Journal of Biogeography (*J. Biogeogr.*) (2007) **34**, 1701–1722

ORIGINAL ARTICLE

Brazilian Páramos IV. Phytogeography of the campos de altitude

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ABSTRACT

Aim This contribution treats the phytogeography of the contemporary campos de altitude flora, with a focus on patterns at the level of genus. Comparative analysis using data from 17 other sites in Latin America is used to describe phytogeographical patterns at the continental scale. Results are combined with those of previous publications to shed light on the biogeographical origins of contemporary floristic patterns in the high mountains of south-east Brazil.

Location The campos de altitude are a series of cool-humid, mountaintop grass- and shrublands found above elevations of 1800–2000 m in south-east Brazil, within the biome of the Atlantic Forest.

Methods Vascular floras are compiled for the three best-known campos de altitude sites, and for 17 other highland and lowland locations in Latin America. Floras are binned into phytogeographical groups based on centres of diversity/origin. Floristic and geographical distances are calculated for all location-pairs; Mantel tests are used to test for relationships between patterns in geographical distance, and floristic and climatic similarity. Multivariate statistics are carried out on the similarity matrices for all genera, and for each phytogeographical group. Predominant life-forms, pollination and dispersal syndromes are determined for each genus in the campos de altitude flora, and proportional comparisons are made between phytogeographical groups. Supporting evidence from previously published literature is used to interpret analytical results.

Results Two-thirds of the genera in the campos de altitude are of tropical ancestry; the remainder are of temperate-zone or cosmopolitan ancestry. Most campos de altitude genera are phanerophytes and hemicryptophytes, insect pollinated, and wind or gravity dispersed, but there are significant differences in the distribution of these traits among phytogeographical groups. The campos de altitude show stronger floristic similarities with other Brazilian mountain sites and distant Andean sites than with nearby low- and middle-elevation sites; these similarities are best explained by climatic similarities. Floristic similarities among sites for temperate genera are better explained by 'sinuous' distance (e.g. measured along the spines of mountain ranges) than by direct distance; similarities in tropical genera are more related to direct distance. Different phytogeographical groups appear to be responding to different climatic signals.

Main conclusions Many taxa currently living at the summits of the south-east Brazilian Highlands trace their ancestry to temperate latitudes. Patterns of endemism and diversity in the south-east Brazilian mountains point to climatically driven allopatry as a principal mechanism for speciation. The tropical component of the campos de altitude flora is primarily derived from drier, highland environments of the Brazilian interior; the temperate component rises in importance with elevation, but never reaches the levels seen in the tropical Andes. Most temperate taxa in the campos de altitude appear to have arrived via

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www.blackwellpublishing.com/jbi
doi:10.1111/j.1365-2699.2007.01732.x

migration through favourable habitat rather than by recent, long-distance dispersal. At least 11% of the plant species in the campos de altitude study sites are directly shared with the Andes. Palynofloras show that the campos de altitude have significantly contracted over the past 10,000 years, as regional temperatures have warmed and become more humid.

Keywords

Atlantic Forest, Brazil, campos de altitude, historical biogeography, palaeoecology, páramo, phytogeography, tropical alpine.

INTRODUCTION

Above *c*. 2000 m elevation, the Atlantic Forest of south-east Brazil gives way to a series of grass- and shrub-dominated formations known as the campos de altitude. The campos de altitude are the highest, coldest biome – and the only representative of the cold-humid tropics (Lauer, 1989) – in eastern South America (Safford, 1999a,b). Scattered among some of Brazil's highest peaks at elevations reaching nearly 3000 m, these mountaintop ecosystems form a classic archipelago of terrestrial habitat islands (Fig. 1). The campos de altitude show strong similarities to higher, more extensive equatorial alpine formations in the Andes and other tropical ranges (Brade, 1956; Troll, 1959; Hueck, 1966; Schnell, 1971; Clapperton, 1993; Safford, 1999a,b, 2001). Ecological congruencies between the campos de altitude and bamboo-dominated páramos in Costa Rica and Colombia are especially striking (Safford, 1999a,b; A. Chaverri & M. Monasterio, personal communication).

Although they are 2000 km from the nearest Andean subranges and separated from the Andes by extensive lowlands, the campos de altitude support many plant and animal taxa that are of Andean or temperate-zone 'origin' (Brade, 1956; Brown, 1987; Martinelli & Bandeira, 1989; Safford, 1999a). The Andean connection in the Brazilian Highlands has attracted the interest of biogeographers for more than 50 years, but little

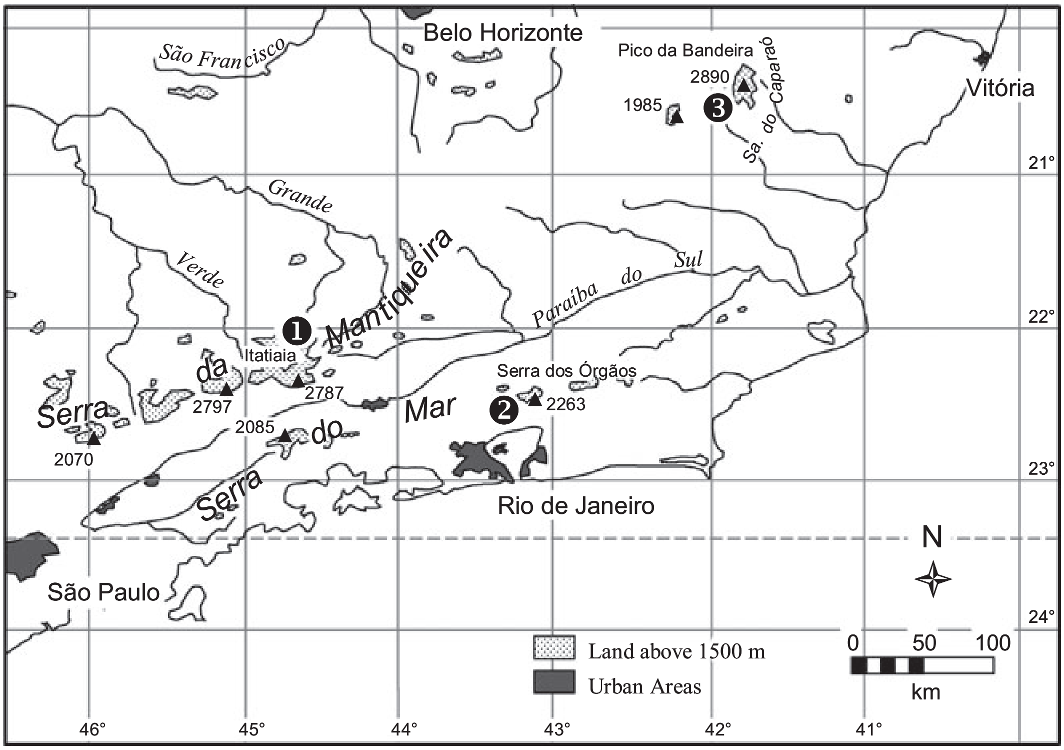

Figure 1 South-eastern Brazil, with locations of the three campos de altitude sites treated in this paper: 1, Serra do Itatiaia; 2, Serra dos Órgãos; 3, Serra do Caparaó.

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attention has been paid to the origins of the floras of the mountains of the south-east. Among many monographs of narrow taxonomic scope, Brade (1956) presented a broader appreciation of the biogeography of the flora of the Parque Nacional de Itatiaia, which harbours the most extensive parts of the campos de altitude. Brade delimited five source areas for the modern mountain flora in Itatiaia: (1) the subtropical rain forest, (2) central Brazil (largely a xerophyllic element), (3) 'Antarctic' (taxa widespread in southern South America, often shared with other southern hemisphere continents), (4) 'austral-Andean' (southern taxa with extensions into the tropical Andes or beyond), and (5) 'Andean' (taxa shared with the tropical Andes, including those Northern Hemisphere taxa that used the Andes as a pathway into southern South America). Brade (1956) and Aubréville (1962) both suggested that the migration of taxa or their ancestors to south-east Brazil must have happened during past periods of colder climates.

A few phytogeographers in southern Brazil have made direct or indirect reference to the campos de altitude in their work. Rambo (1951, 1953, 1956) documented the clear Andean affinity of the dominant species in the southern Brazilian Highlands, and discussed the contributions of various phytogeographical elements to the current flora of the region. Rambo did not consider the biogeography of the campos de altitude, but noted that the mountain floras at campos de altitude sites in São Paulo and Rio de Janeiro were northern extensions of the same patterns he saw in the southern highlands. In an analysis of the origins of the southern Brazilian flora, Smith (1962) found strong biogeographical relationships between southern temperate South America and the Andes on the one hand, and southern Brazil and the mountains of the Brazilian south-east on the other.

From collections made at six campos de altitude localities, Martinelli & Bandeira (1989) reported average local endemism of about 6% and habitat endemism (i.e. species restricted to the campos de altitude) of about 18%. Approximately 10% of the species collected were shared with drier mountain habitats of the Brazilian interior, and about 32% with other eastern Brazilian formations (the Atlantic Forest *sensu lato*); about 16% of the species encountered had an undefined 'widespread distribution'.

In previous contributions to the Brazilian Páramos series, I have described the natural history and conservation status of the campos de altitude (Safford, 1999a), quantitatively characterized the macroclimate of the campos de altitude and compared it with Andean climates (Safford, 1999b), and assessed the impacts of fire on vegetation (Safford, 2001). In other related papers, co-workers and I have described the flora and biogeography of the highland inselberg flora (Safford & Martinelli, 2000) and treated late Quaternary palaeoclimates and vegetation in a number of campos de altitude sites (Behling, 1997; Behling *et al.*, 2007). As the most recent addition to the Brazilian Páramos series, the current contribution synoptically and quantitatively treats the phytogeography of the contemporary campos de altitude flora, with a focus on patterns at the level of genus. Comparative analysis using data from 17 other sites in Latin America is used to elucidate spatio-temporal phytogeographical patterns at the continental scale. Finally, results are combined with those of previous publications to shed light on the biogeographical origins of the contemporary flora of the high mountains of south-east Brazil.

MATERIALS AND METHODS

Vascular plant species lists for the three most extensive campos de altitude (Serra do Itatiaia, Serra dos Órgãos, Serra do Caparaó; Fig. 1) have been compiled by the author over the last 11 years. Sources include field plot and survey data, field observations, herbarium records, published and unpublished literature (see Table S1 in *Supplementary Material*), monographs and personal communications. For the purposes of this study, species lists for the three sites were joined into one combined campos de altitude 'flora', representing approximately 130 km^2 of the perhaps 300 km^2 of total campos de altitude habitat in south-east Brazil. The approximate upper reach of continuous forest was used as the lower elevational limit for the floristic compilation. The forest-limit elevation used for south-east Brazil was 2000 m, which approximates the isotherms for 12°C mean annual temperature and 15°C mean of the warmest month (Safford, 1999b).

