by Campos with *Araucaria* forest and Atlantic rainforest in the background. c Map of southern Brazil with sites mentioned in the text. Palaeoecological records: (star) study site Serra do Tabuleiro 1 Aparados da Serra 2 Lagoa dos Patos 3 Serra do Rio do Rastro 4 Serra da Boa Vista 5 Morro da Igreja 6 Serra dos Campos Gerais 7 Volta Velha 8 Cambará do Sul 9 Serra do Araçatuba 10 Serra Velha 11 Campo Alegre 12 São Francisco de Paula 13 Caverna Botuverá. Sources: Vegetação Original [map]. 1:100,000. [Parque Estadual da Serra do Tabuleiro Produto Básico do Zoneamento, Estado de Santa Catarina]: Folha de referência III.1, 2000. Planiglobe Beta (www.planiglobe.com, Creative Commons Attribution 2.5 License)

to global change. Unfortunately, this ecosystem, which is very rich in species and has a high level of species endemism, is under continuous threat due to human activity since the European colonization at A.D. 1500 (e.g. Morelato and Haddad 2000). Palynological studies can offer palaeoenvironmental information, which is useful for the development of conservation and management strategies.

The Serra do Tabuleiro represents the southern distribution limit of many tropical species and is thus an important phytogeographical divisor (Klein 1962, 1981). The species diversity of trees, shrubs, epiphytes and lianas of the Atlantic rainforest gradually decreases towards the south (Klein 1962). Therefore, new acknowledgements about the development and shifting of the Brazilian subtropical forest ecosystems are surveyed and explained in this work. Moreover, with regard to the modern discussion of global warming, we attempt to provide a basis for the prediction of subtropical vegetation responses to future climate changes.

This study is based on pollen and charcoal records covering the last 39720 years, which are analysed with the help of multivariate analysis. The aim is to reconstruct the development and dynamics of Campos, *Araucaria* forest and Atlantic rainforest, and the inferred climatic change in the southern Brazilian region since the pre-LGM period, for which records in this region are scanty. This study helps to answer the question if the coastal mountain range could have acted as a refugium for forest taxa during the LGM period. Another goal is to detect the effect of future climate change on the dynamics of subtropical grassland vegetation and different forest ecosystems. The significance and influence of fire and human impact during the past will be addressed as well.

Regional setting

The study area

The State Park Serra do Tabuleiro was established in 1975 and covers an area of 87,405 ha, being the largest conservation unit in Santa Catarina State (Oliveira et al. 2006). As part of the park, the investigated peat bog (27°53' 48.46" S, 48°52' 5.33" W) is situated in the Ciama region (860 m a.s.l., Fig. 1). It is located in a small area of Campos, which is surrounded by forest. Currently, the distribution of *Araucaria* forest in the park is restricted to the Ciama region and its surroundings. Due to the proximity to the coast and its isolation from other mountain ranges, the site is adequate to record the development and dynamics of different ecosystems, as well as the fire history of the region.

Nowadays, the local population continues to use the land on which they lived before the establishment of the park in 1975. Forest exploitation on the Serra do Tabuleiro, mainly by logging of *Araucaria angustifolia* and *Ocotea porosa* (Klein 1981) began in the early 20th century in the course of the establishment of the Ciama sawmill. In the 1950s, a road was constructed in the region to facilitate

timber transport. The capital Florianópolis was founded by the first Portuguese settlers in the 17th century and in the 18th century, a new wave of Portuguese settlers colonized the coast more extensively. The first German and Italian settlers arrived in the 19th century (www.angelfire.com/al/Geografia/sc.html).

Modern vegetation

From the coastline to the upper part of the Serra do Tabuleiro at 1,200 m a.s.l., five different phytogeographic units can be observed (Klein 1981). In the eastern part, coastal vegetation (so-called *restinga*) and mangroves occur on a Quaternary sand plain. Atlantic rainforest is the dominating vegetation type on the slopes. Cloud forest grows at altitudes from 700 to 900 m. *Araucaria* forest can only be found in an isolated region at higher altitudes on the western part of the Serra do Tabuleiro. Campos covers the higher altitudes of the Park, where mosaic landscape with forest patches occurs. The water supply for Florianópolis and other surrounding cities comes from streams and rivers which rise at higher altitudes. At present, large areas of natural vegetation can still be found within the park. The local vegetation of the Ciama area is secondary vegetation. It is a transition zone of Atlantic rainforest and *Araucaria* forest with small patches of Campos (Fig. 1). It was not clear to what extent these grassland patches were natural, as in the past, the area was used for timber exploitation by the Ciama sawmill. The *Araucaria* forest is composed of *Araucaria angustifolia*, diverse Myrtaceae and other tree species such as *Calyptanthus concinna*, *Siphoneugena reitzii*, *Myrciaria tenella* and *Mimosa scabrella*. *Ocotea porosa*, *O. puberula*, *Lamanonia speciosa*, *Weinmannia pauliniaefolia*, *Drimys brasiliensis*, *Vernonia discolor*, *Piptocarpha angustifolia*, *Ilex* spp. and *Dicksonia sellowiana* appear associated with *Araucaria* forest along the upper slopes. Characteristic for the transition between the *Araucaria* forest and the Atlantic rainforest are *Clethra scabra*, *Gomidesia sellowiana*, *Myrsine* spp., *Symplocos* spp., *Clusia criuva*, *Merostachys ternata*, *M. speciosa* and *Chusquea* spp. Some species from the Atlantic rainforest can also be found, such as *Alchornea triplinervia*, *Hyeronima alchorneoides*, *Cryptocarya aschersoniana*, *Ocotea* spp., *Nectandra rigida*, *Aspidosperma olivaceum*, *Tapirira guianensis* and *Sloanea guianensis*. Numerous lianas and epiphytes belonging to Bromeliaceae, Orchidaceae, Araceae, Cactaceae, as well as pteridophytes, are typical for the Atlantic rainforest ecosystem. Campos vegetation is formed by forbs and graminoids, mostly by Poaceae, Cyperaceae, Fabaceae, Verbenaceae and Asteraceae (Klein 1978, 1981).

Climate

The climate is characterized as mesothermic (Cfa under 800 m a.s.l. and Cfb above 800 m a.s.l., Köppen) without dry season. Rainfall is uniformly distributed throughout the year with average annual precipitation varying between 1,600 and 1,800 mm/year. Average annual temperatures vary greatly according to the relief: lower regions and the coast have higher temperatures than the highlands, which can have temperatures below 0 °C in cold winter nights. Climate records from Florianópolis in the lowland show a January mean temperature of 24 °C and a July mean temperature of 16 °C (www.inmet.gov.br/html/clima.php). However, moderate summers and cold winters are characteristic for the highlands, while hotter and longer summers characterize the coastal area (due to subtropical latitudes) and the west (due to lower altitudes and continentality).

The study site is located in southern Brazil, which is influenced by the South Atlantic Anticyclone transporting equatorial warm and humid air masses from the tropical Atlantic Ocean over the continent during the whole year. This influence is weaker during the austral winter (June–August) and more frequent during the summer (December–February). Another atmospheric circulation, the Polar Anticyclone with dry and cold air masses, influences the climate of southern Brazil mostly during the winter. These air masses, which are formed in the Antarctic and moves across the South-American continent, provoke strong rainfall when they clash with tropical warm and humid air masses (Nimer 1989).

