Acta Botanica Brasilica - 33(4): 644-653. October-December 201.
doi: 10.1590/0102-33062018abb0333

Updates on extratropical region climbing plant flora: news regarding a still-neglected diversity

Jaqueline Durigon[1*], Patrícia Sperotto[2], Priscila Porto Alegre Ferreira[3], Greta Aline Dettke[4], Renato Aquino Záchia[5], Maria Ana Farinaccio[6], Guilherme Dubal dos Santos Seger[7] and Silvia Teresinha Sfoggia Miotto[8]

Received: September 28, 2018
Accepted: February 18, 2019

ABSTRACT

Most studies concerning climbing plants have focused on lianas, forest ecosystems, and tropical regions. Thus, the majority of existing information is not relevant to all climbing plants (lianas and vines) or all ecoregions of the world (forested and non-forested). We provide an update on floristic and distributional data available for climbing plants in Rio Grande do Sul, Brazil's southernmost state, which is located within subtropical and temperate zones and includes a variety of forest and non-forest vegetation types. A total of 448 climbing plant species were confirmed and documented by voucher specimens, revealing a diversity similar to that registered for trees in the state (533). The significant contribution of climbing species to the regional flora, the differences in floristic composition and species richness among the state's eight vegetation types, and the high number of endangered species found in this extratropical region reveal the requirement to expand studies of climbing plants to include environments beyond tropical forests. Furthermore, the importance of herbaceous climbing species in subtropical and temperate floras demonstrates that they should be included in ecological studies of climbing plants, and that future analyses could detect unique or divergent patterns between herbaceous and woody climbers.

Keywords: Atlantic Forest biome, climbers, lianas, non-forest ecosystems, Pampa biome, subtropical flora, vines

Introduction

More than 25 years ago, when the book "The Biology of Vines" (Putz & Mooney 1991) was published, climbing plants were likely, according to Gentry (1991), "the most under-collected of any major habit group of plants". At the time, the significant contribution of climbing plants to tropical forest biodiversity was recognized, as was some evidence of their ecological role as a food source and structuring component of tropical forests (Putz 1984; Gentry 1991; Hegarty & Caballé 1991). There was no discussion, however, of climbers' community-level effects on trees and their key role in ecosystem-level processes as it is now known (Schnitzer & Bongers 2002; Phillips *et al*. 2005; Schnitzer *et al*. 2015; Schnitzer 2018).

Despite important advances in research regarding climbers in the last few decades, most studies are restricted

1 Instituto de Ciências Biológicas, Universidade Federal do Rio Grande, 96170-000, São Lourenço do Sul, RS, Brazil
2 Programa de Pós-Graduação em Botânica, Universidade Estadual de Feira de Santana, 44036-900, Feira de Santana, BA, Brazil
3 Fundação Zoobotânica do Rio Grande do Sul, 90690-000, Porto Alegre, RS, Brazil
4 Herbário da Universidade Tecnológica Federal do Paraná, 87301-899, Campo Mourão, PR, Brazil
5 Departamento de Biologia, Universidade Federal de Santa Maria, 97105-900, Santa Maria, RS, Brazil
6 Herbário da Universidade Federal de Mato Grosso do Sul, Universidade Federal de Mato Grosso do Sul, 79304- 902, Corumbá, MS, Brazil
7 Centro de Estudos Costeiros, Limnológicos e Marinhos, Universidade Federal do Rio Grande do Sul, 95625-000, Imbé, RS, Brazil
8 Departamento de Botânica, Universidade Federal do Rio Grande do Sul, 91501-970, Porto Alegre, RS, Brazil