For comparison with the campos de altitude flora, species lists were compiled for a cross-section of mountain regions in the tropical Andes and Brazil, from lowland and highland regions in the temperate zone of South America, and from lowland regions and sites in south-east Brazil (regions = 1000s of km^2, sites = 10s of km^2). Table 1 lists the floras and other sources used in the floristic compilation, and summaries of macroclimatic data from each location (literature sources for floristic and climatic data are given in Table S1); Fig. 2 shows their approximate geographical locations. In the tropical Andes, the forest limit was also used as the lower elevation limit. In these locations, the forest limit ranges from 3200 to 3500 m, or approximately the 10°C (mean annual temperature) isotherm; means for the warmest month at these elevations range from 12–19°C (Schwertdfeger, 1976; Sarmiento, 1986). In the temperate zone, where temperature regimes are much more seasonal, locations were selected such that the mean temperature of the warmest month at the lowest sampled elevation was as near to that of the campos de altitude (15°C) as possible – values ranged from 10 to 19°C. Some locations in south-east Brazil (Triângulo Mineiro, Ilha do Cardoso/Maricá, Macaé de Cima, Pico das Almas; see Table 1 and Fig. 1) were chosen based on biogeographical pertinence rather than on climatic parameters and represent 'outgroups' for comparative purposes. The Ilha do Cardoso/Maricá flora is a composite from two separate occurrences of restinga vegetation, one in São Paulo state, the other in Rio de Janeiro (Table 1). Data on macroclimatic parameters from each site were accessed from the literature or, where necessary, generated using regressions based on region-specific lapse rates

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Table 1 Geographical locations treated in this paper, numbers of species and genera per location, and physical and climatic site characteristics. For literature sources see Table S1 in *Supplementary Material.*

Location	Code	Lat./long. (centroid)	No. of spp.	No. of genera	Lowest elev. sampled (m)	Elev. range sampled (m)	Area sampled (km^2)*	Range of mean ppt (mm)	Mean annual temp. (°C)†,‡	Mean temp. warmest month (°C)†,‡	Mean annual temp. at 2800 m (°C)‡	Months with frost†	Months with < 50 mm ppt†	Index of tropicality§
Cordillera de Talamanca, Costa Rica	CR	9°29′ N, 83°30′ W	–	150	3300	500	100	2000–3000	9	12	11	5	2	6
Venezuelan Andes	VZ	8°42′ N, 71°00′ W	668	253	3200	1600	3000	700–2000	10–11	12–15	12	4–7	2	5.8
Cordillera Oriental, Colombia	CO	6°24′ N, 72°21′ W	–	261	3300	1500	8000	1200–2500	8–9	11–13	12	4–6	2	4
Ecuadorean Andes	EC	0°42′ S, 78°23′ W	1675	446	3500	1300	16,000	700–2000	8–9	14	13	4	2	6
Department of Huanuco, Peru	HU	9°40′ S, 77°07′ W	934	385	3500	1300	17,000	500–1000	10	19	14	10	5	3.3
Department of Puno, Peru	PU	14°58′ S, 70°31′ W	751	317	3500	1400	50,000	250–750	9	19	13	10	8	3.3
Argentine puna	AP	24°15′ S, 66°43′ W	645	249	3400	1000	50,000	100–400	9–10	13	13	12	9	2.2
Sierras de Tucumán, Argentina	TU	27°00′ S, 66°00′ W	686	319	1400	1800	5000	1500–2000	13	19	11	9	4	1.2
Rio Atuel Basin, Argentina	RA	34°30′ S, 69°10′ W	518	194	1500	1500	8000	500–1000?	12	18	3	12	9	0.9
Chile, 38° to 45°	CH	41°00′ S, 73°00′ W	756	332	0	1800	120,000	1300–3000	9–12	15–17	0	8–10	0	1
Tierra del Fuego, Argentina and Chile	TF	54°00′ S, 68°30′ W	417	215	0	1000	66,000	500–2500	5–6	9–10	< 0	12	8	1
Province of Buenos Aires, Argentina	BA	35°30′ S, 60°00′ W	1553	574	0	150	308,000	800–1200	17	24	*c.* 0	5	0	0.8
Aparados da Serra, Brazil	AS	29°10′ S, 50°25′ W	896	368	800	600	105	2000	15	20	*c.* 4	8	0	1.4
Ilha do Cardoso and Maricá, Brazil	RE	23°38′ S, 45°26′ W	617	318	0	10	40	1800	21	24	*c.* 5	0	0	1.3
Macaé de Cima, Brazil	MA	22°25′ S, 42°30′ W	956	364	880	840	75	2100	18	21	*c.* 9	1	1	1.8
Campos de Altitude, Brazil	CA	21°46′ S, 43°52′ W	929	332	2000	890	130	1800–3000	12	15	8	7	2	1.3

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Table 1 continued.

Location	Code	Lat./long. (centroid)	No. of spp.	No. of genera	Lowest elev. sampled (m)	Elev. range sampled (m)	Area sampled (km^2)*	Range of mean ppt (mm)	Mean annual temp. (°C)†,‡	Mean temp. warmest month (°C)†,‡	Mean annual temp. at 2800 m (°C)‡	Months with frost†	Months with < 50 mm ppt†	Index of tropicality§
Triângulo Mineiro, Brazil	CE	19°20′ S, 49°00′ W	552	287	600	400	1000s	1600	22	23	*c.* 9	1	4	2.1
Pico das Almas, Brazil	PA	14°00′ S, 42°30′ W	718	327	1500¶	460	140	1300?	18	19	*c.* 10	1	4	2.9

ppt, precipitation.

*Estimate based on best available maps.

†At lowest elevation sampled.

‡Derived using lapse rates, based on nearest set of climate stations.

§Mean diurnal temperature range divided by mean seasonal temperature range.

¶Spp. described as being found in campos rupestres were included even where they grew below 1500 m elevation.

(from, e.g. Sarmiento, 1986; Jørgensen & Ulloa, 1994; Safford, 1999b, etc.; see Table 1). Lat./long. centroids for each site were determined using GoogleEarth (2005).

Lists of vascular plant species were compiled for each location based on the accessible literature (Table S1 in *Supplementary Material*). Floristic lists were sorted by genus and family, and recent changes in taxonomy and nomenclature were applied to bring older floras up to date and to make lists comparable across regions. Species that were obvious human introductions were removed from the data set.

Using the methodology of Cleef (1979, 1983), all sampled genera were assigned to one of seven phytogeographical groups, based on the current centre of diversity for that genus, determined using Mabberley (1996), publications of Cleef and co-workers (e.g. Cleef, 1979, 1983, 2005; van der Hammen & Cleef, 1986; Cleef & Chaverri, 1992) and monographs. The groups used correspond to those used by Cleef and others in phytogeographical studies carried out in the tropical alpine flora: Australantarctic (Southern Hemisphere temperate, hereafter 'AA'); Holarctic (Northern Hemisphere temperate, 'HO'); widespread temperate ('WTe'), Neotropical ('NT'), widespread tropical (at least 5% of the species on a second continent, 'WTr'); endemic (restricted to the region within which a given site is embedded); cosmopolitan (± worldwide distribution, 'CO'). Centres of diversity were used in this study as surrogates for generic centres of origin because we do not know enough about the evolutionary and biogeographical history of most genera to identify centres of origin confidently. Species were not grouped into phytogeographical groups because: (1) the complexity of species distributions, combined with the sheer number of species in this comparison, makes it difficult to bin species into a reasonable number of phytogeographical categories; (2) species lists are not complete for some sites in this study, but it is likely that the list of genera at each site is more or less complete; (3) distributions of genera are more likely than the distribution of species to conserve biogeographical relationships resulting from ancient occurrences of dispersal and vicariance.

For the campos de altitude flora, each genus was coded for life-form (Raunkiær, 1934) and for pollination and dispersal syndromes. For genera with multiple life-forms or pollination/dispersal syndromes, the predominant/modal case was used for the genus as a whole. Comparisons were made between phytogeographical groups as to the proportional representation of life-form, pollination and dispersal classes in each group. Chi-square tests for independence were used to determine if the distributions of these characteristics were statistically similar across phytogeographical groups. For χ^2 tests, due to low expected frequencies, the HO, AA and WTe groups were pooled into a 'temperate' supergroup; the Brazilian, NT and WTr groups were pooled into a 'tropical' supergroup.

A variety of qualitative and quantitative comparisons were made between the floras of the different South American locations at both the genus and species levels. Costa Rica and Colombia were left out of most of these analyses, as reasonably

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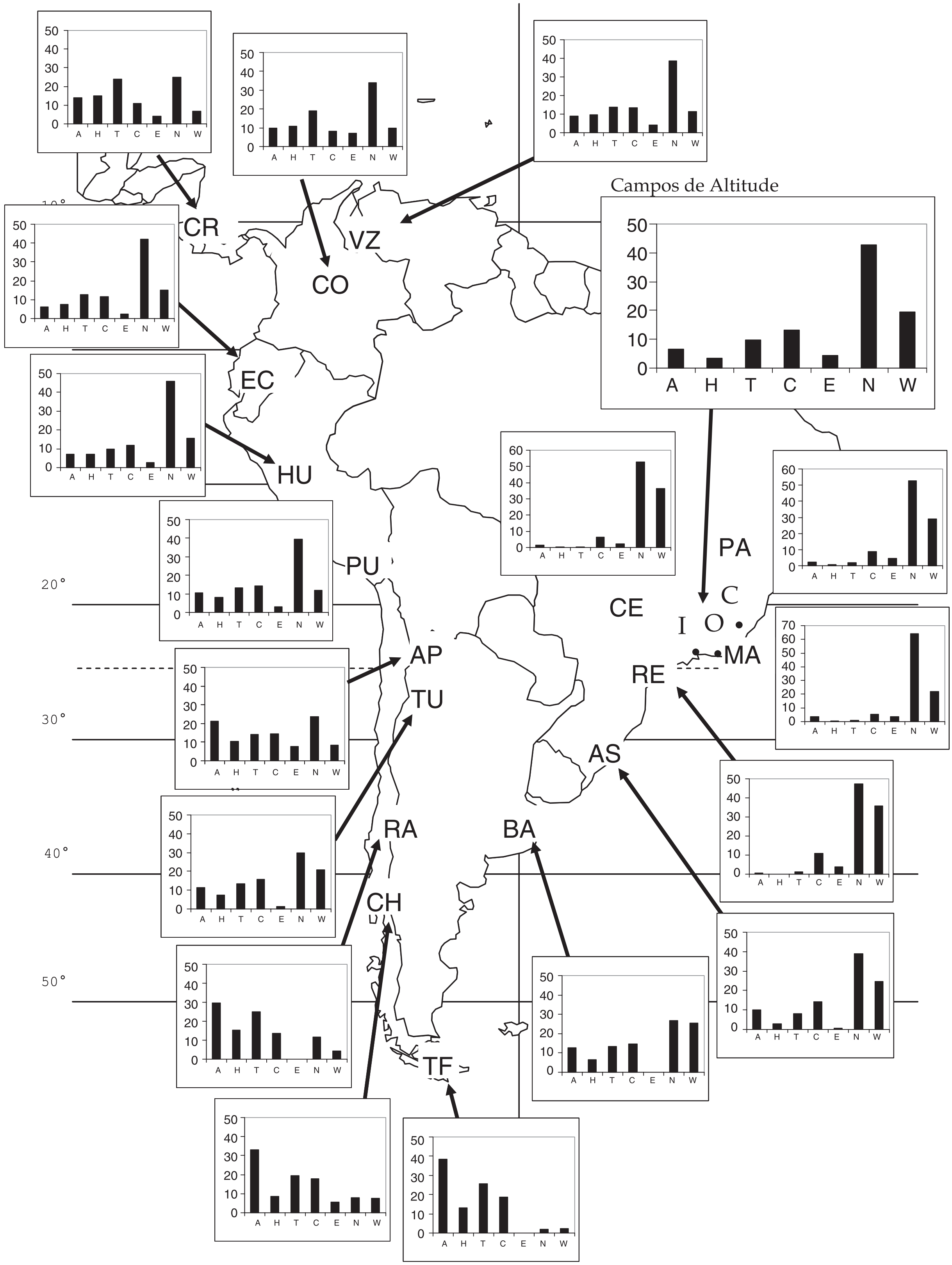

Figure 2 Genus-level phytogeographical spectra for the South American locations compared in this paper. For site identities, refer to the 'Code' column in Table 1. In the diagrams, the *Y*-axis represents per cent of genera, the *X*-axis represents phytogeographical group. From left to right in each diagram, the groups are: A, Australantarctic; H, Holarctic; T, widespread temperate; C, cosmopolitan; E, regional endemic; N, Neotropical; W, widespread tropical. 'I', 'O' and 'C' in south-east Brazil refer to Itatiaia, Serra dos Órgãos and Caparaó, respectively.