Precipitation anomalies are associated with El Niño Southern Oscillation (ENSO) and La Niña events. Excessive rainfall events are related to El Niño, whereas La Niña reduces rainfall in southern Brazil (Grimm et al. 1998, 2000). An excess or scarcity of precipitation in the southern coast of Brazil can also be linked respectively to periods of enhanced or weak activity of the South Atlantic Convergence Zone (SACZ) (Garreaud et al. 2009). Interannual variability of rainfall is also related to anomalies in sea surface temperature (SST), with increased or decreased precipitation respectively associated with warm or cold deviation of SST in the southwestern Atlantic Ocean (Díaz et al. 1998; Barros et al. 2000).

Materials and methods

Fieldwork and subsampling

A sediment core (169 cm long) was obtained from a peat bog in 2005 using a Russian corer. Each sealed 50 cm long core section was transported to the laboratory and stored

under dark and cold conditions until it was opened for sediment description and subsampling. A total of 83 volumetric subsamples (0.25 cm³) was used for pollen and charcoal analysis. Subsamples were taken every 2 cm except between 0 and 8 cm core depth, where two subsamples were taken at an interval of 4 cm. Eight subsamples were sent to the Radiocarbon Laboratory at the University Erlangen-Nürnberg, Germany, for AMS radiocarbon dating. The resulting ages were converted to calibrated calendar years before present using the software CALIB 5.0 (Stuiver and Reimer 1993). We applied the data set of SHCal04 (McCormac et al. 2004) for the ages in the Holocene period as well as for the multivariate data analysis and the one of IntCal04 (Reimer et al. 2004) for the ages in the Pleistocene period. For each calibrated age range a median probability was adopted. The age-depth model was constructed through linear interpolation between the radiocarbon ages.

Pollen and charcoal analysis

Standard pollen preparation procedures with hydrofluoric acid (HF) and acetolysis followed Faegri and Iversen (1989). One tablet of *Lycopodium clavatum* spores was added to each subsample to be able to calculate pollen and charcoal concentrations and accumulation rates (Stockmarr 1971). All *L. clavatum* spores that occur naturally in the area could be differentiated from the acetolysed *L. clavatum* marker due to the dark coloration and the wrinkled aspect of the latter. The pollen residues were mounted in glycerin gelatine and each sample was counted up to at least 300 pollen grains. Pollen and spores were identified using the reference collection available at the Department of Palynology and Climate Dynamics of the University of Göttingen and morphological descriptions by Behling (1993) and Cancelli (2008). The pollen sum (which includes all terrestrial taxa), pollen percentages and concentration were calculated and plotted in TILIA and TILIAGRAPH (Grimm 1991). The frequencies of arboreal pollen (AP), which includes pollen from tree and shrub taxa, and of non arboreal pollen (NAP), which includes pollen from herbs and grasses were plotted in the summary pollen diagram. Pollen grains of Myrtaceae are placed in the AP group. The zonation of the pollen diagrams (C2-I-IV) was based on the cluster analysis using CONISS (Grimm 1987). For the calculation we used a square root transformation for all known pollen taxa that occur in the 83 sample levels and excluded ferns, mosses, aquatics, unknown and not determined/indetermined pollen grains. The charcoal analysis was based on microscopic charred particles (5–150 µm) which were counted on the pollen-slides using the grid count method (Patterson et al. 1987).

Multivariate analysis

Principal coordinates analysis (PCoA) of the counted pollen data set (total of 83 subsamples as units and 120 taxa as variables) was used as the ordination method and was applied to Chord distances between subsamples. All analyses were performed using the MULTIV 2.5 software (Pillar 2006). Aquatic and non-identified pollen grains, as well as all spores, except those of tree ferns, were excluded prior to analysis in order to avoid the interference of local indicators in the results. All taxa present in at least two subsamples were included. Pollen sums were square root transformed before calculating the distances to reduce the importance of dominant taxa. The ordination analysis represents past vegetation dynamics from 39720 to –55 B.P. (A.D. 2005). In addition, we analyzed the vegetation trajectory during the recorded Pleistocene period to the mid-Holocene and over the Holocene. To verify local fire events, correlations between taxa and the concentration of charred particles were performed for the late Pleistocene and Holocene periods.

Results and interpretation

Lithology and chronology

The 169 cm long sediment core consists of seven distinct units (Fig. 2a). At the bottom (169–142 cm), the sediment is composed of light-brown very sandy clay with organic material and small granite stones. From 142 to 70 cm core depth, the sediment consists of brown clay with organic material. Within this section, small amounts of sand and small granite stones occur between 142 and 120 cm. The following interval from 70 to 45 cm is composed of black clay containing a few fine roots. Between 45 and 25 cm, the sediment contains dark-brown decomposed peat containing some fine roots and from 25 to 17 cm, the sediment contains light-brown decomposed peat containing many fine roots. The overlaying section (17–7 cm) consists of brown, decomposed peat rich in fine roots. In the upper part of the core (7–0 cm), there is a layer of weakly decomposed peat with *Sphagnum* sp. covering the top.

The chronology of the sediment sequence is constructed using eight AMS radiocarbon dates (Table 1). The extrapolated basal age at 168 cm core depth corresponds to 39720 B.P. Based on the radiocarbon dates, a continuous sedimentation with no gaps is suggested for the recorded glacial and Holocene periods. Pollen of *Pinus* occurs in the subsamples between 14 and 0 cm core depth, which thus would be after 160 cal. B.P. (~A.D. 1790) indicating a complete core until modern times. The age versus depth relationship (Fig. 2b) shows that sedimentation rates stayed relatively constant through time until 34 cm core depth, when the sedimentation rate increases. Around this point

the sedimentological composition changes from clayey sediment to almost fully decomposed peat after 45 cm core depth and to weakly decomposed peat after 7 cm core depth. As expected, pollen concentration rates decrease significantly during this period.

Description of the pollen diagram

The pollen diagram (Fig. 3) illustrates the percentages of the dominant and most important taxa out of 200 different pollen and spore types found in the core subsamples. A summary pollen diagram (Fig. 4) represents the pollen taxa grouped into different vegetation types, as well as the charcoal data. Based on important changes in the pollen assemblages and on the result of the cluster analysis, four pollen zones have been distinguished (C2-I to C2-IV; Table 2). Pollen concentrations vary between 6.1×10^8 and 4.8×10^{10} grains/cm³ and pollen influx varies between 43,700 and 4,600,000 grains/cm² year.

Zone C2-I (39720–17800 B.P.) is characterized by high percentages of NAP (69–90 %) and minor proportions of AP (6–22 %). Campos taxa are well represented, consisting primarily of Poaceae (49–75 %) and minor pollen proportions of Cyperaceae, different Asteraceae, *Eryngium*-type, Apiaceae, *Xyris*, Iridaceae and *Plantago*. Atlantic rainforest taxa are relatively constant (5–23 %) and are represented mostly by pollen of Myrtaceae, *Weinmannia*-type, *Myrsine* and Melastomataceae. Less frequent (1–5 %) are taxa of the *Araucaria* forest, represented by pollen of *Ilex*, *Mimosa scabrella*-type and *Podocarpus*. A single *Araucaria angustifolia* pollen grain was counted at 142 cm core depth, but single pollen grains were also registered at 168, 166 and 152 cm core depths, as found in an additional scanning process. The tree ferns group reaches up to 8 %, principally due to the rise in spores of Cyatheaceae. Other Pteridophyta, with values between 4 and 15 %, are mainly represented by spores of *Blechnum imperiale*-type, Monolete psilate <50 µm, *Selaginella excurrens*-type and *Isoetes*. Moss spores are poorly represented by low percentages of *Sphagnum* (0–1 %). Concentrations of carbonized particles (9.6×10^{12} – 3.225×10^{14} particles/cm³) and influx (3.1×10^8 – 1.5×10^{10} particles/cm² year) are constantly low during this period.

