The LINNEAN SOCIETY of London BOTANICAL Journal of the Linnean Society

Botanical Journal of the Linnean Society, 2011, **167**, 378–393. With 4 figures

Campos de Cima da Serra: the Brazilian Subtropical Highland Grasslands show an unexpected level of plant endemism

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Received 13 May 2011; revised 8 July 2011; accepted for publication 15 August 2011

A high level of endemic flowering plant species is highlighted for the first time for the southern Brazilian flora. We present a comprehensive list of 1020 endemic taxa and analyse their distribution in different biomes, focusing on the Subtropical Highland Grasslands (Campos de Cima da Serra). Considering all biomes represented in southern Brazil, *c*. 13% of the flowering plant species are endemic, which accounts for more than 5% of the total endemic taxa of Brazil and *c*. 12% of the endemic taxa from the Atlantic Forest hotspot. Like the High Altitude Tropical Grasslands that are found further north in the south-eastern Brazil region, the Subtropical Highland Grasslands are home to an assemblage of tropical and temperate plant lineages. The Subtropical Highland Grasslands are characterized by their transitional nature and by having 296 endemic plant taxa (25% of its flora).

ADDITIONAL KEYWORDS: angiosperms – biogeography – conservation – diversity – endemic species.

INTRODUCTION

South American savannas and grasslands harbour particular floras with a high level of endemism. However, these open vegetations are neglected when compared with the forests with regard to the priority given to research and conservation (Burman, 1991; Safford, 1999, 2007; Bilenca & Miñarro, 2004; Overbeck *et al*., 2007).

The Campos de Cima da Serra are the southern Brazilian Subtropical Highland Grasslands. Studies focusing on this biome have suggested that they are neglected in conservation policies, and that information about their biodiversity is lacking (Giulietti *et al*., 2005; Overbeck *et al*., 2007). A compilation by Boldrini *et al*. (2009) for the Subtropical Highland Grasslands, including two (Rio Grande do Sul and Santa Catarina) of the three states comprising the southern Brazilian Subtropical Highland Grasslands, estimated the existence of 1161 plant species, with 107 (9.21%) considered as endemic. Despite these recent reports, other publications covering grasslands from Brazil have considered the southern Brazilian grasslands as not satisfactorily known (Joly *et al*., 1999; Alves & Kolbek, 2010). In an attempt to delineate the campos rupestres (rocky grasslands embedded within the tropical savannas) in comparison with other grass-rich vegetation from South America, Alves & Kolbek (2010) mentioned the high diversity of endemic species that characterize the grassy vegetation in the high-altitude mountains of south-eastern Brazil (to the north of the area of the current study). However, the Subtropical Highland Grasslands of southern Brazil were not included in their analysis, because the authors considered their flora as poorly known and interpreted it as representing a successional phase to forest vegetation.

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The present study arises from the need to characterize and delimit the southern Brazilian Subtropical Highland Grasslands and to recognize the distribution of the diversity of their endemic plants. We aim to characterize the southern Brazilian flora, looking for candidate plant taxa which could be recognized as indicators of the Subtropical Highland Grasslands biome, and to analyse its floristic similarity with the other adjacent biomes. We address the following questions. How high is the diversity of endemic plants in southern Brazil? Is it possible to characterize the Subtropical Highland Grasslands biome by the means of endemic taxa? Which other biomes are the Subtropical Highland Grasslands related to?

MATERIAL AND METHODS

Study area

The southern Brazilian Subtropical Highland Grasslands comprise 1 374 000 ha (Boldrini *et al.*, 2009), reaching to around 1800 m elevation on their eastern edge. This vegetation lies south of the Tropic of Capricorn, between 24°52′11″S and 29°26′40″S and between 49°27′11″W and 53°43′51″W. The Subtropical Highland Grasslands are underlain by effusive rocks of the Serra Geral Formation that originated between 120 and 135 Mya (Almeida, 2009). The climate is subtropical humid (Cfa) and temperate humid (Cfb) (Peel, Finlayson & McMahon, 2007), with rainfall throughout the year and an average temperature between 12 °C (mean minimum temperature in July, 10 °C) and 18 °C (mean maximum temperature in January, 27 °C) (Behling, 2002; Almeida, 2009).

Species list and distribution

Two large databases concerning South American vegetation have been published recently and cover the study area. The *Catálogo de las Plantas Vasculares del Cono Sur* (Zuloaga, Morrone & Beltrano, 2008) lists all vascular plants from southern South America, including Argentina, Chile, Paraguay, Uruguay and the south of Brazil (Paraná, Santa Catarina and Rio Grande do Sul states). The other database is the *List of Species of the Brazilian Flora* (Forzza *et al.*, 2010), which covers all known plants and fungi from Brazil. Information from these databases was the source to elaborate a consensus checklist of endemic angiosperms from southern Brazil in the study presented here. To achieve this consensus list, all names were checked and the taxa assigned as endemic to southern Brazil were assembled in a new checklist. To combine the lists, an exhaustive search was carried out, and each taxon name was checked in nomenclatural databases (International Plant Names Index (IPNI), 2008; Tropicos, 2011), protologues and taxonomic revisions. In addition, the checklist *Plantas da Floresta Atlântica* (Stehmann *et al.*, 2009), monographs, herbaria records, field observations and personal communications were considered to complement the final list and solve ambiguous and contradictory information amongst the original sources of data. The most recent changes in taxonomy and nomenclature were applied to make lists comparable, according to the Angiosperm Phylogeny Group (APG) III (2009) for family and genus levels and recent taxonomic revisions for genus and species levels. In the same way, data on the geographical distribution for each taxon, including the vegetation in which they occur, were compiled from the most representative herbaria covering the southern Brazilian flora [HBR, ICN, MBM, PACA, RB, SPF (abbreviations from Thiers, 2010)] and from databases of the Missouri Botanical Garden – Brazilian records (MOBOT_BR), Smithsonian Department of Botany – Brazilian records (NMNH-_Botany_BR) and The New York Botanical Garden – Brazilian records (NYBG_BR), accessed through Species Link (CRIA, 2011). This review enabled the improvement of the checklist by eliminating incongruent names from the source lists (not validly published names, synonyms and taxa mistakenly considered as endemics).

Taxa with narrow distributions centred in southern Brazilian vegetation, but not endemic to southern Brazil, were not included in the present analysis. The vegetation in neighbouring regions (e.g. Tropical Forest and Tropical Highland Grasslands, in southeast Brazil) was not fully sampled here, leading to the omission of some taxa which were not exclusive to southern Brazil. Similarly, some taxa restricted to Low Altitude Temperate Grasslands and Temperate Shrubland, but not endemic to southern Brazil because their distribution range crosses the political limits with Uruguay and Argentina within the Pampean Domain, were also not included in the analysis.