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complete species lists were unavailable at the time of analysis. Species and genus lists were compared between locations, and the numbers and identities of shared species and genera were tabulated. The Jaccard index of similarity was calculated for each pairwise comparison (Ludwig & Reynolds, 1988). Distances between locations were calculated in two ways: straight-line distance and sinuous distance following the geographical spine of the Andes. Sinuous distances were also calculated between the Andean and Brazilian locations, following a line from the Sierras de Tucumán and Córdoba through Uruguay and southern Brazil. Distances between locations were determined with GoogleEarth (2005), and measured between the nearest edges of each location (i.e. not between centroids).

Mantel tests were carried out in PC-ORD v.4 (McCune & Mefford, 1999) to test the null hypothesis of no relationship between the geographical distance matrix and the floristic similarity matrix. Different tests were carried out for direct and sinuous distance, and for similarity matrices of seed plants, vascular cryptogams (ferns and fern allies) and the different phytogeographical groups; genera endemic to any one region (e.g. eastern Brazil, Chile, equatorial Andes, puna, etc.) were removed from the data set before analysis. Results were compared with Mantel tests run against a similarity matrix derived from macroclimatic data.

Sixteen locations, i.e. Table 1 excepting CR and CO, were included in a pan-continental TWINSPAN analysis. Each location was ranked by its 25 most important genera (based on species numbers, as a proportion of the total flora), and the resulting lists were pooled, giving 178 total genera. Data were input as a proportion of the total flora of each location, with the following pseudospecies cut-off values: 0, 0.5, 1, 2, 3, and 5. Analysis was carried out in PC-ORD (McCune & Mefford, 1999).

Genera weighted by species at each of the 16 locations were input into cluster analyses; before analysis, genera occurring at only one location were removed, and all remaining data were relativized by standard deviation to more equally weight the contribution of speciose and species-poor genera to the analysis. Agglomerative classifications were carried out in order to group locations by their floristic similarities, using SYN-TAX 5.0 (Podani, 1994). Resemblance between floras was quantified by two similarity indices, the Jaccard index and chordal Euclidean distance (CHED) (Ludwig & Reynolds, 1988). Because the Jaccard index is calculated based on presence–absence, it stresses genus-level (i.e. historical) relationships between sites (e.g. did a genus ever get to a site?); CHED measures genera ranked by their species numbers, and therefore stresses environmental relationships between sites (e.g. how much did a genus speciate after arrival?) and more recent events of dispersal. Each similarity index was calculated for all location–pair combinations. The resultant site-by-site matrices were used in the generation of dendrograms using average linkage (UPGMA) clustering (Ludwig & Reynolds, 1988). Cluster analyses were carried out for all genera combined, for all genera minus vascular cryptograms, for all vascular cryptogams, and for each phytogeographical group.

Using canonical correspondence analysis (CANOCO v. 4.5; ter Braak & Smilauer, 2002), direct environmental gradient analysis was carried out in order to examine floristic affinities among locations and to identify their possible relationships to a suite of climatic factors. Floristic inputs were the same as for the cluster analyses. Climatic inputs were: (1) mean annual precipitation, (2) number of months with > 50 mm precipitation, (3) mean annual temperature, (4) extreme maximum temperature, (5) extreme minimum temperature, (6) index of tropicality (mean diurnal range of temperature/mean seasonal range of mean daily temperatures), and (7) number of months with temperatures < 0°C. Stepwise forward selection was used to rank climatic variables as to their importance in determining floristic data patterns. Statistical significance of each selected variable was determined by a Monte Carlo permutation test.

RESULTS

My current plant list from the three studied Brazilian sites includes 332 genera (Supplementary Table S2) and 928 species of vascular plants (human introductions are excluded). The full list of genera is available in Table S2. The list includes all habitats above 2000 m, including grassland, shrubland, patches of high-elevation forest and aquatic habitat. For a variety of reasons (e.g. insufficient data on species numbers or identities; botanical collections made since the analyses were carried out, etc.), only 300 of these genera were included in most quantitative analyses. In the complete list, 21 genera are considered Australantarctic (‘AA’), 40 are Brazilian (‘BR’), 42 are cosmopolitan (‘CO’), 10 are Holarctic (‘HO’), 121 are Neotropical (‘NT’), 34 are widespread temperate (‘WTe’) and 64 are widespread tropical (‘WTr’).

The distribution of phytogeographical groups at each location is shown in Fig. 2. The diagram from the campos de altitude most closely approximates the diagrams from the Sierras de Tucumán, the tropical Andean locations and the Aparados da Serra. About two-thirds of the vascular plant genera inhabiting the campos de altitude and the Aparados da Serra are derived from tropical stock (BR + NT + WTr); values for the other Brazilian locations are higher, and range from 83% to 91% (Fig. 2). The generic floras of the tropical Andean sites are from 51% to 64% tropical in origin. The proportional representation of the temperate supergroup (HO + AA + WTe) across the studied locations follows a clear gradient from high to low latitude. The northernmost flora (Costa Rica) is 54% temperate genera (15% HO), the southernmost flora (Tierra del Fuego) is 77% temperate genera (39% AA); intermediate values are found in between. Of the Brazilian sites, only the Aparados da Serra and the campos de altitude support significant numbers of temperate genera (about 21% each); the total temperate component is 5% or less of the generic flora in the four other Brazilian locations.

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Overall, about 31% of the genera occurring in the campos de altitude are predominantly phanerophytes, 27% hemicryptophytes and 11% geophytes (Fig. 3a). The distribution of life-forms among the different phytogeographical groups is very different (Fig. 3a): $\chi^2 = 57.2$, d.f. $= 10$, $P < 0.0001$ (temperate supergroup vs. tropical supergroup vs. CO). The tropical groups are the only groups with epiphytes and meaningful numbers of lianes; together with the AA group, they are dominated by phanerophytes. The HO and WTe groups are primarily hemicryptophytes and, with the CO group, they have the smallest proportion of phanerophytes; the HO group also has the highest proportion of therophytic genera. Pollination spectra are likewise different across groups (Fig. 3b; $\chi^2 = 33.1$, d.f. $= 6$, $P < 0.0001$, pooled as above). Overall, 71% of the campos de altitude genera are predominantly insect pollinated, about 13% are wind pollinated and 11% water pollinated (vascular cryptogams); bird and bat pollination together account for 5% of the genera. The HO genera in the campos de altitude appear to be entirely insect pollinated, while the WTe group is more evenly split between wind and insect pollination. The distribution of pollination syndromes is very similar across the AA, NT and WTr groups, with insect and bird pollination dominating in all three cases. Overall, dispersal syndromes are dominated by wind and gravity (in many cases wind-aided), with about 40% of genera in each category (Fig. 3c); endozoochory accounts for 15%, self-dispersal and epizoochory about 2% each. Seed dispersal spectra are not independent of phytogeographical group ($\chi^2 = 9.89$, d.f. $= 4$, $P = 0.041$, pooled as above). The tropical groups support a higher proportion of wind-dispersed genera (mean = 44%) than the temperate groups (28%), which are primarily gravity dispersed (49% vs. 37% in the tropical groups). The CO group has components of all six dispersal syndromes.

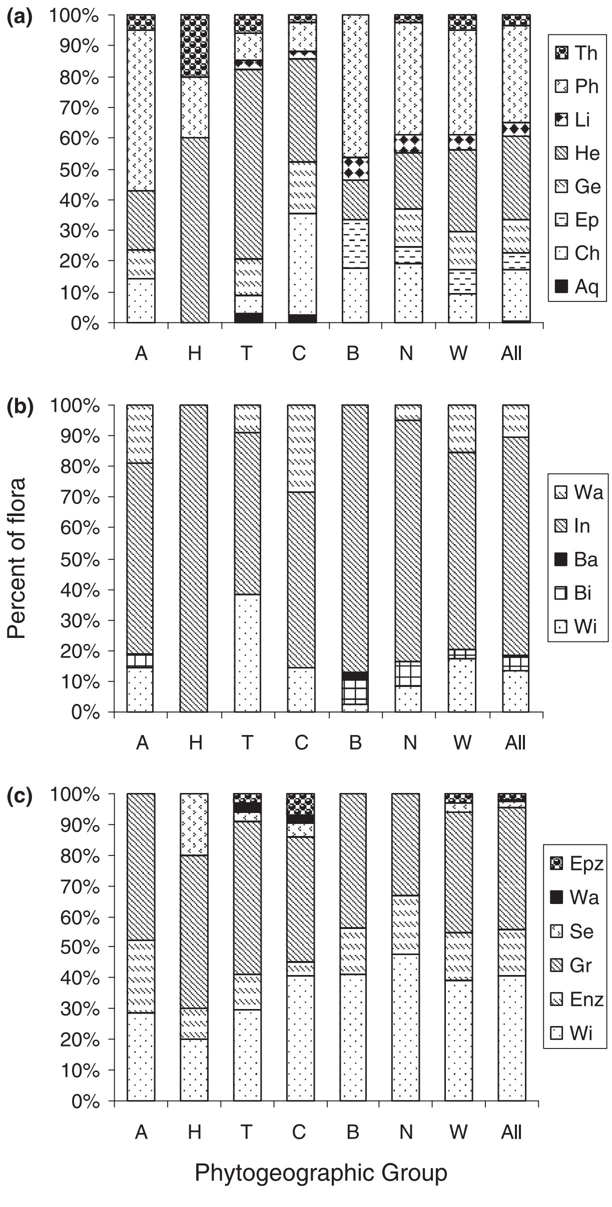

Figure 3 Distributions of (a) life-form, (b) pollination syndrome and (c) dispersal syndrome among the seven phytogeographical groups for the campos de altitude flora. Assignments made at the level of genus (see text). In (a): Th, therophyte; Ph, phanerophyte; Li, liane; He, hemicryptophyte; Ge, geophyte; Ep, epiphyte; Ch, chamaephyte; Aq, aquatic. In (b): Wa, water; In, insect; Ba, bat; Bi, bird; Wi, wind. In (c): Epz, epizoochory; Wa, water; Se, self-dispersed (autochory); Gr, gravity; Enz, endozoochory; Wi, wind.