In Zone C2-II (17800–9900 B.P.) the percentages of NAP increase slightly (84–90 %), while the proportions of AP show a decreasing trend (6–17 %). The Campos taxa are mainly represented by Poaceae pollen with increasing values (65–78 %). Pollen of Cyperaceae, *Eryngium*-type, Apiaceae, Iridaceae and *Plantago* decreases in abundance to ≤2 %. A slight decrease of percentages of the Atlantic rainforest group can be noted. *Alchornea* pollen percentages increase up to 3 % at the top of this zone. Abundances of *Araucaria* forest taxa decrease to 0 %. Tree fern spores are represented by decreasing percentages, mainly by low

Fig. 2 **a** Lithology and location of dated subsamples of the Ciama 2 sediment core (uncalibrated years B.P.) and **b** radiocarbon ages of the Ciama 2 core plotted against depth (cm)

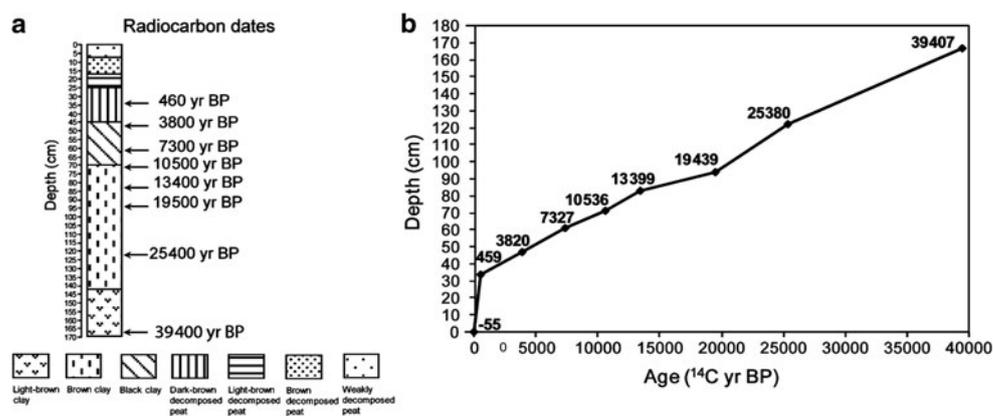


Table 1 Radiocarbon ages and calibrated ages of organic matter from the Ciama 2 core

| Lab. code | Depth (cm) | Age (B.P.) | Age range ^a (cal. B.P.) | Med. prob. (cal. B.P.) | Calibration curve |
|-----------|------------|-------------|------------------------------------|------------------------|-------------------|
| Erl-11255 | 34 | 459 ± 44 | 328–534 | 478 | SHCal04 |
| Erl-12097 | 47 | 3820 ± 39 | 3981–4284 | 4129 | SHCal04 |
| Erl-12656 | 61 | 7327 ± 45 | 7981–8179 | 8092 | SHCal04 |
| Erl-11256 | 71 | 10536 ± 63 | 12240–12786 | 12545 | IntCal04 |
| Erl-12657 | 83 | 13399 ± 72 | 15528–16341 | 15916 | IntCal04 |
| Erl-12098 | 94 | 19439 ± 115 | 22661–23596 | 23126 | IntCal04 |
| Erl-12099 | 122 | 25380 ± 152 | Too old for calibration | | |
| Erl-11257 | 167 | 39407 ± 681 | Too old for calibration | | |

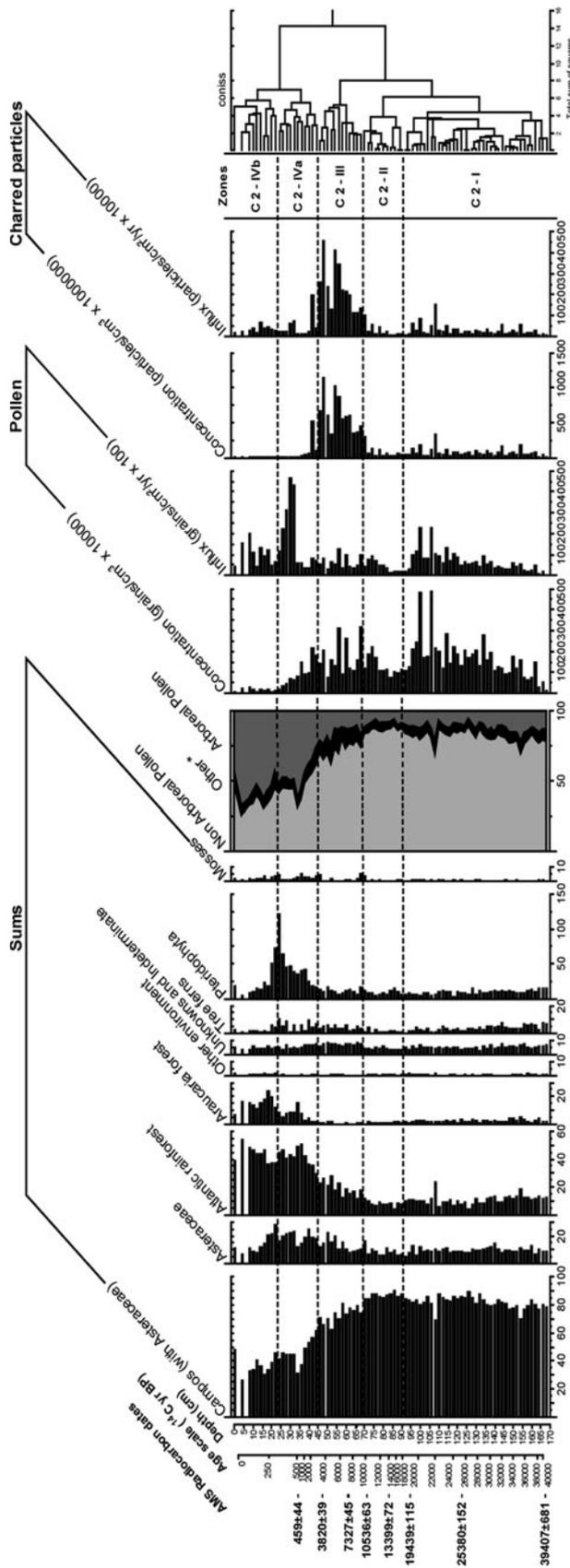
^a Range at standard deviation of 2 σ at 95.4 % probability

values of Cyatheaceae (<4 %). The Pteridophyta group remains stable but abundances of spores of *Blechnum imperiale*-type and *Isoetes* drop at the top of this zone. Mosses are basically represented by *Sphagnum* spores (0–3 %). Charcoal concentration (2.0×10^{13} – 3.0×10^{14} particles/cm³) and charcoal influx (3.8×10^8 – 1.0×10^{10} particles/cm² year) continue to be low during this zone.