Categorization of vegetation

To analyse the distribution of endemics at a finer scale, the vegetation of southern Brazil was classified by a modification of the categories mapped by Leite (2002), who recognized ten different phytoecological units and three transitional vegetation areas in the south of Brazil on the basis of geology, terrain, climate and soil. For the present study, nine categories (biomes) were considered (Fig. 1): Tropical Forest (TRF), Tropical Savanna (TRS), Tropical Coastal Scrub (TCS), High Altitude Tropical Grasslands (HTG, synonymous with Campos de Altitude), Subtropical Seasonal Forest (SSF), Subtropical Mixed Forest (SMF), Subtropical Highland

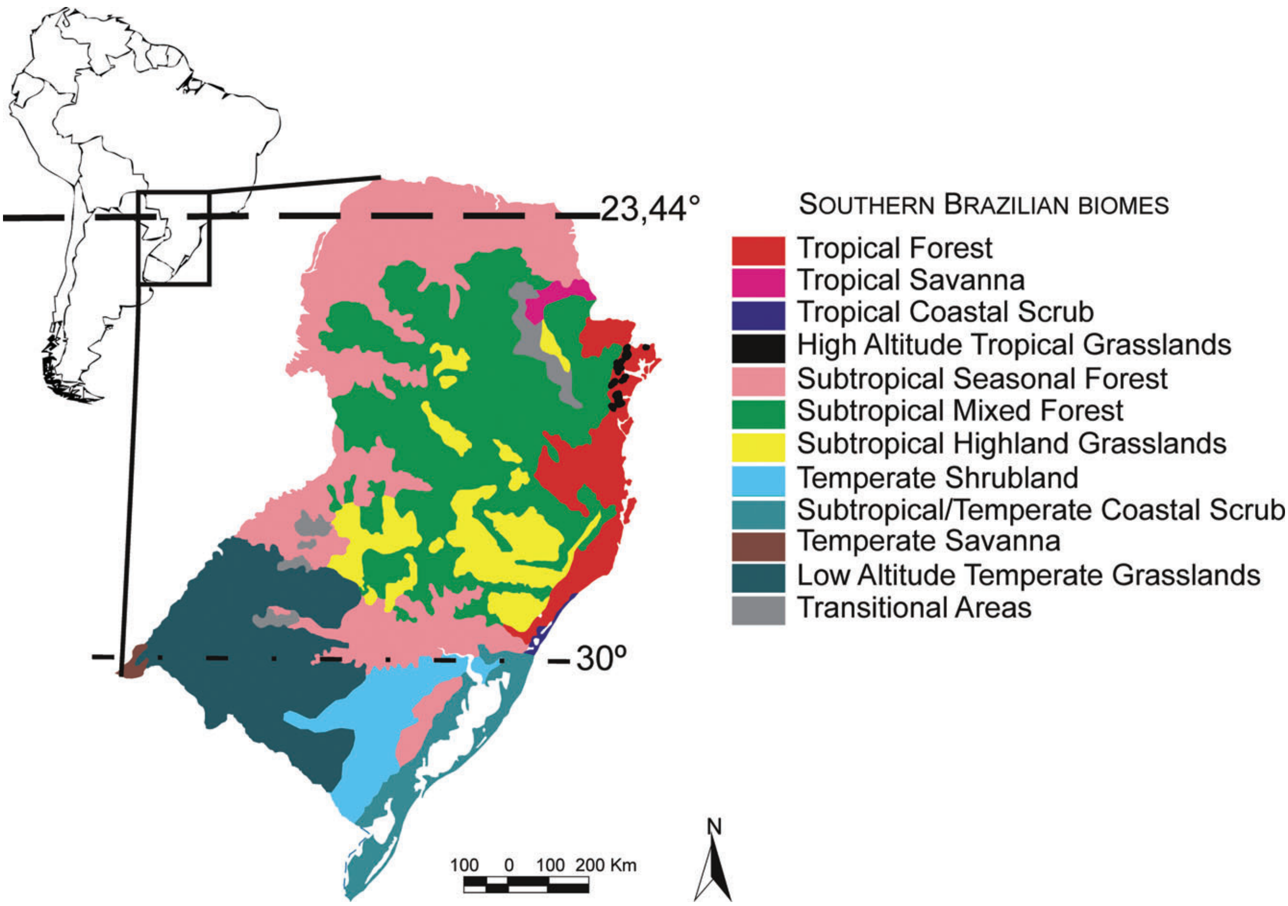

Figure 1. Vegetation in southern Brazil.

Grasslands (SHG, synonymous with Campos de Cima da Serra), Temperate Shrubland (TES) and Low Altitude Temperate Grasslands (LTG). The main differences between this classification and that of Leite (2002) is the separation of the High Altitude Tropical Grasslands and the Subtropical Highland Grasslands and of the Subtropical Scrub and the Low Altitude Temperate Grasslands, and the merging of different seasonal categories applied by Leite (2002) into a single unit called Subtropical Seasonal Forest. Areas defined as transitional by Leite (2002) and areas not relevant in the context of the current work (Subtropical/Temperate Coastal Scrub and Temperate Savanna) were mapped, but not included in the analysis. As the delimitation of the study area (southern Brazil) is essentially political, some of the biomes listed above are continuous in other Brazilian states or in adjacent countries, such as Argentina and Uruguay. For these biomes, only the portion included in southern Brazil was considered and analysed. However, the Subtropical Highland Grasslands, the main subject of this work, are completely included within the study area and were therefore analysed completely.

DATA ANALYSIS

All names were organized in tables, and taxa for which data on geographical distribution were unreliable were excluded from the analysis. The information on geographical distribution was organized into floristic matrices, consisting of binary presence–absence data for 965 taxa (descriptors) and nine sampling units (samples). Similarity between different sampling units was calculated by the Sørensen coefficient, and their relationships were investigated using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA), applied in Fitopac 2.1.2.85 (Shepherd, 2010). To test the sharpness of groups, a method developed by Pillar (1999) was applied, using MULTIV 2.4.2 (Pillar, 2006). The separation of floristic groups, highlighting the indicator taxa for each sampling unit, was carried out using WinTWINS 2.3, TWINSPAN for Windows (Hill & Šmilauer, 2005). The taxa which occur exclusively in each sample were considered as biome indicators. A Venn diagram (Venn, 1981) was elaborated to visualize both exclusive and shared endemic taxa among the main floristic areas identified in the similarity analysis, considering four sampling units: Forests (TRF + SSF + SMF + TCS), Pampas (LTG + TES), High Altitude Grasslands (HAG: HTG + SHG) and Tropical Savanna (TRS).

RESULTS

The list of endemic taxa of angiosperms from southern Brazil, based only on the *Catálogo de las Plantas Vasculares del Cono Sur* (Zuloaga *et al*., 2008), resulted in a total of 1249 taxa, including species, subspecies and varieties. However, when considering the list of endemics based only on the *List of Species of the Brazilian Flora* (Forzza *et al*., 2010), 981 taxa were considered to be endemic to southern Brazil. When compared, the two lists showed only 646 names in common, and 48.27% (603 names) of the taxa cited as endemic from southern Brazil in the *Catálogo de las Plantas Vasculares del Cono Sur* were not considered as endemic in the *List of Species of the Brazilian Flora*. Similarly, 34.14% (335 names) of the taxa listed as endemic from southern Brazil in the *List of Species of the Brazilian Flora* were not considered to be endemic in the first list. Summarizing both lists into a single database, 938 names were incongruent and had to be checked through the review of protologues, taxonomic revisions, analysis of herbarium specimens and personal communication with experts on specific families.

The consensus list of endemic flowering plants from southern Brazil recognizes 1020 taxa at species, subspecies and variety levels, corresponding to 13% of all angiosperms from southern Brazil (7671 taxa) and 5.34% of the total (19 090 taxa) endemic flowering plants from Brazil (Forzza *et al*., 2010). The complete list of endemic flowering plants from southern Brazil is provided as Supplementary Material (Table S1). The most important families with regard to the number of endemic taxa are Asteraceae (115), Orchidaceae (100) and Fabaceae (78), which are recognized as the three richest flowering plant families in the number of species worldwide. The genera with the largest numbers of endemic taxa in southern Brazil are *Mimosa* L. (Fabaceae) with 45 taxa, and *Baccharis* L. (Asteraceae) and *Begonia* L. (Begoniaceae) with 26 taxa each. Considering only the Subtropical Highland Grasslands, the most important families with regard to the number of endemic taxa are Asteraceae (56), Fabaceae (31) and Poaceae (26), and the genera with the highest levels of endemism are *Croton* L. (Euphorbiaceae) with 15 taxa, and *Mimosa* (Fabaceae) and *Nothoscordum* Kunth (Amaryllidaceae) with 14 taxa each.