Jaccard similarities between locations are shown graphically on a map of South America in Figs 4 and 5. For the raw Jaccard values and shared species between locations see Table S3 in *Supplementary Material.* In the genus-level comparison (Fig. 4), three clusters of high similarities are clear: north Andes, south Andes and south-east/southern Brazil. Genus-level similarities > 40% were found for the following location pairs: northern Andes, Ecuador–Venezuela, Ecuador–Huanuco, Ecuador–Puno and Huanuco–Puno; southern Andes, Chile–Tierra del Fuego; south-east/southern Brazil, campos de altitude–Aparados da Serra. The closest genus-level affinities with the campos de altitude are with Aparados da Serra [195 genera shared, 41.4% similarity, 1080/1220 km distant (direct distance/sinuous distance)], Pico das Almas (146 genera shared, 30.4% similarity, 1020 km) and the northern Andean regions and the Sierras de Tucumán (115–158 genera shared, 22.7–26.9% similarity); the Sierras de Tucumán are 2150/2820 km from the campos de altitude and the north Andean locations 2650/4400 to 3900/7170 km distant. The only other locations with genus-level similarities above 20% with the campos de altitude are Buenos Aires and Macaé de Cima.

The highest species-level similarities (Fig. 5) are between Tierra del Fuego and Chile (234 shared species, 25% similarity, 1440 km apart), Huanuco–Puno (299 species, 22%, 900 km) and Ecuador–Huanuco (321 species, 14%, 960/1070 km). Species-level similarities are not especially high among the Brazilian locations. For the campos de altitude, the closest species-level affinities are with the Aparados da Serra (149 species shared, 9.1% similarity) and Macaé de Cima (80 species, 4.5%, 70 km distant). Jaccard similarities between the campos

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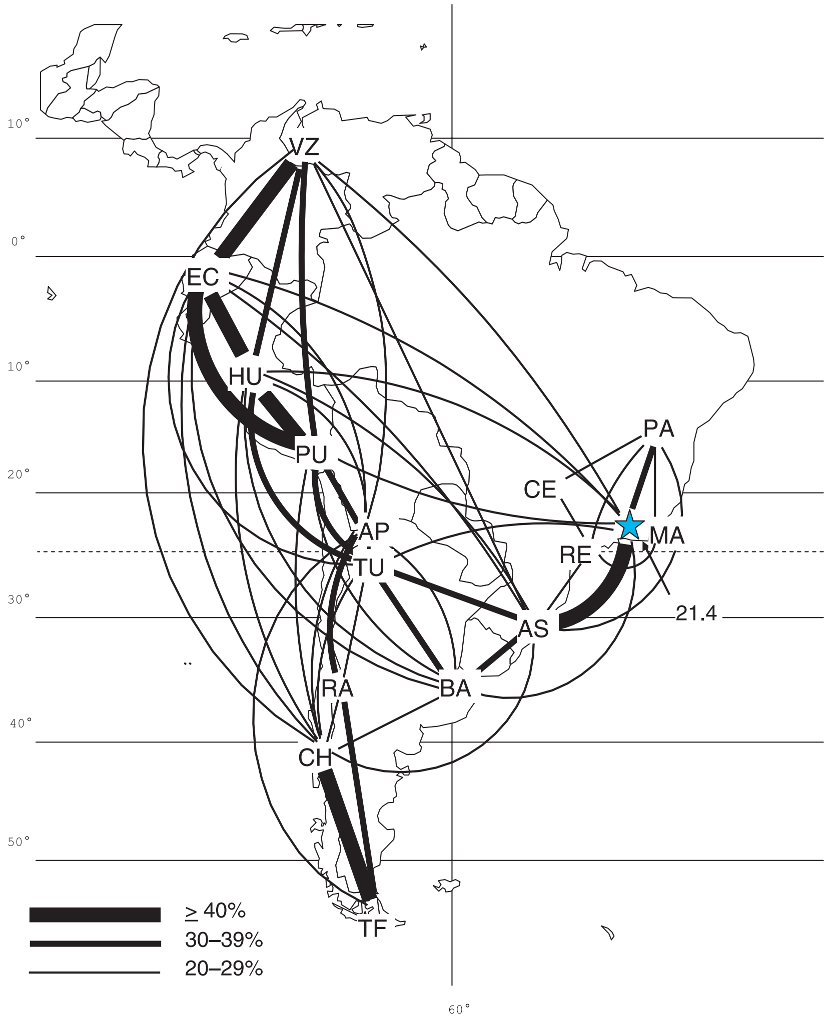

Figure 4 Geographical patterns in Jaccard similarities at the level of genus for the sites treated in this paper. The campos de altitude are represented by a star. '21.4' is the Jaccard similarity between the campos de altitude and Macaé de Cima. Values from Table S2 (in *Supplementary Material*), site codes as in Table 1.

de altitude and the northern Andean locations and the Sierras de Tucumán average 2% (29–51 species shared), higher than similarity with cerrado in the Triângulo Mineiro (0.5%), only 740 km away. Species-level Jaccard similarity with the flora of Buenos Aires (1850/2180 km distant) is as high as with the coastal restinga flora (RE), only 60 km away. The lowest similarities are with Rio Atuel in the dry Argentine Andes, and with Tierra del Fuego. Eighty-six species (45 phanerogams, 41 vascular cryptogams) are shared between at least one of the tropical Andean sites and the campos de altitude, and a further 51 are shared between the campos de altitude and the south Andean sites; in total, 101 separate species (or about 11% of the total flora) were identified that are shared between the campos de altitude and the Andean locations.

Mantel tests (Table 2) exhibited the following patterns:

1 in most comparisons, the sinuous geographical distance matrix has a stronger relationship than direct distance to the floristic similarity matrix; direct and sinuous distance are approximately equal for the tropical genera and for all genera combined,

2 except in two cases, climatic patterns provide the strongest match to the floristic patterns – they are much stronger than the distance measures for the Mantel test including all genera, somewhat stronger than the distance measures for the test with only phanerogamic genera, and they are the only physical matrix significantly related to patterns of distribution for the vascular cryptogams.

3 in the case of the combined-temperate, CO and AA groups there are no strongly significant relationships (i.e. $P < 0.05$), but sinuous geographical distance provides the strongest fit in all three cases.

Figure 6a shows the clustering results from the Jaccard dissimilarity matrix for all genera combined and Fig. 6b shows the results from the CHED matrix for all genera. In both figures, seven basic groups of locations are apparent: a tropical Andean group, a dry Argentine Andean group, a moist southern Andean group, a high-elevation Brazil group, an 'other Brazil' group (Atlantic Forest, restinga and cerrado), and Tucumán–Buenos Aires. The Jaccard-based dendrogram (Fig. 6a) joins the Brazilian high–elevation group to the tropical Andes–Tucumán–Buenos Aires supergroup before it joins either of these groups to the dry Andes, moist southern Andes or lowland Brazil. The CHED-based dendrogram (Fig. 6b) clearly splits the locations into Brazilian and Andean (+ Buenos Aires) supergroups, but maintains the same general subgroups. The TWINSPAN analysis (results not

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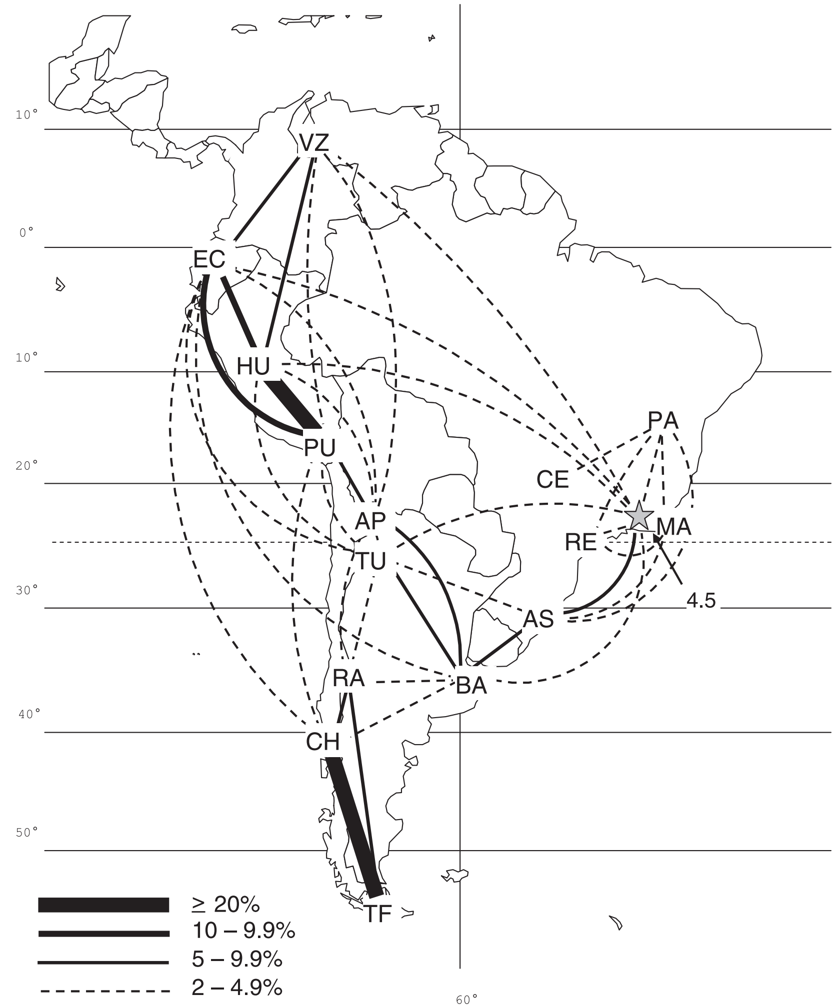

Figure 5 Geographical patterns in Jaccard similarities at the level of species for the sites treated in this paper. The campos de altitude are represented by a star. '4.5' is the Jaccard similarity between the campos de altitude and Macaé de Cima. Values from Table S2 (in *Supplementary Material*), site codes as in Table 1.

shown), which like the CHED analysis is based on a distillation of the raw species data, produced an essentially identical dendrogram to Fig. 6b. The indicator species identified in the TWINSPAN analysis are given in Fig. 6b at their appropriate locations.

The Jaccard dendrogram for the NT phytogeographical group (Fig. 6c) splits the 16 locations into the same groups as the all-genera analysis, but the high-elevation Brazilian locations are grouped with the other Brazilian sites before they are joined to the equatorial Andean regions, Tucumán and Buenos Aires; the southern Andean locations, dry and moist, are outgroups in this analysis. The WTr phytogeographical group clusters as the NT group and is not shown. Figure 6d shows the Jaccard dendrogram for the combined WTe and HO phytogeographical groups. The closest similarity in this phytogeographical group for the cold Brazilian locations (Aparados da Serra and campos de altitude) is with the Andean regions and not with the much nearer Brazilian sites. The dendrogram of the CO phytogeographical group shows much the same pattern, with the cold Brazilian locations now more closely grouped with the Sierras de Tucumán and the equatorial Andean regions (Fig. 6e). The AA dendrogram (not shown) orders the sites from north to south along the Andean axis, with Buenos Aires between Rio Atuél and Chile. The Brazilian high-elevation group is linked with the montane forest at Macaé de Cima (MA), then to the Andean regions; cerrado and restinga are outgroups. The cluster analyses using vascular cryptogamic genera alone groups the campos de altitude with the equatorial Andean regions (Venezuela and Ecuador), and then the Peruvian regions, before joining the three montane locations from Brazil (Fig. 6f).