In Zone C2-III (9900–3300 B.P.) the proportions of NAP decrease down to 63 %, whereas frequencies of AP are represented by increasing values from 10 to 24 %. Campos taxa show a decreasing trend (80–63 %), mainly attributed to lower percentages of Poaceae pollen (65–40 %). Pollen abundances of Asteraceae subf. Asteroideae increase up to 10 % and those of Apiaceae up to 5 %. *Eryngium*-type reaches its highest values (8 %) in this zone. A marked increase of abundances of Atlantic rainforest taxa from 12 to 28 % can be noted. This is mainly due to the increase in *Weinmannia*-type pollen to 14 % at the top of this zone. Pollen percentages of *Myrsine*, Melastomataceae and *Alchornea* and, with lower values, of Moraceae/Urticaceae, *Celtis* and *Trema*-type also increase. Myrtaceae pollen frequencies slightly decrease (4–1 %). Taxa of the *Araucaria* forest (<2 %) are much less frequent. Tree fern taxa increase to 7 %, with higher proportions of Cyatheaceae and lower frequencies of *Nephelea setosa* and *Dicksonia sellowiana*. The group of Pteridophyta is well represented

with values between 6 and 16 %, mainly composed of spores of Monolete psilate <50 μ m. Spore abundances of *Blechnum imperiale*-type increase up to 7 % at the top of this zone. Abundances of spores of *Selaginella excurrens*-type decrease strongly (7–0 %). Moss proportions increase slightly up to 5 %, represented by spores of *Sphagnum* and *Phaeoceros laevis* (not shown in the diagram). Values for concentrations (3.3×10^{14} – 1.15×10^{15} particles/cm³) and influx (1.1×10^{10} – 4.5×10^{10} particles/cm² year) of carbonized particles increase markedly in this zone.

Zone C2-IV (3300 B.P. to the present) is divided into two subzones (IV-a and IV-b). This zone shows a further decrease in NAP down to minimum proportions of 26 %, but they recover higher to the top of the zone reaching values of 48 %. AP increases markedly with values ranging between 26 and 68 %. A strong decrease from 61 to 26 % in Campos taxa is mostly reflected by the decrease of Poaceae pollen (31–7 %). Abundances of Cyperaceae pollen increase markedly compared to the previous zone and reach values of 21 %. Pollen frequencies of the Heliantheae-type also increase (up to 8 %) whereas Apiaceae pollen percentages decrease strongly, reaching a maximum value of 1 %. Pollen abundances of *Eryngium*-type decrease continually from 6 % at the first part of the zone to 0 %, but they increase up to 3 % towards the top of the core. Abundances of Atlantic rainforest taxa show a



◀ **Fig. 4** Summary pollen percentage diagram, including pollen and charcoal concentration as well as pollen and charcoal influx and the cluster analysis dendrogram of the Ciama 2 peat bog. * Other includes pollen grains from taxa that can have different growth forms (tree, shrub, herb or liana) as well as all unknown and indeterminate pollen grains counted in all depth levels of the core

Multivariate analysis

The complete trajectory of pollen composition changes over the last 39720 B.P. is shown in the ordination diagrams (Fig. 5a, b). Axes 1 and 2 explain 58 % of the total variation in the data set with 120 taxa and 83 subsamples. A random phase, with slight changes in vegetation occurs during the glacial period until 12680 B.P. (13470 cal. B.P.) with Campos as the dominating vegetation type in the system. Non-directional changes in pollen composition dynamics at the small temporal scale and a directional trend at the large scale during the end of the Pleistocene (12680 B.P. or 13470 cal. B.P.) until the mid-Holocene (3560 B.P. or 3850 cal. B.P.) can be observed in Fig. 5b. The replacement of the initially predominant Campos (Fig. 5a, on the right-hand side) by forest vegetation (Fig. 5a, on the left-hand side) occurs after 3850 cal. B.P., when Atlantic rainforest and *Araucaria* forest expands. Changes in the pollen composition along a time trajectory from 39720 until 3560 B.P. (3850 cal. B.P.) are depicted on a separate ordination (Fig. 5c, d), in which the two main axes account for 35 % of the total variation. During the period from 39720 until 12680 B.P. (13470 cal. B.P.), corresponding to the pollen zones C2-I and II, the system is dominated by Campos, represented primarily by Poaceae (Fig. 5c). Some taxa belonging to the *Araucaria* forest, like *Illex* and Myrtaceae, are present, but decrease slightly during this period. Myrtaceae may also correspond to species that occur in the Campos vegetation, which can be seen on the right-hand side in Fig. 5c, together with the groups of Cyperaceae and Apiaceae. Subsequent to phases of randomness, an evident change in the vegetation dynamics occurs after 10780 B.P. (11200 cal. B.P.), corresponding to the pollen zone C2-III. The vegetation is characterized by increased quantities of forest taxa, such as *Alchornea*, *Myrsine*, *Weinmannia* and Melastomataceae, which represent the Atlantic rainforest (Fig. 5c, on the left). Another ordination exploring the period of 8930 B.P. (9510 cal. B.P.) to -55 B.P. (A.D. 2005) (Fig. 5e, f) reveals the vegetation dynamics over the Holocene period and towards the end corresponds to the pollen zone C2-IV. The main ordination axes account for 47.6 and 12.6 %, respectively, for the first and second axes. Three phases of strong directionality of vegetation change occur. The first significant directional change in pollen composition appears from 3560 until 1490 B.P. (3850 until 1600 cal. B.P.),

Table 2 Pollen zones of the Ciama 2 core, showing the depth, the converted radiocarbon ages and the number of subsamples for each pollen zone

| Zone | Depth (cm) | Age range (B.P.) | Age range (cal. B.P.) | No. of subsamples |
|--------|------------|------------------|-----------------------|-------------------|
| C2-I | 168–91 | 39720–17800 | | 39 |
| C2-II | 91–69 | 17800–9900 | 21200–10400 | 11 |
| C2-III | 69–45 | 9900–3300 | 10400–3600 | 12 |
| C2-IVa | 45–23 | 3300–290 | 3600–300 | 11 |
| C2-IVb | 23–0 | 290––55 | 300––55 | 10 |

when the vegetation changes from predominantly open Campos (Fig. 5e, on the right), to a more forested one (Fig. 5e, on the left). The Atlantic rainforest expands, mostly represented by *Weinmannia*, whereas the *Araucaria* forest starts to develop, as it is reflected by *Araucaria angustifolia* pollen grains (Fig. 5e). The second directional change follows a random phase and takes place from about 310 until 160 B.P. (A.D. 1630–1790). During this phase, a further development of the Atlantic rainforest and the *Araucaria* forest occurs, which replace in part the Campos. This is represented by the taxa *Lamanonia speciosa*, Myrtaceae, *Symplocos tenuifolia*, *S. lanceolata* and *Ouratea* (Fig. 5e, on the left). Also, *Araucaria* forest is well represented by taxa such as *Mimosa scabrella*, *Ilex* and *A. angustifolia*. From 5 to –55 B.P. (A.D. 1940 to 2005), subsequent to the spatial expansion of the forest, a sharp change in pollen composition takes place, with a tendency towards a pollen composition of Campos vegetation.