Eight genera belonging to six families were recognized as endemic to southern Brazil. All are monotypic in their current circumscription and are distributed in different vegetation formations, as shown in Table 1.

Table 1. Species belonging to endemic monotypic genera in southern Brazil

Family	Species	Biome
Fabaceae	*Sellocharis paradoxa* Taub.	TES
Iridaceae	*Kelissa brasiliensis* (Baker) Ravenna	TES
	Onira unguiculata (Baker) Ravenna	LTG TCS
Malvaceae	*Calyptraemalva catharinensis* Krapov.	TRF
	Tropidococcus pinnatipartitus (A.St.-Hil. & Naudin) Krapov.	SMF TRF
Myrtaceae	*Curitiba prismatica* (D.Legrand) Salywon & Landrum	SMF
Rutaceae	*Raulinoa echinata* R.S.Cowan	TRF
Verbenaceae	*Verbenoxylum reitzii* (Moldenke) Tronc.	TRF

LTG, Low Altitude Temperate Grasslands; SMF, Subtropical Mixed Forest; TCS, Tropical Coastal Scrub; TES, Temperate Shrubland; TRF, Tropical Forest.

Among the biomes from southern Brazil, the Subtropical Highland Grasslands is the richest in endemic flowering plants, with 296 endemic taxa. The second richest is the Tropical Forest with 216 endemic taxa, and the third richest is the Subtropical Mixed Forest with 70 endemic taxa. The other endemic taxa are more or less equally distributed amongst the remaining six biomes. Fifty-five taxa were classified as having deficient data on their geographical distribution because of a lack of reliability of herbarium records or missing data, and these were not considered.

The grasslands of southern Brazil are frequently considered to be a single vegetation unit, known as 'Campos Sulinos' (Southern Grasslands), encompassing both the Subtropical Highland Grasslands (Campos de Cima da Serra) and the Pampas (Low Altitude Temperate Grasslands plus Subtropical Scrub). However, considering the geographical distribution of the endemic flora emphasizes that few taxa exclusive to southern Brazil are shared between the Subtropical Highland Grasslands and the Pampas. The Subtropical Highland Grasslands show a transitional pattern, sharing some taxa with the tropical grasslands from further north in Brazil (High Altitude Tropical Grasslands) and some taxa with the temperate grasslands from the Pampas Domain. Twenty-three taxa are shared with the High Altitude Tropical Grasslands and 12 between the Subtropical Highland Grasslands and the Pampas. However, when the

Pampas is compared with the High Altitude Tropical Grasslands from Serra do Mar, no taxa are shared, highlighting the temperate character of the Pampas and the tropical nature of Serra do Mar, and the discontinuity of distribution of southern Brazilian endemic taxa between them (Fig. 2A). In addition to these shared taxa, the uniqueness of the Subtropical Highland Grasslands is emphasized by the 296 endemic plant taxa, which could be considered as indicator species for the recognition of this biome. A complete list of endemic flowering plants from the Subtropical Highland Grasslands is presented in Table 2.

A comparison of taxa exclusive to southern Brazil, shared between the biomes analysed, shows low floristic similarity, as revealed in Table 3 (maximum Jaccard index of 0.1599 between Tropical Forest and Subtropical Mixed Forest). The present analysis considered only endemic taxa from southern Brazil (13% of the total flora), which probably influenced this low degree of similarity. Although the Subtropical Highland Grasslands share endemic taxa from southern Brazil with all other biomes within this region, there is no one biome to which it has a high degree of floristic similarity. Maximum similarity is with the High Altitude Tropical Grasslands (23 shared taxa), Tropical Forest (35 shared taxa) and Subtropical Mixed Forest (40 shared taxa). Cluster analysis based on UPGMA (cophenetic correlation, 0.8952) is visualized in Figure 3. The first group (forests of Atlantic Domain) is composed of the Tropical Forest, Subtropical Seasonal Forest and Subtropical Mixed Forest, the second group (grasslands of the Atlantic Domain) of the Subtropical Highland Grasslands (Campos de Cima da Serra) and the High Altitude Tropical Grasslands, and the third group (grasslands and savannas of the Pampas Domain) of the Low Altitude Temperate Grasslands plus the Subtropical Scrub. The Tropical Coastal Scrub (coastal vegetation of Atlantic Domain) and the Tropical Savanna (Cerrado Domain) did not group and remained separated.

The TWINSPAN analysis shows similar results where, in the first partition, the Low Altitude Temperate Grasslands and the Subtropical Scrub are separated with an eigenvalue of 0.695 and 19 taxa as indicators. The second partition separates the Tropical Forest, Subtropical Seasonal Forest, Subtropical Highland Grasslands, Subtropical Mixed Forest and Tropical Coastal Scrub from the High Altitude Tropical Grasslands plus the Tropical Savanna, with an eigenvalue of 0.652 and 165 positive preferential species. Finally, the Subtropical Highland Grasslands emerged from the remaining vegetation formations with an eigenvalue of 0.525 and 97 taxa as positive preferentials.

Figure 2B shows a Venn diagram of the four groups clustered in the previous analysis, which are also represented in Figure 4. No southern Brazilian endemic taxa co-occur in all four groups and only two species occur in three different groups: *Mimosa intricata* Benth. (Forests + Pampas + HAG) and *Galianthe verbenoides* (Cham. & Schltdl.) Griseb. (Pampas + HAG + TRS). The High Altitude Grasslands (HTG + SHG) share endemic taxa from southern Brazil with all three other groups, being weakly related to both the Pampas and Tropical Savannas (12 and 11 shared taxa, respectively), and sharing more exclusive species with the Forests (76 shared taxa).

DISCUSSION

A previous study concerning endemic plants from southern Brazil included an analysis of the distribution patterns by Marchioretto & Siqueira (1998) of endemic plants from Rio Grande do Sul state, in which they listed 65 eudicotyledons within different biomes and five endemic taxa from the Subtropical Highland Grasslands. Later, the total plant diversity from the Subtropical Highland Grasslands was estimated to be 1161 plant taxa (including 107 endemic taxa; 9.21%) (Boldrini *et al*., 2009). In the present study, we demonstrate a remarkably higher level of endemism in the Subtropical Highland Grasslands (25.31%; 296 taxa). This may even exceed the endemism in the High Altitude Tropical Grasslands further north in Brazil, where 11% of vascular plant species are endemic to Itatiaia (part of the Serra da Mantiqueira range) in south-east Brazil (Martinelli, Bandeira & Bragança, 1989) and 17–31% of species are endemic in the flora of the High Altitude Tropical Grasslands as a whole (Safford, 1999). Most of the genera sampled by Safford (2007) for the south-east Brazilian High Altitude Tropical Grasslands are the same as those found in southern Brazil, but many exclusive species indicate the distinction between them.