Results of the CANOCO floristic analysis were analogous to the cluster analyses and are not shown. Stepwise selection of environmental variables for the phytogeographical groups showed the following results: mean annual temperature had the closest relationship with the abundances of four of the five groups; the AA and WTe groups were more abundant as mean temperature dropped; and the two tropical groups were more abundant as mean temperature rose. The temperate groups (AA, HO, WTe) all showed positive relationships with the number of months with temperatures < 0°C; the abundance of the HO group also increased as extreme minimum temperatures dropped. In contrast, abundance of the WTr group went up as extreme minimum temperatures rose. Mean

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Table 2 Results of Mantel tests for 16 locations, based on Monte Carlo randomization. Genera endemic to any one region were removed from the data set before analysis.

	r	*p*
All genera ($n = 689$)		
Direct geog. dist.	0.163	0.004
Sinuous geog. dist.	0.188	0.004
Climate	0.232	0.023
All phanerogamic genera ($n = 642$)		
Direct geog. dist.	0.176	0.002
Sinuous geog. dist.	0.200	0.001
Climate	0.215	0.030
All cryptogamic genera ($n = 47$)		
Direct geog. dist.	0.027	0.327
Sinuous geog. dist.	0.043	0.270
Climate	0.226	0.045
All temperate genera ($n = 185$)		
Direct geog. dist.	0.036	0.284
Sinuous geog. dist.	0.075	0.160
Climate	0.019	0.370
All tropical genera ($n = 383$)		
Direct geog. dist.	0.217	0.001
Sinuous geog. dist.	0.215	0.002
Climate	0.331	0.005
Cosmopolitan genera (excluding cryptogams; $n = 60$)		
Direct geog. dist.	0.078	0.107
Sinuous geog. dist.	0.104	0.075
Climate	0.070	0.257
Australantarctic genera (excluding cryptogams; $n = 67$)		
Direct geog. dist.	0.054	0.189
Sinuous geog. dist.	0.093	0.092
Climate	0.111	0.173

r = standardized Mantel statistic.

precipitation was positively related to the abundances of both the NT and AA groups.

Tables 3 and 4 list those campos de altitude species that are shared with at least two other locations. In the phanerogams (Table 3), three species groups are apparent: (1) species shared primarily with the tropical Andes, (2) species shared primarily with Argentina and Chile, and (3) species shared primarily with other south-east and southern Brazilian sites. Among vascular cryptogams (Table 4), there is a clear 'Andean' group, and a smaller group shared primarily with Argentina and Chile.

DISCUSSION

Environmental and floristic similarities with Andean sites

A number of authors have referred to the unexpectedly strong floristic and climatic connections between the maritime–temperate Andes of Chile and the southern Brazilian mountains (Rambo, 1951, 1953; Smith, 1962; Hueck, 1966; Klein, 1975; Golte, 1978). The same biogeographical and climatic relationships are found between the campos de altitude and maritime–temperate Chile (Brade, 1956; Safford, 1999a,b). As Figs 4 and 5 and Table 2 show, species- and genus-level connections between Brazil and southern temperate and southern Andean sites are about as strong in the campos de altitude as they are in the southern mountains (e.g. Aparados da Serra), even though the former are more than 1000 km and 7° of latitude further north than the latter. The campos de altitude attain much higher altitudes than the southern Brazilian mountains (> 2000 m vs. *c.* 1000 m in the Aparados da Serra), hence floristic distance increases less rapidly than geographical distance; in essence, the campos de altitude are 'islands' of temperate climate above the tropical Atlantic Forest.

Although there is a clear floristic/climatic relationship between maritime–temperate Chile and the campos de altitude, similarities in climate and flora are even more pronounced between the campos de altitude and the tropical Andean mountains (Figs 2 and 3a,b; Tables 1 and 2). Safford (1999b) used an analysis of macroclimatic patterns to show that, environmentally, the campos de altitude are essentially a high-latitude variant of tropical Andean *páramo* with exaggerated seasonality. Other authors have made reference to páramo-campos de altitude parallels in vegetation physiognomy, climate, soils, physical habitat and fire ecology (e.g. Brade, 1956; Troll, 1959; Hueck, 1966; Schnell, 1971; Safford, 1999a, 2001; M. Monasterio, personal communication). Congruencies in climate and environment between the wet tropical Andean and Central American sites and the campos de altitude are underlined by strong genus- and species-level floristic connections between the vascular cryptogamic floras of these regions (Fig. 6f & Table 4). More than 40 vascular cryptogam species are shared between the high-elevation tropical Andean regions and the campos de altitude [not all are shown in Table 4, as some are shared with only one site, and some with areas (e.g. Bolivia) not analysed in this paper]; many more taxa are closely related. Close connections also exist between the bryophyte floras of the tropical Andean highlands and the south-east Brazilian mountains; Frahm (1991) cites numerous examples of vicariance, especially in the genera *Atractylocarpus* and *Campylopus*. Bryophytes release large quantities of microscopic spores that are viable for long time periods and can be blown long distances by wind. To such plants, wide geographical distances between suitable habitats are often minor impediments to colonization (Sauer, 1988; Barrington, 1993); their joint presence in two floras may thus owe more to environmental similarities than to shared biogeographical history. The same holds for most of the phanerogamic taxa in Table 3: 45% (10/23) of the species in Table 3 shared with the tropical Andes are from genera in the family Asteraceae, and much of the rest of the list comprises ruderal species. Like many cryptogams, their distribution at least partly obeys Beijerink's rule (originally applied to microbes): 'everything is everywhere, and the environment selects'.

Phytogeographical groups – tropical component

In the tropical Andean and cold Brazilian locations (campos de altitude and Aparados da Serra) analysed in this study, between

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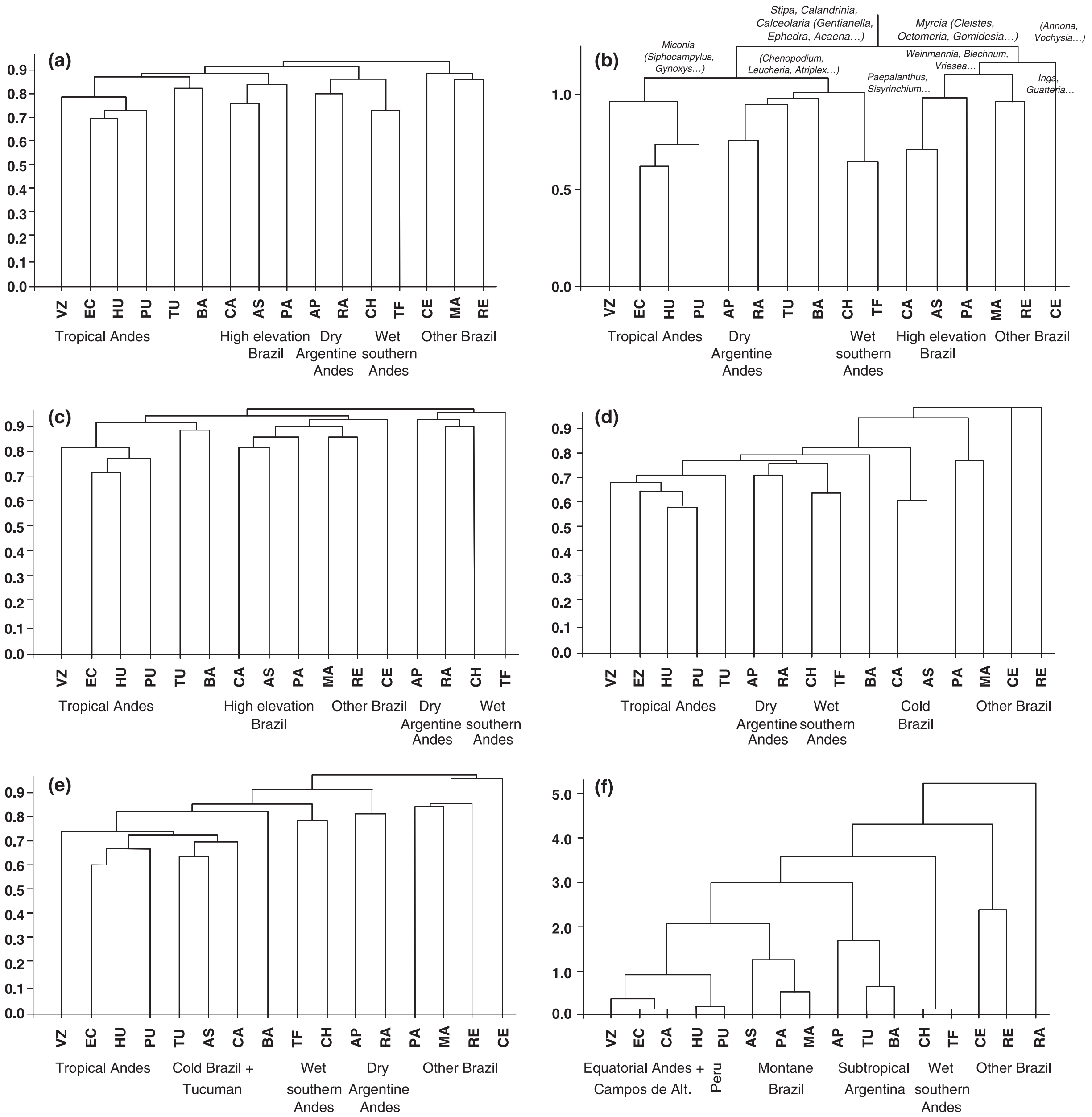

Figure 6 Dendrograms from cluster analyses of the generic floras of 16 South America sites; site codes as in Table 1. The *Y*-axis represents the similarity between sites: (a) all genera, Jaccard index (presence–absence); (b) all genera, chordal Euclidean distance (genera weighted by species); (c) Neotropical genera, Jaccard index; (d) widespread temperate and Holarctic taxa, Jaccard index; (e) cosmopolitan genera, Jaccard index; (f) vascular cryptogam genera, chordal Euclidean distance. In (b), indicator species for the major clustering divisions are indicated on the diagram.

half and two-thirds of the genera present above the limit of closed forest have tropical roots (see also Rambo, 1953; Brade, 1956). Although some genera are restricted to forest habitats, the tropical component of the campos de altitude flora is skewed strongly toward taxa with adaptations to open habitats, such as grassland and shrubland formations. Nearly 50% of the NT genera in the campos de altitude are wind dispersed, as are about 40% of the BR and WTr groups (Fig. 3). Although the dominant single life-form among the tropical genera is phanerophytes, the number of low-growing plants (hemicryptophytes, geophytes, chamaephytes) is higher in sum (84 vs. 100 genera), especially among the NT and WTr groups. Many of the hemicryptophytes and geophytes (and some of the epiphytes, which are often also epilithic) are found on and around extensive rock outcrops ('inselbergs') which characterize the campos de altitude landscape (Safford & Martinelli, 2000). In addition, many of the phanerophytes are asteraceous (e.g. *Baccharis*, *Vernonia*, *Vanillosmopsis* and the tribe

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Table 3 Phanerogamic species shared between the campos de altitude and at least two other locations. Species tabled manually to best represent floristic patterns. For the high-elevation sites, '+' indicates present at elevations lower than the sampled area.