Environmental reconstruction based on the palaeoecological record

A grassland landscape predominated in the southern Brazilian highlands throughout the pre-LGM and LGM period from 39720 B.P. until 21200 cal. B.P. (zone C2-I). The vegetation was mainly composed of grasses (Poaceae) and different forbs of the Asteraceae family, but also of Cyperaceae, Apiaceae and other plants characteristic of grassland ecosystems. Some species of Myrtaceae, placed in the Atlantic rainforest group, probably belonged to the grassland vegetation during the recorded last glacial. They might have been shrub species (e.g. *Campomanesia* spp.) that grew in open grassland vegetation at this time. The multivariate analysis of the pollen data indicates a predominance of Campos taxa during the palaeovegetational trajectory spanning over glacial times (from 39720 to 12680 B.P. or 13470 cal. B.P.; zone C2-I-II). As indicated by a random phase, only small changes in pollen composition that therefore do not reflect marked changes in vegetation dynamics occurred during the last glacial period. Steady cold climatic conditions at this time may have only produced small-scale compositional changes

Table 3 Abbreviations of the pollen taxa shown in the ordination diagrams

| Abbreviation | Pollen and spore taxa |
|--------------|-----------------------------------|
| Alcho | <i>Alchornea</i> |
| Apiac | Apiaceae |
| Arauc | <i>Araucaria angustifolia</i> |
| Astsu | Asteraceae subf. Asteroideae |
| Celti | <i>Celtis</i> |
| Cyath | Cyatheaceae |
| Cype | Cyperaceae |
| Dicks | <i>Dicksonia sellowiana</i> |
| Eryng | <i>Eryngium</i> -type |
| Helia | Heliantheae-type |
| Holo | <i>Holocheilus</i> -type |
| Ilex | <i>Ilex</i> |
| Irida | Iridaceae |
| Lama | <i>Lamanonia speciosa</i> -type |
| Melas | Melastomataceae |
| Misca | <i>Mimosa scabrella</i> -type |
| Myrsi | <i>Myrsine</i> |
| Myrta | Myrtaceae |
| Nephe | <i>Nephelea setosa</i> |
| Ourat | <i>Ouratea</i> -type |
| Oxali | <i>Oxalis</i> -type |
| Plant | <i>Plantago</i> |
| Pluch | Plucheae-type |
| Poac | Poaceae |
| Symla | <i>Symplocos lanceolata</i> -type |
| Symte | <i>Symplocos tenuifolia</i> -type |
| Tetru | <i>Tetrorchidium rubrivenium</i> |
| Trema | <i>Trema</i> -type |
| Trixi | <i>Trixis</i> -type |
| Vernu | <i>Vernonia nudiflora</i> -type |
| Weinm | <i>Weinmannia</i> -type |

in the highlands. During the pre-LGM and LGM period, the Atlantic rainforest was represented by low frequencies of *Weinmannia*, *Myrsine*, Melastomataceae, *Alchornea*, Moraceae/Urticaceae, *Celtis*, *Symplocos tenuifolia* and *Mimosa taimbensis*. Small populations of arboreal taxa probably occurred on the slopes of the mountain range at lower elevations or even formed small gallery forests along rivers or streams in the lowland, thereby creating refugia. It might be possible that these taxa existed in deep valleys of the Serra do Tabuleiro where humidity was retained. Some (sub-) tropical forest species such as *Roupala*, *Drimys brasiliensis*, *Mimosa taimbensis*, *Sebastiania commersoniana* (not shown in the pollen diagram) and *Symplocos lanceolata* were not present during the LGM period. Other sensitive arboreal species such as *Alchornea* and *Myrsine* were represented by diminished abundances, sometimes with only one pollen grain in

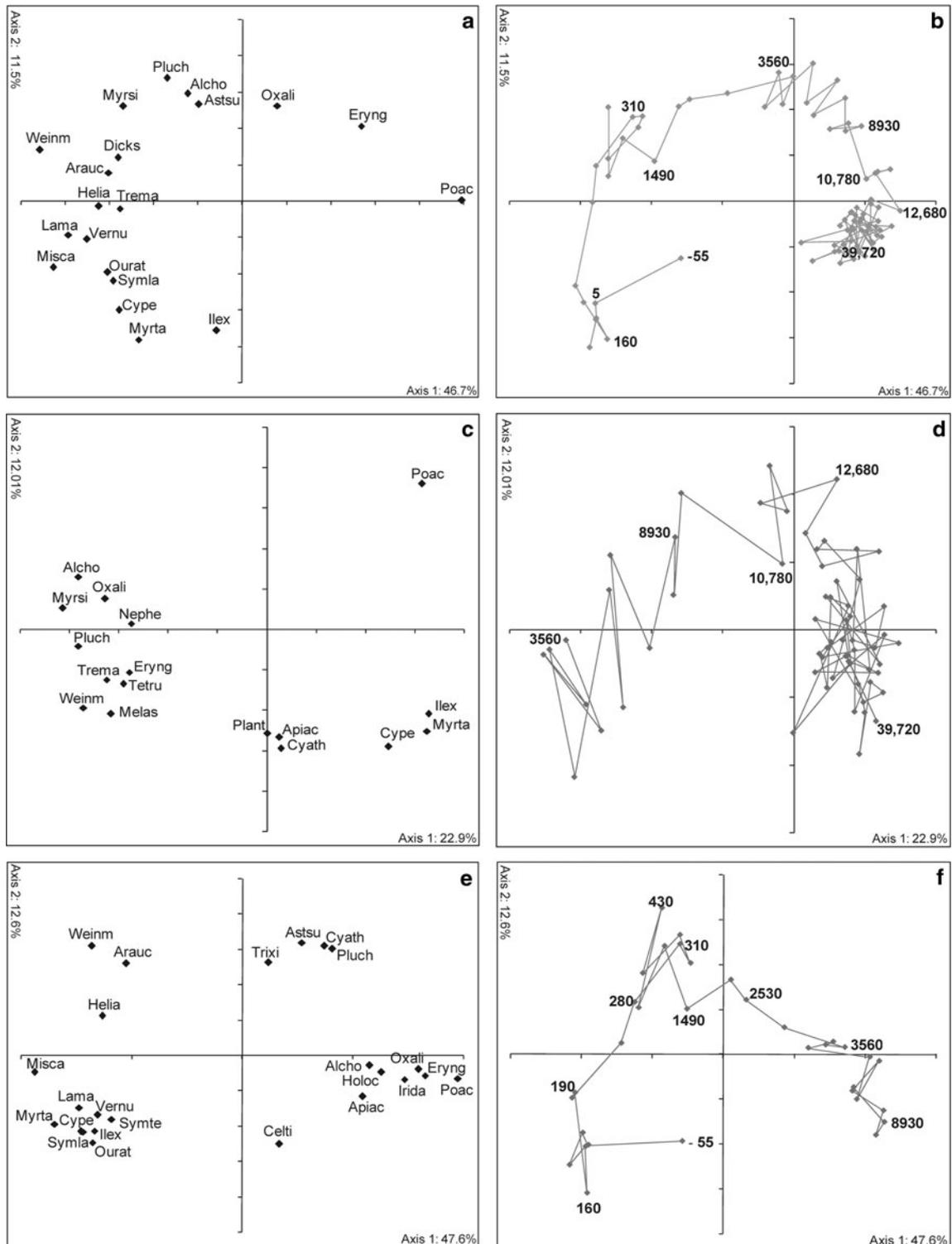


Fig. 5 Ordination diagrams based on principal coordinate analysis (PCOA) applied to chord distances between sampling units from the Ciama 2 core. Pollen data were previously square-root transformed. The complete vegetation trajectory for the last 39720 B.P. is mapped in the diagrams **a**, **b** with 83 sampling units and 120 taxa including counted pollen types and tree fern spores. Sampling units are identified by age (radiocarbon years). Other separated ordinations

using the same method map the trajectory over the Pleistocene until the mid-Holocene in **c**, **d**, with 62 sampling units and 102 taxa, and over the complete Holocene in **e**, **f**, with 33 sampling units and 87 taxa. Only taxa with the highest correlation ($-0.5 \leq r \leq 0.5$) are shown in positions proportional to their correlation level to each ordination axis in **a**, **c** and **e**. Taxa abbreviations are shown in Table 3