The Subtropical Highland Grasslands contain a marked diversity of endemic flowering plants, especially at the eastern edge of the plateau of the highlands, e.g. from Campos dos Padres and Serra do Corvo Branco in Santa Catarina state to Serra da Rocinha and Cambará do Sul in Rio Grande do Sul State. Although these grasslands are within the Atlantic Forest Domain (Oliveira-Filho & Fontes, 2000), the results here suggest an endemism centre distinct from the High Altitude Tropical Grasslands in the Serra do Mar range, in the north-east of Santa Catarina and the east of Paraná. The Subtropical Highland Grasslands contain a high level of endemic plant taxa, which should be considered as particularly important for conservation approaches and future

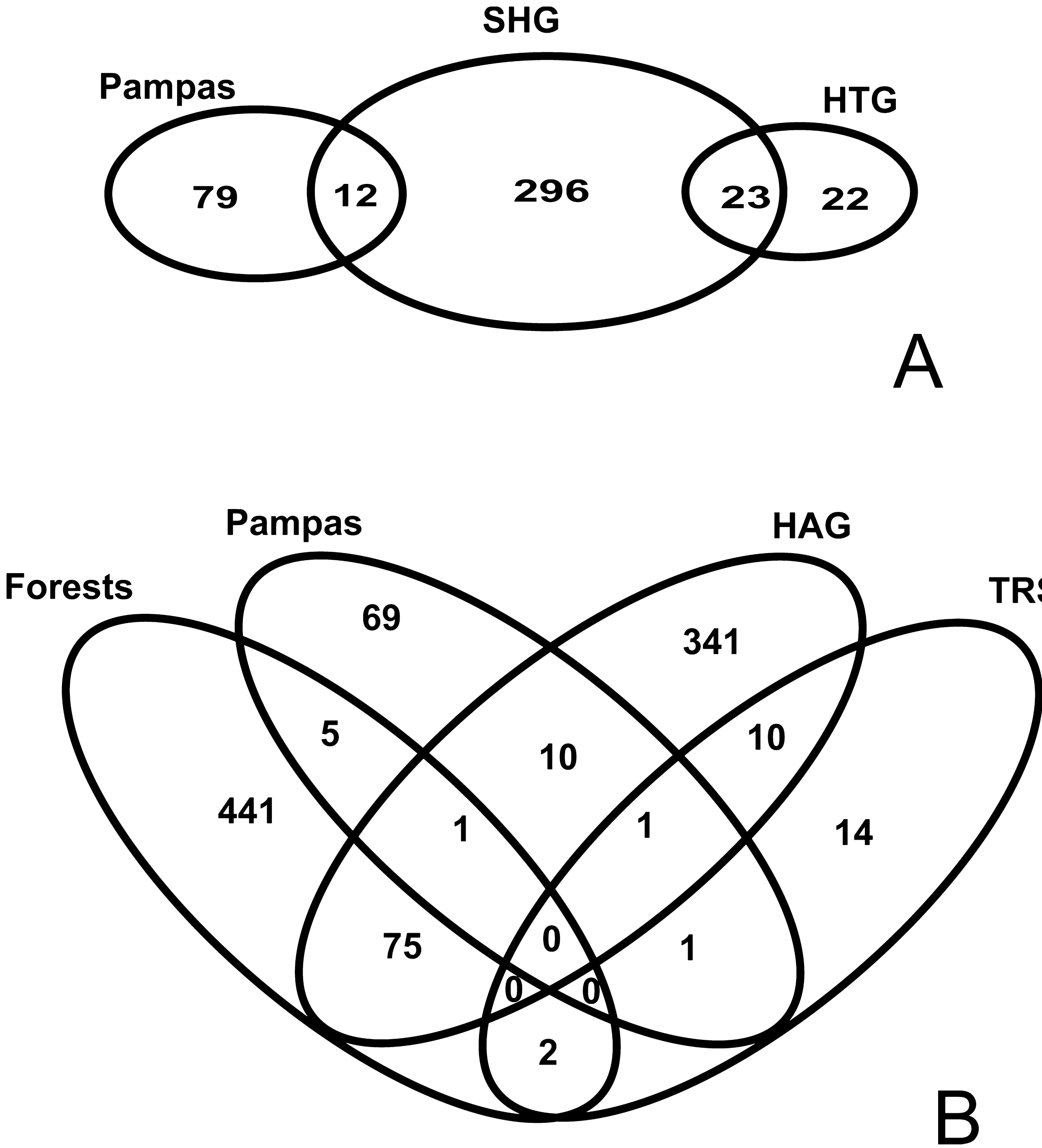

Figure 2. A, Exclusive and shared southern Brazilian endemic taxa between the grassland formations. B, Distribution of exclusive and shared southern Brazilian endemic taxa, considering the four major vegetation clusters from southern Brazil. Forests, Tropical Forest, Subtropical Seasonal Forest, Subtropical Mixed Forest and Tropical Coastal Scrubs; HAG, High Altitude Grasslands (SHG plus HTG); HTG, High Altitude Tropical Grasslands; Pampas, Low Altitude Temperate Grasslands and Temperate Shrubland; SHG, Subtropical Highland Grasslands (Campos de Cima da Serra); TRS, Tropical Savanna.

Table 2. Endemic flowering plants from the Subtropical Highland Grasslands, southern Brazil

Alstroemeriaceae	*Alstroemeria malmeana* Kraenzl.
Amaryllidaceae	*Hippeastrum santacatarina* (Traub) Dutilh
	Nothoscordum aparadense Ravenna
	Nothoscordum cambarense Ravenna
	Nothoscordum capivarinum Ravenna
	Nothoscordum catharinense Ravenna
	Nothoscordum collinum Ravenna
	Nothoscordum curvipes Ravenna
	Nothoscordum exile Ravenna
	Nothoscordum gracilipes Ravenna
	Nothoscordum leptogynum Ravenna
	Nothoscordum luteomajus Ravenna
	Nothoscordum nutans Ravenna
	Nothoscordum stenandrum Ravenna
	Nothoscordum tibaginum Ravenna
	Nothoscordum uruguaianum Ravenna
	Zephyranthes lagesiana Ravenna
	Zephyranthes paranaensis Ravenna
Anacardiaceae	*Schinus spinosus* Engl.
Apiaceae	*Eryngium corallinum* Mathias & Constance
	Eryngium falcifolium Irgang
	Eryngium ramboanum Mathias & Constance
	Eryngium smithii Mathias & Constance
	Eryngium urbanianum H.Wolff
	Eryngium zosterifolium H.Wolff
	Lilaeopsis tenuis A.W.Hill
Apocynaceae	*Oxypetalum coalitum* E.Fourn.
	Oxypetalum malmei Hoehne
	Oxypetalum morilloanum Fontella
Asteraceae	*Achyrocline luisiana* Deble
	Austroeupatorium rosmarinaceum (Cabrera & Vittet) R.M.King & H.Rob.
	Baccharis apicifoliosa A.A.Schneid. & Boldrini
	Baccharis chionolaenoides D.B.Falkenb. & Deble
	Baccharis deblei A.S.Oliveira & Marchiori
	Baccharis hypericifolia Baker
	Baccharis megapotamica var. *weirii* (Baker) G.M.Barroso
	Baccharis pseudovillosa Teodoro & Vidal
	Baccharis scabrifolia G.Heiden
	Baccharis scopulorum A.A.Schneid. & G.Heiden
	Baccharis trilobata A.S.Oliveira & Marchiori
	Baccharis uleana Malag.
	Baccharis wagenitzii (F.H.Hellw.) Joch.Müll.
	Barrosoa ramboi (Cabrera) R.M.King & H.Rob.
	Calea ilienii Malme
	Calea monocephala Dusén
	Carelia ramboi Cabrera
	Chromolaena kleinii (Cabrera) R.M.King & H.Rob.
	Chromolaena oinopolepis (Malme) R.M.King & H.Rob.
	Chromolaena palmaris (Sch.Bip. ex Baker) R.M.King & H.Rob.
	Chromolaena umbelliformis (Dusén ex Malme) R.M.King & H.Rob.
	Chrysolaena nicolackii H.Rob.
	Conyza reitziana Cabrera
	Dendrophorbium subnemoralis (Dusén) A.M.Teles
	Gochnatia argyrea (Dusén ex Malme) Cabrera
	Hatschbachiella polyclada (Dusén ex Malme) R.M.King & H.Rob.
	Heterocondylus reitzii R.M.King & H.Rob.