* Corresponding author: jaquelinedurigon@gmail.com

to tropical regions, forest ecosystems, and woody climbers (lianas) only. That is, the existing data concerning climbing plant diversity, and nearly all the distribution and floristic patterns found, cannot be applied to all ecoregions of the world or to climbers as a whole (woody and herbaceous climbers; i.e. lianas and vines). For example, despite sharing many species with the tropics, climbing flora of extratropical regions can exhibit a distinctive taxonomic and ecological diversity of climbing plants (Durigon *et al*. 2014a; Gallagher 2015). In extratropical South America, the floristic pattern contrasts with those described for tropical regions, with differences in the most speciose families and species composition (Durigon *et al*. 2014a). In addition, the percentage of vines in the climbing flora can be significantly higher in temperate sites in comparison to tropical sites worldwide (Hu *et al*. 2010; Gallagher *et al*. 2011; Gallagher & Leishman 2012), reaching up to 85 % of climbing species in areas from South America (Durigon *et al*. 2014a). Whereas lianas decrease in abundance and diversity with increasing latitude because of freezing-induced embolism (Schnitzer 2005; Schnitzler *et al*. 2016), vines can be less limited, considering their lower susceptibility to temperature and water oscillations (Bhattarai & Vetaas 2003; Hu *et al*. 2010). In temperate areas of South America, the remarkable success of vines can be also attributed to their high frequency in the non-forest ecosystems that cover a large part of the area (Durigon *et al*. 2014a).

Despite being located mostly within tropical latitudes and recognized worldwide for its high diversity of tropical ecosystems and species, Brazil possesses a region with subtropical moist climates that was only recently highlighted as encompassing a distinct biodiversity (Overbeck *et al*. 2007; Pillar *et al*. 2009; Iganci *et al*. 2011). The southern region of Brazil (Paraná, Santa Catarina, and Rio Grande do Sul states) represents both a climatic transition, between tropical and temperate zones, and a biogeographic transition, between tropical-like forests in the north and grassland formations in the south. It is a convergence area of different floristic elements and, notably, the southern distribution limit of several tropical Atlantic species (Rambo 1960; Jurinitz & Jarenkow 2003). Around the 30°S, there is a marked biogeographic discontinuity in which temperate grasslands, steppes, and savannas become important physiognomic elements (Villagrán & Hinojosa 1997; Iganci *et al*. 2011). This transition may exclude some of the woody climbing species adapted to mature inner forest (Gentry 1991; Jiménez-Castillo & Lusk 2013). Moreover, most herbaceous species, in addition to being able to live in drier and/or colder climates, are able to climb the variety of small-diameter supports available among different temperate vegetation types (Durigon & Waechter 2011; Durigon *et al*. 2014a).

Climbing plant diversity and ecology in South Brazil have been addressed by punctual studies restricted to forest ecosystems, which still retain many northern tropical elements (Citadini-Zanette *et al*. 1997; Durigon *et al*. 2009; Durigon & Waechter 2011; Seger & Hartz 2014; Guerra *et al*. 2015; Oliveira *et al*. 2016; Seger *et al*. 2017), thus preventing a more comprehensive analysis of southern climbing flora richness and distribution. Conversely, the extensive work of taxonomic cataloging Brazilian flora in recent years (Forzza *et al*. 2010; Brazil Flora Group 2015; Flora do Brasil 2020) has generated a large amount of new occurrence data by state, allowing for the development of some regionalized biodiversity estimates, even for poorly known groups such as climbing plants. For example, in the state of Rio Grande do Sul, preliminary analyses have revealed a climbing richness that approaches that of arboreal species recorded for the state (Durigon *et al*. 2014b).

In Rio Grande do Sul, the southernmost state of Brazil, the physiognomic division between forest and non-forest environments approaches the regional division between northern and southern halves of the state, and between the biome classifications of Mata Atlântica (Atlantic forest) and Pampa, respectively. The registry of climbing occurrence data in this area and the analysis of the distribution of climbing richness across different types of vegetation can therefore contribute to a re-evaluation of the importance that is given to climbers in non-forest ecosystems and, ultimately, in regions outside the tropics. The main objective of the present study was to systematize and update existing knowledge regarding climbing plants in an extratropical region of Brazil, in order to subsidize advances in research and conservation policies for a neglected plant group in an equally neglected biome, as is the case for the Pampa biome. A substantiated list of species in the state of Rio Grande do Sul is provided, including information on climbing species richness, distribution, conservation status, and ecological attributes, in addition to indications of specialized literature for taxonomic identification of the species registered.