Phanerogams	VZ	CO	EC	HU	PU	AP	RA	TU	BA	CH	TF	AS	MA	PA	RE	CE
Erechtites valerianifolia	+	+	+	+	+							X		X	X	
Hydrocotyle ranunculoides	+	X	+	+	X				X	X		X				
Juncus microcephalus	X	X	X	X	X					X		X		X		
Galium hypocarpium	X	X	X	X	X			X	X	X		X		X		
Pseudognaphalium cheiranthifolium	X	X	X	+	+			X	X	X		X				
Achyrocline satureioides	X	X	+	+	+				X			X		X	X	X
Gordonia fruticosa	+	X	X	+									X	X	X	
Peperomia galioides	X		X	X	X									X		
Sisyrinchium iridifolium	X		X	+					X							
Chaptalia nutans	X		+						X			X		X		
Gamochaeta purpurea	X		X							X		X				
Plantago australis		X	X	X	X											
Castilleja arvensis		+	X	+												
Myrsine ferruginea		+	+	X				X				X	X			
Peperomia glabella		+	+										X	X		
Austroeupatorium inulaefolium		+	+	+	+			X	X						X	
Baccharis genistelloides s.l.		X	X	+	X				X			X			X	
Arenaria lanuginosa		X	X	X	X			X				X				
Gamochaeta americana		X	X	X	X	X			X	X	X			X		
Achyrocline alata			X	X	X			X				X		X		
Conyza bonariensis			X	X				X	X	X		X		X		
Coccocypselum condalia			+	X								X				
Paronychia chilensis			X				X		X	X		X				
Campovassouria cruciata								X	X			X				
Gamochaeta spicata								X	X	X						
Cissus striata								X	X	X		X	X			
Bromus brachyanthera								X	X			X				
Habenaria montevidensis								X				X	X			
Eryngium paniculatum									X	X						
Carex fuscula									X	X						
Smilax campestris									X					X		X
Griselinia ruscifolia										X		X	X			
Weinmannia paulliniifolia												X	X	X	X	
Symphyopappus itatiayensis												X	X		X	
Podocarpus lambertii												X	X	X		
Myrceugenia alpigena												X		X		
Myrsine guianensis													X	X	X	
Vanillosmopsis erythropappa													X			X

Eupatorieae) and other shrubs (e.g. *Vellozia*, some Myrtaceae) found primarily in rocky, open habitats; the biogeography of most of these genera shows a strong connection with the Brazilian Plateau rather than with lowland forest (Barroso, 1973; Kirkbride, 1976; Judd, 1984; Almeida *et al.*, 2004). Finally, there is a component of tropical grasses, e.g. *Axonopus*, *Aristida*, *Eragrostis*, *Ichnanthus*, *Paspalum*, with distributions centred in drier subtropical and tropical formations of the interior. The importance of the Brazilian Plateau, or 'campos' element in the Brazilian montane flora has also been clearly described by Brade (1956) for Itatiaia, and Rambo (1951, 1953) and Rizzini (1979) for the mountains of southern Brazil. Cleef *et al.* (1993) describe a 'savanna' element in the páramo flora of the northern Andes, but typical low-elevation savanna (cerrado or llanos) has very little floristic relationship to high-mountain habitats in south-east Brazil (Table 2 & Figs 4–6; see also Eiten, 1970)

There is also a wet, tropical element in the Brazilian montane flora (Rambo, 1953; Brade, 1956). Genera from this subgroup are mostly relatively widespread in eastern Brazil (see

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Table 4 Cryptogamic species shared between the campos de altitude and at least two other locations. Species tabled manually to best represent floristic patterns. For the high-elevation sites, '+' indicates present at elevations lower than the sampled area.

Cryptogams	VZ	CO	EC	HU	PU	AP	RA	TU	BA	CH	TF	AS	MA	PA	RE	CE
Grammitis flabelliformis	X	X	X	X	X											
Grammitis moniliformis	X	X	X	X	X											
Grammitis strictissimum	X	X	X	X	X											
Lycopodium jussiaei	X	X	X	X	X											
Culcita coniifolia	X	X	X	+	+											
Asplenium monanthes	X	X	X	X	X			X	X	X		X				
Dryopteris paleacea	X	X	X	X	X			X				X				
Lycopodium clavatum	X	X	X	X	X							X	X			
Athyrium filix-femina	X	X	X	X				X				X				
Lophosoria quadripinnata	X	X	X	+	+					X		X				
Woodsia crenata	X	X	X	X	X	X		X	X			X				
Dicksonia sellowiana	X	+	X	+	+							X	X			
Hymenophyllum polyanthos	X	X	X	+	+							X		X		
Lycopodiella alopecuroides	X		X	X	+							X		+	X	
Hymenophyllum fucoides	X		X	X	X							X				
Hymenophyllum rufum	X		X									X	X			
Asplenium auritum	+		X										X			
Campyloneurum angustifolium		+	X	X	X							X				
Histiopteris incisa		X	X	X	X					X		X		X		
Pteridium aquilinum		X	X	X	X			X	X			X	X	X		X
Plagiogyria semicordata		X	X	X												
Blechnum schomburgkii			X	X	X							X		X		
Eriosorus cheilanthoides			X	X	X											
Asplenium harpeodes			X	X	X							X	X			
Blechnum penna-marina				X	X			X		X	X	X				
Rumohra adiantiformis				+	+					X	X	X		X		
Hymenophyllum peltatum					X					X	X					
Elaphoglossum gayanum								X	X	X						
Hypolepis rugulosa								X	X	X						
Selaginella muscosa									X			X	X			

Table S2) and occur primarily in the cloud forest belt that fringes the lower elevations of the campos de altitude and ascends in some places along waterways and in protected hollows. Taxa in this group include many genera of the families Myrtaceae, Melastomataceae, Rubiaceae and Bromeliaceae, and also a suite of arboreal genera found in high montane forests throughout Latin America and even worldwide, including *Myrsine*, *Maytenus*, *Ilex*, *Symplocos*, *Clethra* and *Gordonia*.

Phytogeographical groups – temperate component

About 21% of the campos de altitude generic flora is derived from temperate taxa originating from outside Brazil, and another 13% is cosmopolitan (Fig. 2). Allowing that some of the Australantarctic taxa are relict species from ancient southern South American temperate forests, somewhere between one-fifth and one-third of the genera in the campos de altitude flora have temperate latitude origins. This value rises slightly as one proceeds south to Aparados da Serra, and is even higher in the tropical Andean locations, where 26–32% of the genera are temperate in origin (Fig. 2). This pattern – where the closest relatives of many local taxa are found in distant, more temperate climes – is common to all high tropical mountains, and is even more pronounced in the alpine zones of tropical East Africa and New Guinea, where nearly 70% of genera are of temperate zone origin (Hedberg, 1964; Cleef, 1983; Smith & Cleef, 1988).

At least 11% of the species in the three most extensive campos de altitude appear to be shared directly with either the temperate or tropical Andes (the real value is higher, as this study includes only nine locations in the Andes). Rambo

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(1951, 1953) made much of the fact that about 10% of the flora of the State of Rio Grande do Sul had clear Andean affinities, but many of the taxa he identified were congeners with Andean cousins rather than shared species. Using Rambo's rationale, something like 20% of the campos de altitude species have 'Andean affinities'. This result makes it clear that there are two centres of 'Andean vegetation' in Brazil: the southern mountains and campos, and the high peaks of the south-east, with the latter supporting even stronger connections at the species level.

The primary pre-adaptation required for all prospective plants at high elevation is frost tolerance. The rarity of frost tolerance in the lowland flora of the wet tropics helps explain the relative importance of temperate biogeographical elements in tropical alpine floras (Hedberg, 1964; Smith & Young, 1987; Rundel *et al.*, 1994). This pattern is clearly behind patterns of tropical vs. temperate origins of highland floras in south-east and southern Brazil as well (Rambo, 1951; Brade, 1956; Safford, 1999a,b). Absolute minima in the campos de altitude reach below −10°C, and upwards of 60 days of frost may occur in a year, many more days than at elevations with equivalent mean annual temperatures in the equatorial Andes (Safford, 1999a,b). These 'extreme' conditions result in the increased dominance of cold-adapted taxa in the campos de altitude *vis-à-vis* lower habitats at the same latitude. Figure 7 compares phytogeographical spectra for five sites in south-east Brazil, ranged along an elevation gradient from sea level to 2400 m. The drop in dominance of tropical taxa with elevation is obvious, as is the rise in importance of temperate and cosmopolitan genera.

Surprisingly, temperate genera in the campos de altitude flora are primarily gravity-dispersed; there are also many endozoochorous and self-dispersed taxa (Fig. 3). Mantel tests (Table 2) showed that sinuous geographical distance provides the best explanation (if not strongly significant) for patterns of distribution for the temperate (and cosmopolitan) genera. These results underline the fact that the majority of temperate taxa in the campos de altitude flora did not show up recently 'on the wind', but rather required terrestrial links with similar habitats to move from western South America to eastern South America. The current distributions of many temperate genera retain strong signals of ancestral routes of migration between the temperate climates of west and east South America: the obvious 'gate' is through the northern Argentine and Paraguayan lowlands (for graphic examples of this Andean–southern temperate–south-south-east Brazil distribution pattern see Brade, 1956; Smith, 1962; Rizzini, 1979; Brown, 1987; Longhi-Wagner & Zanin, 1998; Safford, 1999a).

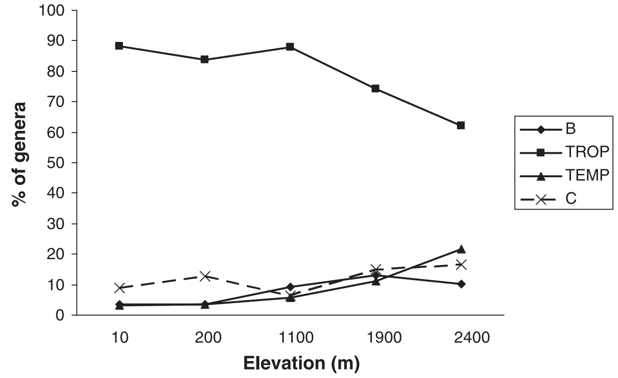

Figure 7 Geographical origin of genera at five sites in south-east Brazil, arranged by elevation. B, Brazilian taxa; TROP, tropical taxa (Neotropical + widespread tropical); TEMP, temperate taxa (Holarctic + Australantarctic + widespread temperate); C, cosmopolitan taxa. For site details and original data see Safford & Martinelli (2000).