Table 4 Pollen taxa with the highest positive or negative correlations to charcoal concentration during the Pleistocene and Holocene period. All pollen taxa found in at least 50 % of the subsamples were used for the analysis

| Pleistocene 39720–10200 B.P. | | Holocene 9600 B.P. until present | |
|---------------------------------|----------|----------------------------------|----------|
| Taxa | <i>r</i> | Taxa | <i>r</i> |
| <i>Weinmannia</i> -type | 0.57396 | Poaceae | 0.75412 |
| <i>Alchornea</i> | 0.36713 | <i>Eryngium</i> -type | 0.65964 |
| Asteraceae subf. Asteroideae | 0.35346 | Melastomataceae | 0.50486 |
| <i>Baccharis</i> -type | 0.33598 | Cyperaceae | −0.43453 |
| <i>Myrsine</i> | 0.27903 | <i>Blechnum imperiale</i> -type | −0.45904 |
| <i>Holocheilus</i> -type | 0.27424 | <i>Araucaria angustifolia</i> | −0.46249 |
| Iridaceae | 0.25451 | <i>Ilex</i> | −0.4772 |
| <i>Blechnum imperiale</i> -type | −0.34302 | <i>Lamanonia speciosa</i> -type | −0.48713 |
| Poaceae | −0.40661 | Heliantheae-type | −0.50711 |
| | | Myrtaceae | −0.5557 |
| | | <i>Lycopodium clavatum</i> -type | −0.58425 |
| | | <i>Weinmannia</i> -type | −0.58822 |
| | | <i>Mimosa scabrella</i> -type | −0.61206 |

the whole period. These slight differences in the pollen spectra reflect colder and drier climatic conditions for the LGM in comparison to the pre-LGM on the Serra do Tabuleiro. Only a few pollen grains of *Araucaria angustifolia* and *Podocarpus* during the last glacial period suggest the presence, probably in scattered patches, of these trees in the lower regions of the Serra do Tabuleiro.

The slight decrease of Atlantic rainforest taxa such as *Weinmannia*, *Myrsine*, *Symplocos tenuifolia* and *Mimosa taimbensis* during the zone C2-II (21200–10400 cal. B.P.) suggest that a dry phase lasted throughout the late glacial period. Forest taxa, such as *Ilex*, together with Cyperaceae and tree ferns (Cyatheaceae), decreased during this period, thus indicating drier conditions. This hypothesis is also supported by the increase of Poaceae. However, a drier phase from 21200 to 10400 cal. B.P. cannot be recognized in the ordination diagrams, as Poaceae were the dominant taxon in the system throughout the last glacial stage.

The beginning of the Holocene was characterized by an increase in frequencies of tree pollen such as *Weinmannia*, *Myrsine* and *Alchornea*, thus reflecting the early development of Atlantic rainforest from the lowland over the slopes. Between 10400 and 3600 cal. B.P. (zone C2-III), Campos taxa, such as some Asteraceae, *Eryngium*, Apiaceae, Iridaceae and *Plantago*, as well as forest taxa, such as Melastomataceae, Moraceae/Urticaceae, *Celtis* and *Trema*, rose in abundance simultaneously with tree ferns, thereby indicating a climatic improvement to wetter and warmer conditions. This vegetational change, implying forest development/expansion, but also reflecting the maintenance of a forest-grassland mosaic could be due to an increase in precipitation at the Pleistocene/Holocene transition. The multivariate analysis gives clear evidence for a marked change of vegetation dynamics after 11200 cal. B.P. Better climatic conditions with higher humidity

permitted a forest development, which is indicated by a large-scale directional trend during the end of the Pleistocene (13470 cal. B.P.) until the mid-Holocene (3850 cal. B.P., Fig. 5c, d). This directional change was characterized by the increase in forest taxa such as *Alchornea*, *Myrsine*, *Weinmannia* and Melastomataceae mentioned above, thus suggesting the expansion of Atlantic rainforest.

From 3600 cal. B.P. until the present (zone C2-IV), a continuous development/expansion of Atlantic rainforest took place, and *Araucaria* forest began to develop and expand as well. At this time, the study bog was covered by *Sphagnum* and *Blechnum imperiale*. An evident directional change of vegetation dynamics happened from 3850 to 1600 cal. B.P. when Atlantic rainforest continued to expand mostly due to *Weinmannia* and Myrtaceae, while the *Araucaria* forest group started to develop mainly with the pioneer taxa *Mimosa scabrella* and *Araucaria angustifolia* (Fig. 5e, f). Forest development and expansion was probably related to increased moisture levels during this period. The establishment of a forest environment throughout the mid/late Holocene (3600–300 cal. B.P.; subzone C2-IVa) is indicated by the decrease of proportions of Poaceae, some Asteraceae, Apiaceae, *Eryngium* and other Campos taxa, whereas Myrtaceae and *Weinmannia* greatly increased. *Araucaria* forest began to develop at approximately 2160 cal. B.P. and reached its maximum expansion in the study area after 300 cal. B.P. (A.D. 1650).

Major changes in forest composition occurred during the last 360 years (subzone C2-IVb). After the change of the predominant Campos vegetation to a forest system, another directional change in vegetation dynamics occurred from 320 to 160 cal. B.P. (A.D. 1630 to 1790). During this period, Atlantic rainforest and *Araucaria* forest expanded further, thereby replacing Campos. This can be observed by the increased abundances of *Lamanonia speciosa*, Myrtaceae,

Symplocos tenuifolia, *S. lanceolata*, *Ouratea*, *Mimosa scabrella*, *Ilex* and *Araucaria angustifolia* (Fig. 5e). Later, ecosystem disturbance occurred, resulting in forest opening. This disturbance is indicated by the increase of *Trema* and *Mimosa scabrella*, coinciding with the decrease of *Araucaria angustifolia* and *Podocarpus*. Both *Trema* and *Mimosa scabrella* are known as pioneer species that establish after disturbance, thus representing forest exploitation by European settlers and logging in the last years. An abrupt decrease of *Blechnum imperiale* after 260 cal. B.P. (A.D. 1690) also indicates bog disturbance. From A.D. 1940 to 2005, a strong directional phase in vegetation dynamics revealed by changes in pollen composition indicates a trend of Campos species returning to the Ciama area (Fig. 5e, f). The higher occurrence of Poaceae at the top of subzone C2-IVb may indicate the opening of the forest due to human activity.

Palaeofires

Two main phases could be distinguished in the curves of charcoal concentration and influx based on the counted charcoal particles. The first phase, with relatively constant low proportions of microcharred particles, corresponds to the recorded last glacial period. The second phase is marked by a rising trend of microcharcoal fragments starting about 10360 cal. B.P. Higher concentrations of charred particles until 3570 cal. B.P. suggests that fire was very common in the region during this time. Fire events continued to be common in the Serra do Tabuleiro during the late Holocene, as indicated by high frequencies of charred particles for the last centuries. This cannot be easily recognized in the charcoal concentration and influx curves, as there is a dissimilar time resolution of about 500 years from the 34 cm depth in the core upwards in comparison to the millennial timescale of the deeper samples, which expressed slow sedimentation rates.

Results of unexpected correlations between pollen taxa and charcoal concentration (Table 4) during the Pleistocene (zone C2-I and C2-II) support the assumption that fire was almost absent during glacial periods on the Serra do Tabuleiro. Forest taxa, such as *Weinmannia*, show a highly positive correlation with charcoal concentration, while Poaceae as a Campos taxon and *Blechnum imperiale* as a fern that grows in peat bogs are negatively correlated to charcoal concentration. On the other hand, results of correlation analyses between pollen taxa and charcoal concentrations during the Holocene (zone C2-III and C2-IV) show a strong positive correlation of Poaceae with charred particles, while forest taxa such as *Mimosa scabrella*, *Weinmannia* and Myrtaceae show a strong negative correlation with charcoal concentration (Table 4). These results

indicate that fires occurred locally or regionally during the Holocene.