Table 2. *Continued*

	Hieracium commersonii var. *megapotamicum* Malme
	Hieracium ignatianum Baker
	Hieracium urvillei Sch.Bip.
	Holocheilus monocephalus Mondin
	Hysterionica pinnatiloba Matzenb. & Sobral
	Hysterionica pinnatisecta Matzenb. & Sobral
	Lepidaploa pseudomuricata H.Rob.
	Leptostelma catharinensis (Cabrera) A.M.Teles & Sobral
	Lessingianthus reitzianus (Cabrera) H.Rob.
	Malmeanthus catharinensis R.M.King & H.Rob.
	Mikania nana W.C.Holmes
	Neocabreria catharinensis (Cabrera) R.M.King & H.Rob.
	Noticastrum decumbens (Baker) Cuatrec.
	Panphalea araucariophila Cabrera
	Panphalea ramboi Cabrera
	Panphalea smithii Cabrera
	Perezia catharinensis Cabrera
	Perezia eryngioides (Cabrera) Crisci & Martic.
	Senecio conyzifolius Baker
	Senecio promatensis Matzenb.
	Senecio ramboanus Cabrera
	Senecio rauchii Matzenb.
	Stevia tenuis Hook. & Arn.
	Vernonanthura perangusta (Malme) A.J.Veja & Dematt.
	Vernonanthura rigiophylla (Kuntze) H.Rob.
	Vernonia viminea Ekman ex Malme
	Viguiera meridionalis Magenta
	Viguiera paranensis (Malme) J.U.Santos
	Viguiera santacatarinense (H.Rob. & A.J.Moore) A.A.Sáenz
Bromeliaceae	*Dyckia cabrerae* L.B.Sm. & Reitz
	Dyckia crocea L.B.Sm.
	Dyckia dusenii L.B.Sm.
	Dyckia fosteriana var. *robustior* L.B.Sm.
	Dyckia frigida Hook.f.
	Dyckia ibiramensis Reitz
	Dyckia irmgardiae L.B.Sm.
	Dyckia remotiflora var. *angustior* L.B.Sm.
Cactaceae	*Frailea curvispina* Buining & Brederoo
	Parodia carambeiensis (Buining & Brederoo) Hofacker
	Parodia haselbergii subsp. *graessneri* (K.Schum) Hofacker & P.J.Braun
	Parodia haselbergii (Haage ex Rümpler) F.H.Brandt subsp. *haselbergii*
	Parodia rechensis (Buining) F.H.Brandt
Campanulaceae	*Lobelia paranaensis* R.Braga
	Siphocampylus densidentatus E.Wimm.
Caprifoliaceae	*Valeriana bornmuelleri* Pilg.
	Valeriana chamaedryfolia Cham. & Schltdl.
	Valeriana eichleriana (Muell.) Graebn.
	Valeriana glechomifolia F.G.Mey.
	Valeriana muelleri Graebn.
Caryophyllaceae	*Paronychia revoluta* C.E.Carneiro & Furlan
Cyperaceae	*Eleocharis kleinii* Barros
	Rhynchospora pseudomacrostachya Gerry Moore, Guagl. & Zartman
	Rhynchospora smithii W.W.Thomas
	Schoenus lymansmithii M.T.Strong
Ericaceae	*Gaultheria ulei* Sleumer
	Gaultheria corvensis (R.R.Silva & Cervi) G.O.Romão & Kin.-Gouv.

Table 2. *Continued*

Eriocaulaceae	*Eriocaulon magnificum* Ruhland var. *magnificum*
	Eriocaulon ulaei var. *radiosum* Ruhland
	Eriocaulon ulaei Ruhland var. *ulaei*
	Paepalanthus albovaginatus Silveira var. *albovaginatus*
	Paepalanthus albovaginatus var. *albobracteatus* Tissot-Sq.
	Paepalanthus albovaginatus var. *fuscobracteatus* Tissot-Sq.
	Paepalanthus bellus Moldenke
	Paepalanthus catharinae Ruhland var. *catharinae*
	Paepalanthus leiseringii var. *kleinii* Moldenke & L.B.Sm.
	Paepalanthus tessmannii Moldenke
	Syngonanthus caulescens var. *proliferus* Moldenke
Escalloniaceae	*Escallonia ledifolia* Sleumer
Euphorbiaceae	*Acalypha apetiolata* Allem & Waechter
	Bernardia alarici Allem & Irgang
	Bernardia flexuosa Pax & K.Hoffm.
	Bernardia geniculata Allem & Waechter
	Bernardia hagelundii Allem & Irgang
	Chiropetalum foliosum (Müll.Arg.) Pax & K.Hoffm.
	Chiropetalum molle (Baill.) Pax & K.Hoffm.
	Chiropetalum phalacradenium (J.W.Ingram) L.B.Sm. & Downs
	Croton calyciglandulosus Allem
	Croton catharinensis L.B.Sm. & Downs
	Croton confinis L.B.Sm. & Downs
	Croton dusenii Croizat
	Croton ericoideus Baill.
	Croton helichrysum Baill.
	Croton ichthygaster L.B.Sm. & Downs
	Croton kleinii L.B.Sm. & Downs
	Croton leptophyllus Müll.Arg.
	Croton myrianthus Müll.Arg.
	Croton patrum L.B.Sm. & Downs
	Croton polygonoides L.B.Sm. & Downs
	Croton quintasii Allem
	Croton ramboi Allem
	Croton thymelinus Baill.
Fabaceae	*Adesmia araujoi* Burkart
	Adesmia arillata Miotto
	Adesmia ciliata Vogel
	Adesmia paranensis Burkart
	Adesmia psoraleoides Vogel
	Adesmia reitziana Burkart
	Adesmia rocinhensis Burkart
	Adesmia sulina Miotto
	Adesmia tristis Vogel
	Adesmia vallsii Miotto
	Crotalaria hilariana Benth.
	Desmodium craspediferum A.M.G.Azevedo & Abruzzi de Oliveira
	Lupinus paranensis C.P.Sm.
	Lupinus reitzii Burkart ex. M.Pinheiro & Miotto
	Lupinus rubriflorus Planchuelo
	Mimosa bathyrrhena Barneby
	Mimosa chartostegia Barneby
	Mimosa dolens var. *pangloea* Barneby
	Mimosa dryandroides var. *extratropica* Barneby
	Mimosa eriocarpa Benth.
	Mimosa glabra Benth.

Table 2. *Continued*

	Mimosa hatschbachii Barneby
	Mimosa involucrata Benth.
	Mimosa kuhnisteroides Barneby
	Mimosa macrocalyx var. *pectinata* Burkart
	Mimosa oblonga var. *pinetorum* Barneby
	Mimosa pseudolepidota (Burkart) Barneby
	Mimosa regnellii var. *exuta* Barneby
	Mimosa regnellii var. *grossiseta* Barneby
	Vicia graminea var. *nigricarpa* N.R.Bastos & Miotto
	Vicia hatschbachii Burkart ex Vanni & D.B.Kurtz
Gesneriaceae	*Sinningia leopoldii* (Scheidw. ex Planch.) Chautems
Hypericaceae	*Hypericum cordatum* subsp. *kleinii* N.Robson
Iridaceae	*Calydorea basaltica* Ravenna
	Calydorea crocoides Ravenna
	Cypella aquatilis Ravenna
	Sisyrinchium bromelioides R.C.Foster subsp. *bromelioides*
	Sisyrinchium coalitum Ravenna
	Sisyrinchium decumbens Ravenna
	Sisyrinchium densiflorum Ravenna
	Sisyrinchium rambonis R.C.Foster
Lamiaceae	*Cunila fasciculata* Benth.
	Cunila platyphylla Epling
	Cunila tenuifolia Epling
	Glechon elliptica C.Pereira & Hatschbach
	Hedeoma polygalifolia Benth.
	Hesperozygis kleinii Epling & Játiva
	Hesperozygis rhododon Epling
	Hesperozygis spathulata Epling
	Hyptis apertiflora Epling
	Peltodon rugosus Tolm.
	Rhabdocaulon erythrostachys Epling
	Salvia congestiflora Epling
	Salvia cordata Benth.
	Salvia scoparia Epling
Linaceae	*Linum smithii* Mildner
Lythraceae	*Cuphea hatschbachii* Lourteig
	Cuphea iguazuensis Lourteig
Malvaceae	*Modiolastrum palustre* (Ekman) Krapov.
	Pavonia commutata Garcke
	Pavonia ramboi Krapov. & Cristóbal
	Pavonia reitzii Krapov. & Cristóbal
	Pavonia renifolia Krapov.
Melastomataceae	*Leandra camporum* Brade
	Leandra dusenii Cogn.
	Leandra luctatoris Wurdack
	Tibouchina kleinii Wurdack
Myrtaceae	*Psidium reptans* (D.Legrand) Soares-Silva & Proença
Onagraceae	*Fuchsia hatschbachii* P.E.Berry
Orchidaceae	*Brachystele bicrinita* Szlach.
	Cyclopogon vittatus Dutra ex Pabst
	Cyrtopodium brandonianum subsp. *lageanum* J.A.N.Bat. & Bianch.
	Cyrtopodium kleinii J.A.N.Bat. & Bianch.
	Habenaria dutraei Schltr.
	Habenaria schnittmeyeri Schltr.
	Habenaria ulaei Cogn.
	Pelexia burgeri Schltr.