Materials and methods

Study area

Rio Grande do Sul is Brazil's southernmost state, located roughly between 27°S and 33°S. According to Köppen's classification, the predominant climate is subtropical humid (Cfa), with a temperate humid climate (Cfb) restricted to some elevated areas located in the northeast and south of the State (Alvares *et al*. 2013). The seasonality is essentially thermal, with no climatic dry season (Leite & Klein 1990).

Two biomes are officially recognized as occurring within state territory — the Mata Atlântica and Pampa biomes, in the northern and southern halves, respectively — with both showing inner heterogeneities that are considered to be different vegetation types or phytoecological units (Leite 2002; Hasenack *et al*. 2010). In general, the Mata Atlântica biome encompasses mainly forest vegetations, including rain forests and seasonal forests. Its floristic composition is highly influenced by tropical forest taxa that have migrated

along two different routes: the western one formed by the seasonal forests of the Paraná and Uruguay River basins, and an eastern route comprising the rain forests of the Atlantic mountain slopes (Rambo 1961). These tropical-like forests that border the eastern and western parts of northern Rio Grande do Sul are segregated by a mosaic-like landscape of highland grasslands and forests characterized by the presence of temperate taxa, such as *Araucaria angustifolia* (Bertol.) Kuntze and *Podocarpus* L'Hér. ex Pers (Boldrini *et al*. 2009). In contrast, in the Pampa biome, a variety of non-forest vegetation types covers the state's southern half, including temperate grasslands, savannas, and coastal scrub (Hasenack*et al*. 2010; Iganci *et al*. 2011).

Data collection and analysis

A preliminary checklist of climbing plant species occurring in the state of Rio Grande do Sul was obtained from two databases: the Catálogo de Plantas e Fungos do Brasil (Forzza *et al*. 2010) and the Catálogo de las Plantas Vasculares del Cono Sur (Zuloaga *et al*. 2008). The species citations for the state were revised based on specific literature for genera and families, information obtained from regional herbarium collections (ICN, HAS, MPUC, HVAT, PACA, SMDB, FUEL, HBR, FLOR, FURB, CTBS, UPCB, and MBM), and records available in the SpeciesLink Database (CRIA 2012). The species occurrence was confirmed by the existence of correctly identified voucher specimens collected in Rio Grande do Sul, thus eliminating spurious data. Climbing species names were updated by consulting the Flora do Brasil online database (Flora do Brasil 2020) and specialized literature. Furthermore, field observations and analyses of national and international herbarium collections (HB, R, RB, SP, LP, CTES, SI, MVFA, MVJB, and MVM) were carried out in search of new occurrences that could complement the revised checklist. All herbaria acronyms follow Thiers (2018).

Because most of the literature used for climbing species taxonomic identification is dispersed in a variety of monographs, revisions and floras of different scales and taxonomic levels were consulted. Taxonomic information concerning the registered species was systematized, with at least one literature source selected and cited for each genus as a subsidy for species identification.

The distribution of confirmed species across the state's different vegetation types was determined based on occurrence data obtained from the SpeciesLink database and from the consulted herbarium collections. The classification into vegetation types was adapted from Leite (2002) and Iganci *et al*. (2011), resulting in eight different