Discussion

Late quaternary vegetation dynamics

During the recorded glacial period (39720 B.P. to 10400 cal. B.P.), grassland vegetation, dominated by Poaceae, covered the highlands of southern Brazil. The low representation of AP, together with the high quantity of grasses in the pollen record, indicates that cold and dry climatic conditions prevailed in this region during this period. Roth and Lorscheitter (1993) proposed drier conditions before the Holocene for the Aparados da Serra region in the southern Brazilian highlands based on a reduced forest cover and an expansion of grassland. Several authors agree that cold and dry climatic conditions prevailed in southern Brazil during the last glacial period (e.g. Behling 1998, 2002; Leonhardt and Lorscheitter 2010; Jeske-Pieruschka and Behling 2012). Additional information on a late Pleistocene dry period comes from a geomorphic study of the northern highlands of Santa Catarina state (Campo Alegre, Oliveira et al. 2008). According to Behling et al. (2004), climate in the southern Brazilian highlands was dry and cold during the pre-LGM, but even drier and colder during the LGM. These results are in accordance with ours, which demonstrate colder and drier climatic conditions during the LGM in comparison to the pre-LGM on the Serra do Tabuleiro. With respect to palaeoclimate, Behling and Negrelle (2001) propose an annual average cooling of 5–7 °C for the LGM period in the southern Brazilian lowlands. According to our results, a treeless landscape continues to dominate the southern region of Brazil under a continuously cold and dry climate during the late glacial period. Other palaeoecological studies have confirmed drier conditions for the highlands of southern Brazil throughout this period (e.g. Behling 1995, 1997, 2007).

The Serra do Tabuleiro could have acted as a refugium for forest taxa during the LGM. The proximity to the Atlantic Ocean could have provided milder climatic conditions that would have favored the survival of some trees during this period. Some orographically protected areas, such as deep valleys, where a microclimate with higher levels of humidity favored tree survival under regionally dry conditions, could be hypothesized as refugia. However, the very low proportions of AP including (sub-) tropical sensitive tree species as *Alchornea* and *Myrsine* among others, suggested that the coastal mountain range of Serra do Tabuleiro was not a glacial refugium for Atlantic rainforest taxa during the LGM. Furthermore, if the Serra do Tabuleiro had been a glacial refugium for forest taxa, then the small arboreal populations existing there up to this period would have expanded rapidly since the

beginning of the Holocene when moister and milder climatic conditions arose. The conifers *Araucaria angustifolia* and *Podocarpus* had probably been present as small populations in protected valleys or on slopes at lower elevations of the Serra do Tabuleiro during the last glacial period. Taking *Araucaria angustifolia* as an indicator species for moist and cold forest, since it can neither tolerate temperatures lower than $-10\text{ }^{\circ}\text{C}$ nor an annual precipitation lower than 1,400 mm or a marked dry season (Hueck 1966), climate was cold on the Serra do Tabuleiro during the last glacial. Lower precipitation and higher temperature levels can affect *Araucaria angustifolia* growth (Silva et al. 2009). According to Leonhardt and Lorscheitter (2010), a warmer climate affects the reproductive capacity of *Araucaria* forest taxa.

Holocene vegetation dynamics

The Atlantic rainforest that characterizes the region today started to move from the lowland over the slopes in the early Holocene. Our results indicate that between 10400 and 3600 cal. B.P., due to warmer and wetter climatic conditions, the Atlantic rainforest probably extended over the coastal slopes of the Serra do Tabuleiro. However, the amount of Poaceae pollen remained high during late Holocene despite the expansion of forest. Thus, the interpretation that a mosaic of natural grassland and forest remained during late Holocene at the studied site is compatible with our pollen record. Indeed, other studies have indicated that grassland vegetation continued to dominate the landscape of the southern Brazilian highlands. It would be reasonable to interpret that prolonged phases of drought continued to prevail in the region despite of milder and moister conditions since the early Holocene. Further, the occurrence of fire during the Holocene may have restricted forest expansion over grassland (Oliveira and Pillar 2004; Blanco personal communication). Ledru et al. (2009) stated that, although changes in insolation are the most important climatic factor controlling rainforest dynamics in the southern tropics, changes in precipitation rates and/or seasonality greatly affect the tropical rainforest. A pollen profile from São Francisco de Paula, on the eastern plateau of southernmost Brazil (Serra Geral), indicates that temperature and moisture increased at the beginning of the Holocene (Leonhardt and Lorscheitter 2010). The pollen record from Serra Velha on the lower slope of the Serra Geral about 330 km south of the Ciama 2 site shows the occurrence of Atlantic rainforest taxa at about 8800 and 5000 B.P., indicating the migration of tropical species from east to west since the early Holocene (Leal and Lorscheitter 2007). However, Behling (1995) demonstrated for the highlands of Santa Catarina state that Campos vegetation continued to prevail until ca. 1000 B.P. on Morro da Igreja and Serra do Rio do Rastro, while an expansion of Atlantic rainforest taxa followed by *Araucaria* forest occurred at the beginning of the Holocene in

the Serra da Boa Vista. The latter site is located 50 km inland from the Atlantic Ocean and ~ 35 km from the Ciama 2 site, which in turn is situated just 25 km away from the coast. The proximity of these sites to the Atlantic Ocean may have provided higher moisture, as they have been influenced by the warm and humid Tropical Atlantic Air Mass since the early Holocene. Observations of wetter climatic conditions in the lowlands and on the Atlantic slopes of the southern Brazilian highlands since the beginning of the Holocene come from Behling (1998). In the southern Atlantic lowlands, Atlantic rainforest started to develop after 12300 B.P. as a part of a successional sequence. However, a dense forest did not become established until after the marine regression at about 6100 B.P. (Behling and Negrelle 2001). A wet climate has been recorded since about 4000 B.P. for the southernmost Brazilian coastal lowlands (Lagoa dos Patos, Cordeiro and Lorscheitter 1994). These results differ from Behling (1998) and Ledru et al. (1998) who suggest dry climatic conditions for southern Brazil during the early/mid Holocene. Other studies report drier conditions and a longer annual dry season for the southern Brazil highlands during the early and mid-Holocene (Behling 1997, 2002, 2007; Behling et al. 2001, 2004). However, these studies cover sites that are further inland than Ciama 2. Our results from the Serra do Tabuleiro, which is located much closer to the Atlantic Ocean, indicate that humidity levels rose gradually throughout the Holocene.

Forest establishment during the mid/late Holocene was related to increased moisture levels during this period. A comparison with a high-resolution oxygen and carbon stable isotope record from cave calcite from Caverna Botuverá, at a distance of 80 km from the Ciama 2 site, reveals that the local temperature can be affected by the summer monsoonal precipitation as well as by winter extratropical circulation patterns (Cruz et al. 2005, 2006). Negative $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values in this speleothem record indicate that increased rainfall coincided with a marked forest expansion across the Serra do Tabuleiro during the mid-Holocene. From 3600 cal. B.P. to the present, the Atlantic rainforest continues to develop/expand while the *Araucaria* forest began to develop initially at about 2160 cal. B.P., reaching its maximum expansion after 300 cal. B.P. (A.D. 1650). Hence, a pronounced development of the *Araucaria* forest happened much later in the Serra do Tabuleiro than in the Serra Geral further south, and just within the northwestern part of the park. The isolated occurrence of *Araucaria* forest and its very late expansion despite favorable climatic conditions suggest that the Serra do Tabuleiro was not a refugium for *Araucaria* forest taxa during glacial times.