Members of the Australantarctic (AA) group have strong preferences for mild to cool temperatures and relatively high-precipitation regimes (see the CANOCO results and Cleef, 2005). This is apparent not only from their respective physiologies (Golte, 1978; Hawkins *et al.*, 1991) but can be seen in grosser form in their elevational distribution, which rises from sea level in southernmost South America to perhaps 1500 m in south-east Brazil, to over 3000 m in the Colombian Andes. The ancient core of this group, which includes *Drimys*, *Weinmannia*, *Griselinia*, *Araucaria*, *Podocarpus* and a few cyathids, was an integral part of the southern Cretaceous–Early Tertiary flora of Australia, Antarctica and southern South America (Menéndez, 1969: Raven & Axelrod, 1974). The early adaptations of these genera to mild, maritime climates have left an indelible imprint on their current distributions (Raven & Axelrod, 1974; Golte, 1978; Mohr & Lazarus, 1994). In South America, fossil remnants of this flora have been documented across the continent from present-day Chile to southern Brazil. There are few adventive species in the AA flora, and a great many genera have diaspores that are much too large for more than local dispersal (Brown & Lomolino, 1998; Fig. 3c). Some of the AA taxa produce edible fruits (*Fuchsia*, *Gaultheria*, *Escallonia*) and thus could conceivably be dispersed much farther, but only a few AA genera are truly efficient dispersers (e.g. *Gleichenia*, *Cortaderia*, *Sisyrinchium*).

The patterns seen in the representation of the temperate phytogeographical groups in Fig. 2 can be explained as the result of three primary factors. First, continuous habitat connections between east and west South America have been lacking since the end of the last glaciation. Beginning with the rise of the central Andes in the Miocene, an arid 'diagonal' stretching from northern Argentina to north-east Brazil appears to have acted as a biogeographical 'gate', opening for montane taxa only during periods of global cooling (Smith, 1962; Raven & Axelrod, 1974; Spichiger *et al.*, 2004). Second, there has been a limited amount of time available for migration of temperate taxa from North America. The Panamá landbridge is thought to have closed about 3.5 Mya (Coates & Obando, 1996), and opportunities for island hopping across the Antilles must have been limited for all but the most dispersible taxa. Finally, the Brazilian sites are far from the northern tip of the continent: the campos de altitude are more than 5000 km in a direct line from the Panamá–Colombia border, and 7500 km along the spine of the Andes and across

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the Argentine–Paraguayan lowlands. Differences in the relative importance of temperate and tropical groups in the Andean vs. Brazilian mountain locations are due to a number of other geographical and historical factors as well, including the lower elevation and more limited area of the Brazilian mountains and the fact that rates and amounts of orographic uplift in the Andes were much greater than in Brazil. Simpson (1983) noted that uplift in the tropical Andes was very rapid and selective pressures were extreme; time for adaptation to these novel ecological conditions by local tropical taxa was very short. As a result, many high-elevation niches were filled by southward-migrating Holarctic and temperate taxa pre-adapted to extreme environmental conditions.

Plant endemism

Patterns of endemism in the south-east Brazilian mountains point clearly to allopatry as a primary mechanism for species differentiation, driven by the interaction between long-term climate cycling (see below), mountain uplift and the insular nature of high-elevation habitats in this part of South America (see Bigarella *et al.*, 1975; Klein, 1975; Simpson, 1979; Vanzolini & Williams, 1981; Whitmore & Prance, 1987; as well as numerous monographs). Only 0.5% of Brazil reaches elevations above 1200 m (Almanaque Abril, 1994), and areas with elevations above 2000 m are very restricted in size and often extremely disjunct. The total areal extent of the campos de altitude is probably less than 350 km^2 (Safford, 1999a). Distances between contiguous areas > 5 km^2 above 2000 m range from tens to hundreds of kilometres.

In Fig. 7, it can be seen that the importance of the east Brazilian group increases with elevation. This underlines the montane nature of endemism in the Atlantic rainforest (Martinelli & Bandeira, 1989; Por, 1992). Although restricted endemism in eastern Brazil peaks between *c.* 500 and 1500 m elevation, there are also a high number of species and even genera that are endemic to the campos de altitude. Endemic genera include *Magdalenaea* and *Nothochilus* (Scrophulariaceae), *Itatiaia* (Melastomataceae), *Worsleya* (Amaryllidaceae) and *Glaziophyton* (Poaceae: Bambuseae); all of these are restricted to very small ranges and all are monotypic. From my current species lists, the percentage of local endemic species in the three best-collected campos averages *c.* 4% (Serra dos Órgãos) to 7% (Itatiaia and Caparaó). Martinelli & Bandeira (1989) give similar numbers for five Serra do Mar sites and the Serra do Itatiaia. Their analysis suggested that about 20% of the species they sampled were endemic to the campos de altitude habitat type – on average 23% of the sampled floras were identified as either locally endemic or habitat endemic.

Endemic plant species in the campos de altitude are concentrated in the Neotropical families. In the three sites included in this study, there are at least 15 local endemics in the Melastomataceae (seven in *Tibouchina*, five in *Leandra*), 11 in the Asteraceae (three each in *Senecio* and *Baccharis*), six in the Eriocaulaceae (all *Paepalanthus*), six in Velloziaceae (all *Barbacenia*), six in Poaceae:Bambuseae (five *Chusquea*), and five in Bromeliaceae (three *Tillandsia*). Noteworthy non-Neotropical families with multiple endemics at higher elevations of south-east Brazil include Ericaceae, Lycopodiaceae, Cactaceae, Orchidaceae, Onagraceae (*Fuchsia*) and the ferns in general (see Safford, 1999a for sources).

Safford & Martinelli (2000) describe patterns of endemism in the inselberg flora of south-east Brazil. Inselbergs occur throughout eastern Brazil, and are common at all altitudes. Above 2000 m, these large rock outcrops support a flora that is proportionally more dominated by tropical genera than are the surrounding grass- and shrublands. This is apparently because adaptations to superxeric rupicolous conditions in the Brazilian highland flora (e.g. succulence, pseudobulbs, poikilohydry, auxiliary water storage, CAM CO_2 fixation) are found almost exclusively in tropical families (Safford & Martinelli, 2000). Endemism among the inselberg flora in south-east Brazil is closely correlated with the rupicolous lifestyle and is primarily restricted to a few Neotropical monocot families: Bromeliaceae, Orchidaceae, Velloziaceae and Araceae. Some of these epilithic taxa are facultatively epiphytic, and others are derived from epiphytic stock (Safford & Martinelli, 2000).

Three basic ancestral groups can be identified for those endemic taxa that are not derived from eastern Brazilian or Neotropical stock: (1) woody or tree-fern Australantarctic taxa that are relict from early Tertiary forests, (2) taxa that came overland from west South America primarily during the late Tertiary and Quaternary, and (3) taxa that arrived by long-distance dispersal. Woody and tree-fern genera in the Australantarctic group (Group 1) typically support only a few species per genus and exhibit strong evolutionary conservatism (Raven & Axelrod, 1974; Golte, 1978; Landrum, 1981). Connections with western South America in this group are mostly at the genus level or above. The long-distance-dispersal group (Group 3) is primarily vascular cryptogams and ruderal phanerogams, and includes most of the species shared between the campos de altitude and the western South America sites (Tables 3 and 4). There are relatively few south-east Brazilian endemics in this group – the distributions of these taxa reflect environmental similarities more than biogeographical history. Of the three groups, the highest number of Brazilian Highland endemics is found in that set of genera that came overland in pulses as cooler environments periodically expanded during glacial cycling beginning in the late Tertiary (Group 2). Smith (1962) noted that genera in this group included species whose distributions bridged the geographical gap between the Andes and southern Brazil, while others were widely disjunct with distinct species on either side. The diversity of distributions found in this group suggested to Smith that a long time had elapsed from the first migration of this group to the last, with the broadly distributed species belonging to recent migrations and the more diverse disjuncts belonging to older migrations. Many Australantarctic, Holarctic and widespread temperate genera fit in this group, as do a few tropical genera as well (see, e.g. Rambo, 1951; Brade, 1956; Smith, 1962; Berry, 1989).

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Biogeography and palaeoclimates – Tertiary

Maack (1949); Rambo (1953); Smith (1962) and Rizzini (1979) all arrived at the conclusion that campos (grasslands) were among the first phanerogamic formations on the southern Brazilian highlands, having arisen in semiarid areas during the late Cretaceous or early Tertiary. Based on fossil data (Rambo, 1953; Menéndez, 1969; Rizzini, 1979) a cool-temperate Australantarctic element (*Araucaria*, *Podocarpus*, etc.) was also in southern Brazil at this time, probably restricted to more maritime slopes and refuges from the volcanic outpourings that covered this part of Brazil in the Jurassic and Cretaceous. Rambo (1953) and Rizzini (1979) suggested that a 'distinct Brazilian montane flora' can trace its roots only to the mid-Tertiary, but mountains high enough to intercept maritime moisture probably existed by the early Tertiary (de Almeida, 1976; de Almeida & Carneiro, 1998). Although areas of central and eastern Brazil experienced hot, drought-like conditions through much of the mid to late Tertiary (see Safford, 1999a), taphofloras substantiate that Australantarctic taxa continued to survive in southern and eastern Brazil throughout the era (Rambo, 1951; Menéndez, 1969; Rizzini, 1979; Romero, 1986). Whether all of these taxa were continuously present, or whether there were multiple recolonizations, sufficiently mesic climatic conditions must have prevailed in the coastal highlands and atop the highest parts of the Brazilian Plateau. Taphofloras indicate that these cooler, moister 'refugia' provided habitat for grassland associations as well (Rizzini, 1979), hence these putative formations may represent a sort of 'ancestral' campos de altitude.

As semiarid conditions developed during the Tertiary, the steadily rising mountains along the eastern edge of the Brazilian Plateau became progressively more important as orographic refuges for taxa adapted to moister and/or cooler conditions. The existence of these refugia in the Brazilian Highlands was not only of local importance. Uplift of the Brazilian mountains pre-dated the rise of the central and northern Andes by many millions of years. The central Andes were at no more than 1000 m elevation in the early Miocene, and still less than 2000 m at the end of the Miocene. The northern Andes are the youngest part of the range, having been uplifted primarily in the last 5–7 Myr; elevations in the mid-Miocene have been estimated at 500–700 m, and at 1000–2000 m at the beginning of the Pliocene (Gregory-Wodzicki, 2000). With the rise of the northern Andes, eastward-flowing drainages developed and the Amazon Sea emptied to the east, probably beginning in the middle Miocene (Webb, 1995; Hoorn, 2006). The tropical forests of eastern South America were an important source for biological colonization of the Amazon Basin as the waters receded, but the Brazilian Highlands also provided much of the germplasm for northern Andean montane habitats as they developed through the late Tertiary. Although researchers have focused on the 'Andean' component of the Brazilian Highland flora, many of these taxa are actually Brazilian in origin, having arisen in eastern South America and colonized the tropical Andes as appropriate habitats emerged in the late Tertiary. In some cases separate and parallel evolutionary tracks ensued, but in others multiple recolonizations of the opposite side of the continent occurred. Strong evidence of Brazilian origin exists for many South American tropical-montane taxa, including 'classic páramo genera' such as *Chusquea* and *Jamesonia* (Tryon, 1944; Vuilleumier, 1969; Grant, 1995; Kelchner & Clark, 1997; Ballard *et al.*, 1999; Aedo, 2001; Sanchez-Barracaldo, 2004). Even *Drimys* appears to have colonized the tropical Andes by way of the Brazilian mountains (Ehrendorfer *et al.*, 1979).