Table 2. *Continued*

	Pelexia robusta (Kraenzl.) Schltr.
	Pelexia tenuior Schltr.
	Sarcoglottis glaucescens Schltr.
	Sarcoglottis juergensii Schltr.
	Stigmatosema garayana Szlach.
	Stigmatosema hatschbachii (Pabst) Garay
	Veyretia undulata Szlach.
Oxalidaceae	*Oxalis bisecta* Norlind
	Oxalis praetexta Progel
Plantaginaceae	*Mecardonia pubescens* Rossow
	Plantago turficola Rahn
	Scoparia pinnatifida Cham.
Poaceae	*Agrostis ramboi* Parodi
	Aulonemia ulei (Hack.) McClure & L.B.Sm.
	Bothriochloa velutina M.Marchi & Longhi-Wagner
	Briza brachychaete Ekman
	Briza scabra (Nees ex Steud.) Ekman
	Calamagrostis longiaristata var. *minor* Kämpf
	Calamagrostis reitzii Swallen
	Chusquea hatschbachii L.G.Clark & Blong
	Chusquea windischii L.G.Clark
	Digitaria purpurea Swallen
	Eustachys paranensis A.M.Molina
	Melica spartinoides L.B.Sm.
	Panicum magnispicula Zuloaga, Morrone & Valls
	Paspalum barretoi Canto-Dorow, Valls & Longhi-Wagner
	Paspalum ramboi I.L.Barreto
	Paspalum redondense Swallen
	Piptochaetium alpinum L.B.Sm.
	Piptochaetium palustre Muj.-Sall. & Longhi-Wagner
	Poa reitzii Swallen
	Poa umbrosa Trin.
	Stipa brasiliensis A.Zanin & Longhi-Wagner
	Stipa planaltina A.Zanin & Longhi-Wagner
	Stipa rhizomata A.Zanin & Longhi-Wagner
	Stipa vallsii A.Zanin & Longhi-Wagner
	Thrasyopsis juergensii (Hack.) Soderstr. & A.G. Burm.
	Trisetum juergensii Hack.
Polygalaceae	*Polygala altomontana* Lüdtke, Boldrini & Miotto
	Polygala densiracemosa Lüdtke & Miotto
Polygonaceae	*Rumex sellowianus* Rech.f.
Portulacaceae	*Portulaca diegoi* Mattos
	Portulaca hatschbachii D.Legrand
Rubiaceae	*Galianthe elegans* E.L.Cabral
	Galianthe latistipula E.L.Cabral
	Galianthe reitzii E.L.Cabral
	Galium hatschbachii Dempster
	Galium ramboi Dempster
	Galium rubidiflorum Dempster
	Galium smithreitzii Dempster
	Oldenlandia dusenii Standl.
Scrophulariaceae	*Buddleja cestriflora* Cham.
	Buddleja cuneata Cham.
	Buddleja hatschbachii E.M.Norman & L.B.Sm.
	Buddleja kleinii E.M.Norman & L.B.Sm.
	Buddleja ramboi L.B.Sm.

Table 2. *Continued*

Solanaceae	*Calibrachoa cordifolia* Stehmann & L.W.Aguiar
	Calibrachoa dusenii (R.E.Fr.) Stehmann & Semir
	Calibrachoa sellowiana (Sendtn.) Wijsman
	Calibrachoa sendtneriana (R.E.Fr.) Stehmann & Semir
	Calibrachoa serrulata (L.B.Sm. & Downs) Stehmann & Semir
	Calibrachoa spathulata (L.B.Sm. & Downs) Stehmann & Semir
	Nierembergia hatschbachii A.A.Cocucci & Hunz.
	Petunia saxicola L.B.Sm. & Downs
Verbenaceae	*Glandularia catharinae* (Moldenke) N.O'Leary & P.Peralta
	Glandularia dusenii (Moldenke) N.O'Leary & P.Peralta
	Glandularia hatschbachii (Moldenke) N.O'Leary & P.Peralta
	Lippia paranensis (Moldenke) T.R.S. Silva & Salimena
	Verbena caniuensis Moldenke
	Verbena subpetiolata N.O'Leary
Xyridaceae	*Xyris dissitifolia* Kral & Wand.
	Xyris hatschbachii L.B.Sm. & Downs

Table 3. Comparison between the endemic flora from nine different vegetation formations in southern Brazil

Vegetation formation	TRF	SSF	SHG	HTG	SMF	TCS	LTG	TES	TRS
TRF	**217**	*0.0638*	*0.0488*	*0.0026*	*0.1599*	*0.0667*	*0*	*0*	*0.0055*
SSF	25	**39**	*0.0229*	*0*	*0.0901*	*0.0530*	*0*	*0.0152*	*0.0096*
SHG	35	11	**296**	*0.0529*	*0.0729*	*0.0327*	*0.0068*	*0.0218*	*0.0256*
HTG	1	0	23	**22**	*0*	*0*	*0*	*0*	*0*
SMF	71	21	40	0	**70**	*0.0216*	*0*	*0.0043*	*0.0100*
TCS	25	7	15	0	5	**25**	*0.0215*	*0*	*0*
LTG	0	0	3	0	0	2	**25**	*0.0588*	*0*
TES	0	2	10	0	1	0	5	**39**	*0.0247*
TRS	2	1	11	0	2	0	0	2	**13**

Bold type, number of endemic taxa from southern Brazil by vegetation formation; roman type, number of exclusive taxa from southern Brazil shared by pairs of vegetation formations; italic type, indices of similarity (Sørensen coefficient). HTG, High Altitude Tropical Grasslands; LTG, Low Altitude Temperate Grasslands; SHG, Subtropical Highland Grasslands (Campos de Cima da Serra); SMF, Subtropical Mixed Forest; SSF, Subtropical Seasonal Forest; TCS, Tropical Coastal Scrub; TES, Temperate Shrubland; TRF, Tropical Forest; TRS, Tropical Savanna.

studies concerning patterns of diversification in a subtropical transitional environment.

Safford (2007) listed 928 species of vascular plant for the High Altitude Tropical Grasslands from southeast Brazil, about 21% of which belong to temperate genera. These High Altitude Tropical Grasslands show a genus-level similarity of 41.4% (195 genera shared) with the Subtropical Highland Grasslands, but a species-level similarity of only 9.1% (149 species shared). Overall, the Subtropical Highland Grasslands present a larger number of temperate taxa, probably reflecting their more southerly latitude and subtropical nature, as well as their more proximal position to the probable migration path of temperate taxa into Brazil (Safford, 1999, 2007).