Pollen data from other sites in the southern Brazilian highlands agree in suggesting that forest expansion started in the mid-Holocene and reached its expansion maximum after 1500 cal. B.P. (Behling 1995, 1997, 2007; Behling et al. 2004; Jeske-Pieruschka and Behling 2012). However, as shown in our study, the Atlantic rainforest began to move from the

lowland upwards across the slopes under milder and wetter conditions in the early Holocene. A continuous forest development/expansion of the Atlantic rainforest and a first development of the *Araucaria* forest is reported for the mid/late Holocene for the region, indicating an amelioration of climate towards moister conditions. Higher precipitation levels, without a major annual dry season that allowed marked forest expansion since late Holocene times were also inferred by Behling (1997) at Serra dos Campos Gerais for the last 1500 B.P. and by Behling (2007) at Serra do Araçatuba after 2000 B.P., both in Paraná state. For Santa Catarina (Behling 1995) and the Rio Grande do Sul highlands (Behling et al. 2001), the major *Araucaria* forest expansion occurred later than in Paraná (situated further north than Santa Catarina), i.e. during the last 1000 B.P., thus under modern climatic conditions.

Based on the increase of *Weinmannia*-type pollen frequencies, Behling et al. (2004) suggest a warmer phase during the little ice age (LIA) for the southern Brazilian highlands. This finding is consistent with our data, in which we found an increase of certain woody taxa that are characteristic of moister and warmer conditions, such as *Weinmannia*. An interpretation inferred from a lake sediment from São Paulo state indicates a warmer and probably wetter period for southeastern Brazil between ~370 and 340 B.P., which fits into the LIA (Pessenda et al. 2010). The LIA is known as a period of cooling in Europe between about A.D. 1200 and 1700.

Considerable vegetational changes occurred due to ecosystem disturbance over the last 360 years, resulting in forest opening. The disturbance of the native forest in the Ciama region during the last centuries can be related to the activities of Portuguese settlers from the coast, who might have exploited the forest throughout the 17th and 18th centuries. Ecosystem disturbance has also taken place because of the construction of a road for timber transport by the company Ciama in the 1950s. By successive timber exploitation and burning, additional open areas were created, which under cattle grazing may have been converted into anthropogenic grassland (Klein 1981) formed by species from nearby Campos.

Palaeofires and implication for human occupation in southern Brazil

Charcoal particles were relatively rare during glacial times. Power et al. (2008) recorded the lowest fire occurrence during the glacial period under a cooler and drier-than-present global climate. The charcoal can be interpreted as a wind-blown intake from fire events across larger distances, assuming that natural fires were very unlikely in these highland environments during glacial periods. Local palaeofires could not be detected based on the concentration of charred particles, as the counted particles sizes (5–150 μm) were mostly too small to give certainty about this. The counted sedimentary charcoal fragments

(normally <50 μm) indicate distant or regional fire events (Clark and Royall 1995; Carcaillet et al. 2001).

During the Holocene, fire events were very common in the region from ca. 10400 until 3600 cal. B.P. It is likely that Amerindians may have caused these fires. Prous and Fogaça (1999) provide evidence for human presence in Minas Gerais, central Brazil, at the end of the Pleistocene (between 12000 and 11000 B.P.). The authors also pointed out that human occupation in southern Brazil can be recorded since ca. 8000 B.P., when the Umbu and Humaitá cultures arrived. Available evidence suggests that fires of anthropogenic origin can be dated back to the beginning of the Holocene in Paraná state (Behling 1997) and to after 7400 B.P. in Rio Grande do Sul state (Behling et al. 2004). Prehistoric fires continued to be common during the late Holocene. However, it would be reasonable to interpret these fires in the Serra do Tabuleiro as being of anthropogenic origin during the late Holocene, as climate was moist in the early/mid-Holocene and more humid during the late Holocene.

Insights from the results for future conservation in the State Park Serra do Tabuleiro

The remaining areas of natural Campos at higher elevations of the State Park Serra do Tabuleiro will probably disappear in the future due to progressive forest expansion over Campos under the modern, humid climatic conditions (e.g. Hueck 1966; Lindman 1906; Rambo 1956a, b). Nonetheless, this biodiverse ecosystem can be maintained by human interference, such as the promotion of fire and grazing (e.g. Behling and Pillar 2007; Behling et al. 2007; Jeske-Pieruschka et al. 2010; Overbeck et al. 2005; Pillar 2003; Pillar and Vález 2010). If fire and/or grazing by large grazers are not allowed, then the restricted areas of Campos in the park might be maintained by mowing (Fidelis et al. 2012).

Observations of *Araucaria* forest replacing Campos areas are also recorded by Hueck (1953) and Klein (1960), as well as by Oliveira and Pillar (2004). Furthermore, the first two authors notice that the Atlantic rainforest restricts both the Campos and the *Araucaria* forest in its ongoing vegetation succession. Here, we provide evidence for a progressive replacement of Campos and *Araucaria* forest by Atlantic rainforest in the southern Brazilian highlands if climate becomes warmer under the effects of global change. At present times, frequent frost during the winter months continues to limit the survival of tropical species on the highlands. However, if climate becomes drier and/or longer periods of drought become more frequent, both ecosystems, the *Araucaria* forest as well as the Atlantic rainforest, will show a hindered development due to water deficits. To sum up, the present landscape, shaped by a Campos-*Araucaria* forest mosaic on the southern Brazilian highlands, will be replaced by Atlantic rainforest under warmer climatic conditions. On

the other hand, the forest ecosystem will retreat under drier climatic conditions. Hence, future climate changes will play a crucial role in vegetation composition and dynamics in the subtropical southern Brazilian highlands.

Conclusions

The pollen and charcoal record from the coastal mountain range of Serra do Tabuleiro reveals palaeoenvironmental changes in southern Brazil during the last 39720 B.P. The results indicate that a treeless landscape continues to dominate under a cold and dry climate throughout the last glacial period until 13470 cal. B.P. A climatic amelioration towards warmer and wetter conditions during the transition from the Pleistocene to the Holocene period provided adequate conditions for the initial colonization of the slopes by trees at about 10400 cal. B.P., with tropical species migrating from the lowland and the coast across the slopes. The proximity to the Atlantic Ocean could also have enhanced the migration of forest taxa from the northern regions to the south due to moderate and moister conditions at the coast. The Atlantic rainforest expanded three times, at the beginning of the Holocene, during the mid/late Holocene, and during the last centuries. The *Araucaria* forest expanded twice during the late Holocene, each time showing differences in floristic composition. The Atlantic rainforest began to develop during the early Holocene and expanded further during the mid-Holocene in the region. As its initial development and expansion is reported for the mid-Holocene in the highlands of Rio Grande do Sul state, located further south, the observations indicate that the Atlantic rainforest shifted from the north to more southerly regions. Therefore, the Serra do Tabuleiro can be seen as a migratory corridor for the tropical species. We concluded that, under the effects of global warming, the Atlantic rainforest will expand through migration of many tropical plant species into the southern regions of Brazil, replacing *Araucaria* forest and, if grazing and fire are suppressed, replacing the Campos in *Araucaria*-Campos mosaics on the highlands. The consequence would be a change of the entire southern Brazilian highland landscape.

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