Biogeography and palaeoclimates – the Quaternary

In eastern South America, we are beginning to learn enough about the last glacial cycle (end of the Wisconsinan/Würm) to ascertain how recurrent glacial events during the Quaternary affected plant distributions in the highlands of south-east Brazil. The Last Glacial Maximum (LGM) occurred between *c.* 24,000 and 18,000 yr BP, when air temperatures in eastern South America were 5–7°C lower than today (Webb *et al.*, 1997; Behling, 1998). Using lapse rates (Safford, 1999b), temperatures that currently occur at the (partly anthropogenic) forest limit at *c.* 2000 m (mean annual temperature = *c.* 12°C) could have occurred at elevations as low as 700–800 m, and the permanent snow line (the 0°C isotherm) may have dropped to the level of the higher summits in the Serra da Mantiqueira (2800–2900 m). Long-lasting winter snow cover would have been a perennial occurrence in the higher mountains (but glaciation, theorized by some early researchers with little or no evidence, could never have occurred under this scenario), and the effects of freezing temperatures would have exerted a strong selective force across wide swathes of the Brazilian south-east and south.

The effects of climate cycling on the campos de altitude and other upper montane vegetation types in south-east Brazil can be seen in palynofloras sampled from higher elevations in the Serras da Mantiqueira and do Mar (Fig. 8; see also Behling *et al.*, 2007). Both cores in Fig. 8 show a clear trend beginning at around the Pleistocene/Holocene boundary of decreasing dominance of grassland and increasing values for forest taxa. The rate of change increases in the mid-Holocene, following a pattern of increased precipitation seen in cores from all over tropical South America (Marchant & Hooghiemstra, 2004). The overwhelming dominance of grassland taxa in the high mountain flora during the LGM and into the mid-Holocene is an indication of much cooler and drier climates than today (trending warmer in the Holocene), and corroborates the findings of other palaeoecological studies (Webb *et al.*, 1997; Behling, 1998, 2002; Ledru *et al.*, 1998). Behling (1997, 2002) has found strong evidence that currently forested elevations above 700–1000 m in south and south-east Brazil supported expanses of campos during the LGM. It seems clear that during glacial maxima many currently isolated mountaintop habitats were ecologically linked by similar environments, at least along the axes of the major mountain ranges. With multiple recurrences of this scenario throughout the latest Tertiary

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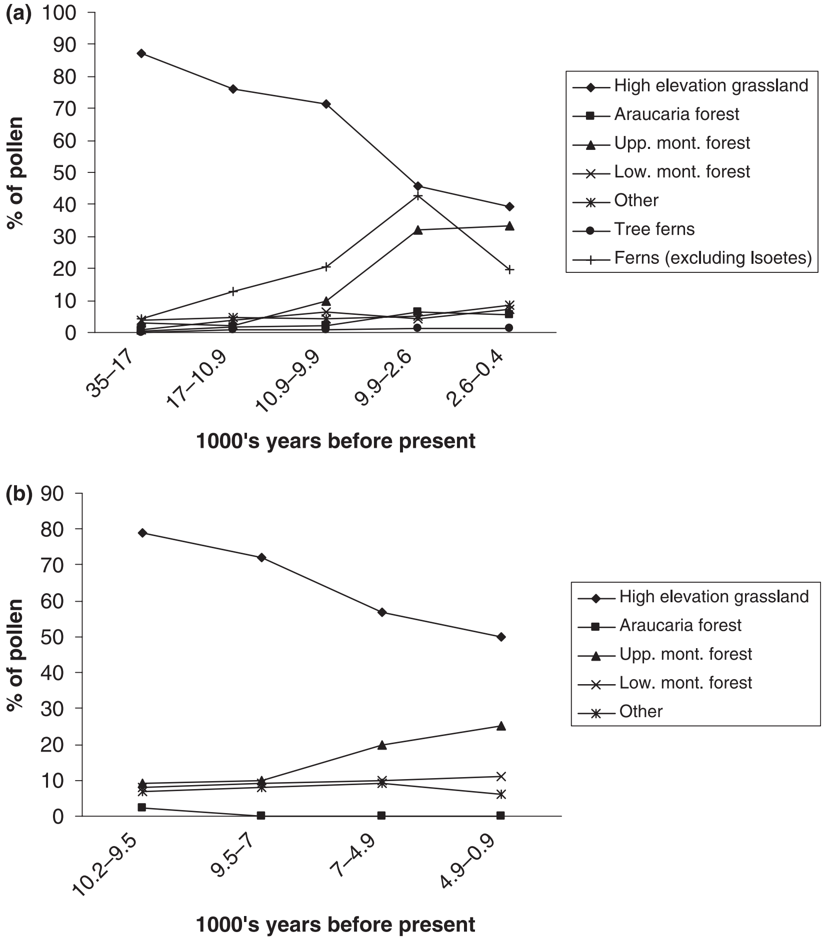

Figure 8 Late Quaternary changes in vegetation at two campos de altitude sites in south-east Brazil. (a) The record from 35,000 yr BP to 400 yr BP at a site near Morro da Itapeva, in the Serra da Mantiqueira (Behling, 1997). (b) The record from 10,200 yr BP to 900 yr BP at a site in the Serra dos Órgãos (Behling *et al.*, in prep.). Each point along the *X*-axis is the mean of values for the block of time indicated.

and Quaternary, opportunities for migrations, colonizations, extinctions and genetic differentiation would have been myriad.

The distributions of many plant taxa throughout the south-east highlands of Brazil exactly support such a scenario of repeated connections and disconnections between montane ecosystems across current geographical gaps. The montane bamboo genus *Chusquea* section *Swallenochloa*, a dominant taxon in most of the campos de altitude and many humid Andean páramos, has approximately 13 species in eastern Brazil. Four of these are widespread, eight are known only from single mountain ranges, and one is distributed among three sites. The evidence suggests allopatric differentiation from a single widely distributed ancestor (Clark, 1992). The genus *Fuchsia* section *Quelusia* (Onagraceae) follows a similar pattern, with one widespread species and seven locally restricted species that are interpreted as vicariants derived by allopatric differentiation from the widespread parent (Berry, 1989). The ericaceous genus *Gaylussacia* has speciated explosively in the Brazilian mountains (Luteyn, 1989), with about 15 species found in the campos de altitude sites considered in this study, some of them endemic to small areas. Even the ancient genus *Drimys* (Winteraceae) shows subspecific differentiation in south-east Brazil that is most parsimoniously explained by Pleistocene climate cycling (Ehrendorfer *et al.*, 1979).

These biogeographical patterns extend to animals, both vertebrate and invertebrate. The frog genera *Cycloramphus* and *Hylodes* contain a number of species restricted to high-elevation streams in the campos de altitude and related habitats in south-east Brazil: Heyer (1982) and Heyer & Maxson (1983) ascribe their existence to climate-driven habitat change in the Pleistocene. Sick (1984) describes biogeographical patterns in the distributions of Brazilian birds, citing numerous examples of Andean–south-eastern Brazilian disjunctions in the families Rhinocryptidae, Furnariidae, Turdidae and Motacillidae. Most of Sick's examples involve taxa of low mobility, which theoretically should favour genetic differentiation in cases of geoclimatic vicariance, and indeed many of the treated species are restricted to relatively small ranges in the Brazilian Highlands. Regarding butterflies, Brown (1987) noted the existence of 'south-Andean elements' (e.g. *Tatochila*, pronophiline satyrs) in high-elevation 'pseudopáramos' (i.e. campos de altitude) as far north as the Serra do Caparaó, with subspecific differentiation between the different mountain groups. Silveira & Cure (1993) found that the bee fauna of high-altitude areas of the Brazilian south-east showed very similar patterns to butterflies. One pattern was of

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high-elevation endemics found only on scattered mountain-tops; another was of common species found only above 1400 m that were shared between south-east Brazil and points south, including Argentina and Chile.

CONCLUSION

1. The current biota of the campos de altitude is the product of the interactions of plate tectonics, climate change, mountain uplift, geographical distance, historical chance and other factors. The current floras of both the Andes and the highest Brazilian peaks are 'hybrids' of tropical, temperate and cosmopolitan evolutionary stock, vestiges of long histories of environmental flux and biological migration. As is the case in most high tropical mountains, many of the plant and animal taxa currently living at the summits of the south-east Brazilian Highlands are traceable in their ancestry to temperate latitudes.
2. Patterns of endemism and diversity in the south-east Brazilian mountains point to climatically driven allopatry as the principal mechanism for speciation.
3. The tropical component of the campos de altitude flora is composed largely of taxa with connections to drier, more open habitats of the interior highlands. Other important tropical groups include taxa adapted to xeric rock outcrops, and taxa restricted primarily to forested conditions.
4. The temperate component of the south-east Brazilian flora increases in importance with elevation, but never reaches the levels seen in the much higher and more extensive Andean ranges.
5. Most temperate, and many cosmopolitan, plant taxa in the campos de altitude appear to have arrived via migration through favourable habitat rather than by recent, long-distance dispersal. Past climate change is necessary to explain the presence of many of these taxa in the south-east Brazilian mountains. The migration path for many of these taxa was clearly through the northern Argentine/Paraguayan lowlands and the highlands of Uruguay and south Brazil.
6. Floristic similarity at the level of genus is higher between the campos de altitude and very distant sites in the tropical Andes than between the campos de altitude and low- and middle-elevation sites in central and eastern Brazil.
7. A high number of bryophyte, fern, and ruderal phanerogam species are shared between the Andes and the campos de altitude. At least 11% of the vascular species in the three campos de altitude sites treated in this paper are shared directly with the Andes; at least 20% of the species have very close Andean 'affinities'. Together with the campos and highlands of south Brazil, the campos de altitude represent a focus of 'Andean vegetation' in Brazil.
8. Previous contributions have described ecological similarities between the campos de altitude and the páramos of the equatorial Andes (Safford, 1999a,b, 2001). As demonstrated in this contribution, floristic patterns strongly substantiate these parallels, and establish that this relationship is the product of both current environmental similarities and shared biogeographical history.
9. The campos de altitude are currently at their Holocene ebb. Palynofloras show that these habitats have significantly contracted over the past 10,000 years, as regional temperatures have warmed and become more humid. Current rates of climate change suggest that these habitats may disappear altogether in the not too distant future.

ACKNOWLEDGEMENTS

Thanks to A. Cleef, H. Behling, R. Esteves, L. Leoni, M. Modenesi, T. Moulton, L.S. Sarahyba, E. Vohman and a whole host of others for field help, botanical expertise and critical reads of early versions of this manuscript. Two anonymous referees and M.B. Bush provided helpful critiques of final drafts.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online from http://www.Blackwell-Synergy.com:

Table S1 Literature sources for floristic and climatic data treated in this paper (see Table 1). Sources for each location are arranged alphabetically. Where no bibliographic information follows author names, the full citation has already been given earlier in the table.

Table S2 Genera represented in the floras of the three largest campos de altitude (Serra do Itatiaia, Serra dos Órgãos, Serra do Caparaó), arranged by phytogeographical group.

Table S3 Floristic similarities between locations. The upper matrix is at the level of genus, the lower matrix at the level of species. First numbers refer to the number of taxa shared; numbers in parentheses are Jaccard similarities. Site codes as in Table 1.

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Editor: Mark Bush

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