The main groups are the same in the cluster and TWINSPAN analyses. The forest biomes group together in both analyses, as do the two formations that comprise the Pampas. The main differences are related to the Subtropical Highland Grasslands (Campos de Cima da Serra) which remain isolated in the TWINSPAN analysis and not related to the High Altitude Tropical Grasslands, which are grouped with the Tropical Savanna. The exclusive and shared taxa between clustered biomes can be observed in Figure 2B.

The Atlantic Forest Domain has a total of 885 endemic taxa in southern Brazil, corresponding to 11.72% of the total endemic plants of the Atlantic Forest hotspot, whereas the Subtropical Highland Grasslands have a total of 296 endemic taxa, corresponding to 4% of the total endemic plants of the Atlantic Forest hotspot. This calls into question policies for conservation that reflect a single, widely

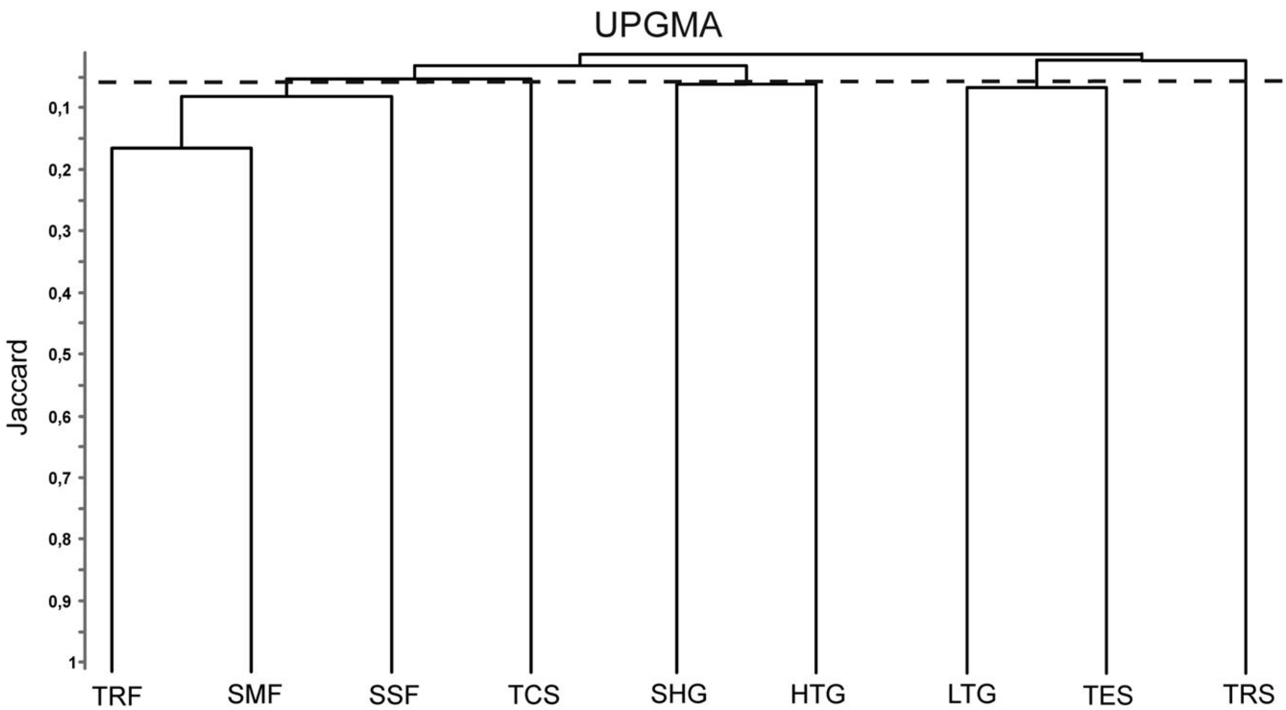

Figure 3. Groups formed in the similarity analysis using Jaccard coefficient and Unweighted Pair Group Method with Arithmetic Mean (UPGMA) as a cluster analysis. The broken line indicates the groups formed in the analysis of sharpness. HTG, High Altitude Tropical Grasslands; LTG, Low Altitude Temperate Grasslands; SHG, Subtropical Highland Grasslands (Campos de Cima da Serra); SMF, Subtropical Mixed Forest; SSF, Subtropical Seasonal Forest; TCS, Tropical Coastal Scrub; TES, Temperate Shrubland; TRF, Tropical Forest; TRS, Tropical Savanna.

defined Atlantic Forest Domain (e.g. following the definition of Oliveira-Filho & Fontes, 2000), and suggests that it might be better to consider High Altitude Tropical Grasslands, Subtropical Highland Grasslands, Tropical Forest, Subtropical Seasonal Forest, Subtropical Mixed Forest and Tropical Coastal Scrub separately. In addition, the Subtropical Highland Grasslands are frequently considered together with grasslands from the Pampas (LTG + TES), being collectively termed the 'Campos Sulinos'. Beyond the physiognomic distinctiveness between the Subtropical Highland Grasslands and Pampas, our results show a strong floristic distinction between them, and they share only 12 taxa. It is clear that, in southern Brazil, different lineages containing endemic taxa are narrowly distributed in different vegetation formations, which are threatened by both human land uses and the increasing predominance of invasive species because of climate change. It is vital, therefore, that conservation policies directed at preserving full plant diversity take these floristic differences into account.

According to the biogeographical classification of South America by Cabrera & Willink (1980), the latitude 30°S is the approximate border between the northern biogeographical provinces Atlántica and Paranense, part of the Amazonian Domain, essentially tropical and dominated by forest, and the southern provinces Pampeana and Espiñal, which represent an extension of the more continental and xerophytic open vegetations of the Chaco Domain.

Although the flora of the high-altitude grasslands contains a large number of endemic taxa, phytogeographical connections with similar habitats in the Andes (Rambo, 1951, 1953, 1956; Smith, 1962; Safford, 1999, 2007) and central Brazil (Smith, 1962) are evident. More than one-third of the flora from southern Brazil clearly belong to temperate Austral-Antarctic and Andean lineages (e.g. *Adesmia* DC., *Araucaria* Juss., *Gunnera* L.), which could be evidence that these groups constitute the major focus of secondary radiation of Andean and Austral-Antarctic taxa into eastern South America (Rambo, 1953; Safford, 1999, 2007; Waechter, 2002). At the same time, between one-half and two-thirds of the genera in the Subtropical Highland Grasslands, and in the high-altitude grasslands in south-east Brazil, may have tropical ancestry as congeneric species grow in tropical regions (Safford, 2007).

Phylogenetic studies of biogeography could help to elucidate these deeper phytogeographical connections. Possible candidate genera are *Lupinus* L.,

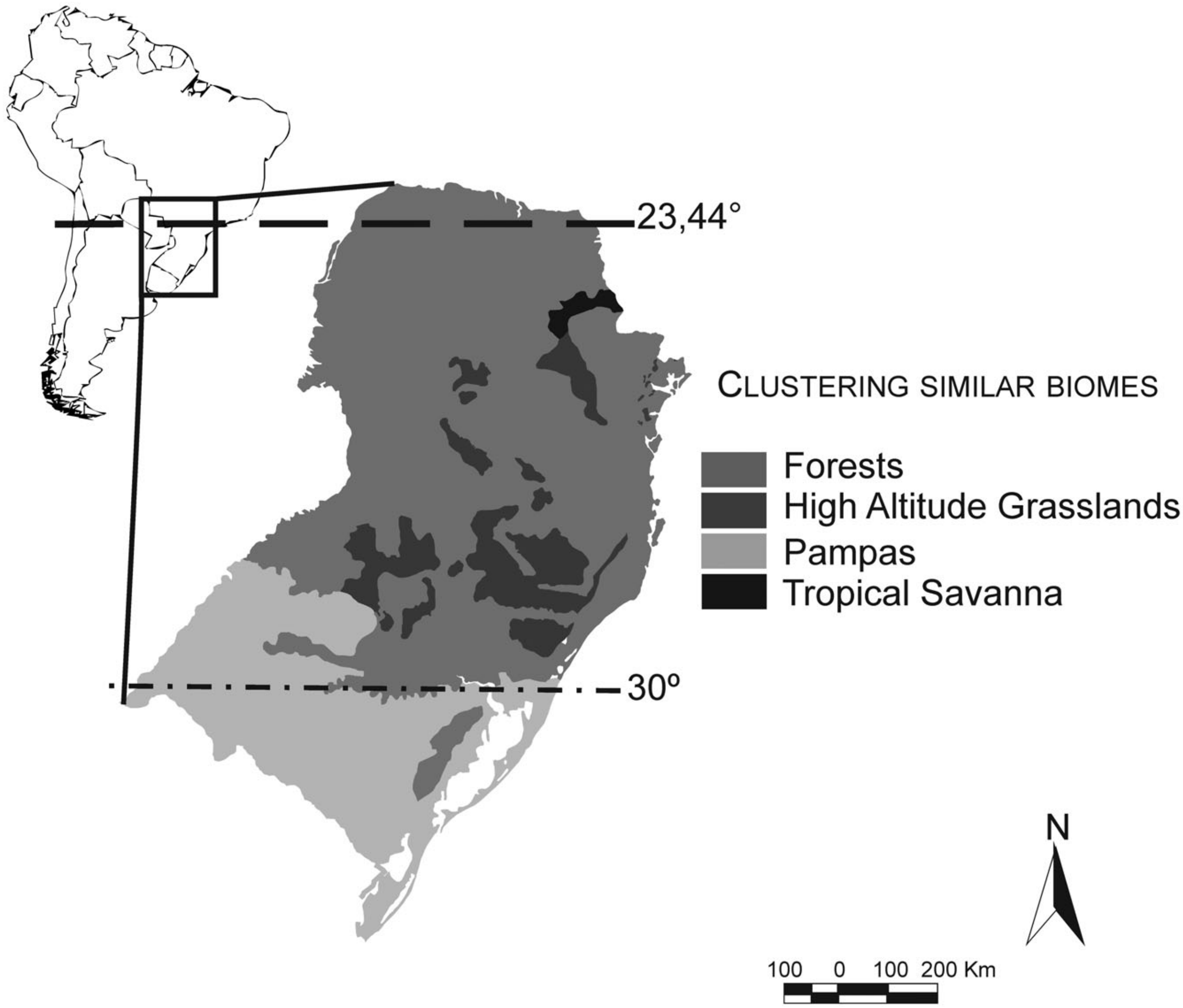

Figure 4. Vegetation in southern Brazil grouping the most similar biomes recognized by the cluster analysis of endemic flowering plants.

Mimosa and *Baccharis*. In *Lupinus* (Fabaceae), many species have a wide distribution in southern Brazil, occurring from the Pampas to the central Brazilian Cerrado (Hughes & Eastwood, 2006), and some species are endemic to the Subtropical Highland Grasslands. In *Mimosa*, many species from southern Brazil are part of lineages which spread from temperate grasslands in lowlands of Argentina and Uruguay to the Cerrado (Simon *et al*., 2009). *Baccharis* has numerous endemic taxa from southern Brazil, showing distribution patterns related to both temperate and tropical grasslands from the Pampas, Subtropical Highland Grasslands and High Altitude Tropical Grasslands (Heiden *et al*., 2007).

Urtubey *et al*. (2010) analysed the diversity patterns of Asteraceae from South America by a panbiogeographical approach and recognized two main nodes that were interpreted as biotic convergence zones. One is located exactly on the transition tropical/temperate area in the subtropics of Brazil, within the Subtropical Highland Grasslands. In this transitional zone, Safford (1999) suggested that climate fluctuations in the Late Tertiary and Quaternary caused floristic changes in the regions now occupied by the high-altitude grasslands. In cool dry periods, such as Pleistocene glacial times, they were colonized by both cool-temperate Andean and Austral-Antarctic taxa, and xerophilous vegetation from the Brazilian Plateau. In warmer, wetter periods, such as Pleistocene interglacials, more humid-adapted forests would have spread. This picture of alternate dominance of the landscape by forests or grasslands is supported by palaeobotanical evidence (Smith, 1962; Behling, 2002; Safford, 2007).

According to Safford (1999), the presence of shared genera of highly dispersive groups, such as Asteraceae and Poaceae, between similar habitats can be explained by the ecological compatibility of the available habitat. However, Safford (1999, 2007) agreed with Rambo (1951, 1953) that the presence in southern Brazil of Andean and Austral-Antarctic genera that lack efficient long-distance dispersal mechanisms is best explained by the existence of direct terrestrial connections during past periods of favourable climate at different periods of both the early and late Cenozoic, and probable multiple times within the Pleistocene. This hypothesis could also be tested by phylogenetic analyses of key exemplar taxa.

The diversification of lineages in the Subtropical Highland Grasslands could have been caused by geographical isolation of vegetation in times of varying climate. In warm, wet conditions favouring the expansion of rain forests, representing barriers to the dispersal of grassland species, allopatry in the grasslands could have been a primary mechanism for species differentiation, producing the large numbers of endemic species demonstrated in this study. This hypothesis could be tested by phylogenetic and population genetic studies of genera with numerous endemic species in the Subtropical Highland Grasslands, such as *Adesmia* series *Psoraleoides* Burkart (Miotto & Waechter, 1996).

CONCLUSIONS

An unexpected diversity of endemic plants is listed for the transitional tropical/temperate vegetation zone in southern Brazil. The Subtropical Highland Grasslands are a distinct vegetation type defined by numerous endemic taxa, and are restricted to isolated patches surrounded by ecologically and floristically distinct formations.

Collectively, the main vegetation types in southern Brazil that are covered in this article harbour 1020 endemic flowering plants, which are distributed within nine biomes. Considering all plant taxa endemic to southern Brazil, few taxa are shared between biomes, but cluster analysis grouped forest biomes (TRF + SSF + SMF + TCS) separate from the High Altitude Grasslands (SHG + HTG) and from the Pampas and Tropical Savanna.

Although the Subtropical Highland Grasslands share taxa with other grasslands and forests, such as the High Altitude Tropical Grasslands and the Low Altitude Temperate Grasslands, they support at least 296 endemic taxa, which is much higher than previous estimates. The transitional character and singularity of the Subtropical Highland Grasslands are indicated by the fact that they harbour both tropical and temperate plant lineages and show surprisingly low species-level similarities with other southern and south-eastern Brazilian grassland systems. Overall, the large number of endemic taxa in the Subtropical Highland Grasslands suggests that this grassland system has been extant for some time in southern Brazil, and does not simply represent a successional stage of disturbed forest.

ACKNOWLEDGEMENTS

The authors would like to thank the Coordenação de Aperfeiçãoamento de Pessoal de Nível Superior – CAPES, Fundação de Amparo à Pesquisa do Estado de São Paulo – FAPESP (2010/00519-8) and Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq, for the provision of grants and post-graduate scholarship support, N. D. dos Santos, J. R. Lima and J. Durigon for comments and suggestions on statistical analysis, and the anonymous referees for their valuable suggestions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. List of endemic flowering plants from southern Brazil and their distribution in different vegetation formations. HTG, High Altitude Tropical Grasslands; LTG, Low Altitude Temperate Grasslands; SHG, Subtropical Highland Grasslands (Campos de Cima da Serra); SMF, Subtropical Mixed Forest; SSF, Subtropical Seasonal Forest; TCS, Tropical Coastal Scrub; TES, Temperate Shrubland; TRF, Tropical Forest; TRS, Tropical Savanna.

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