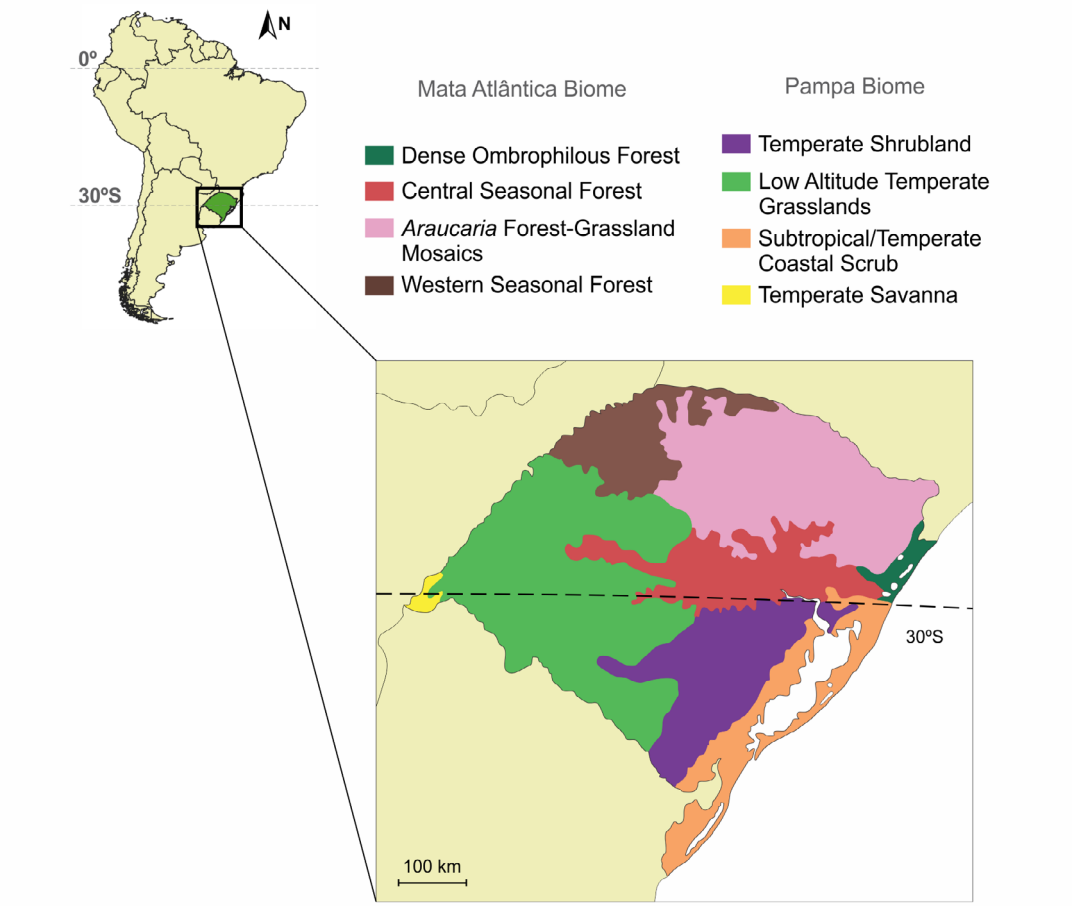

Figure 1. Vegetation types of Rio Grande do Sul state.

units: Dense Ombrophilous Forest (DOF), *Araucaria* Forest-Grassland Mosaics (FGM), Central Seasonal Forest (CSF), and Western Seasonal Forest (WSF) in the Mata Altântica biome; and Subtropical/Temperate Coastal Scrub (SCS), Temperate Shrubland (TES), Low Altitude Temperate Grasslands (LTG), and Temperate Savanna (TMS) in the Pampa biome (Fig. 1). It is important to note that most Mata Atlântica vegetation types (DOF, CSF, and WSF) are characterized by forest vegetations, with the exception of the FGM, which instead corresponds to the mosaics formed by subtropical highland grasslands with shrubby and forest vegetation belonging to *Araucaria* forest. In the Pampa biome, there are distinct forest-grassland mosaics formed by shrubby and seasonal forests, which were considered to be part of the TES unit.

To analyze the floristic affinities between the eight vegetation units, a matrix of species presence/absence was constructed and used to calculate the complement of Jaccard's similarity index. A cluster analysis was also performed using Ward's clustering criterion, and the significance of the formed groups was evaluated by a group partition sharpness analysis (Pillar 1999). All tests were applied with R Statistical Environment (R Development Core Team 2018).

Ecological characteristics and species conservation status

Climbing species were classified into growth forms (i.e., lianas and vines), following Gentry (1991). Lianas are woody, relatively thick-stemmed climbers that more commonly inhabit forest interiors, whereas vines are herbaceous/subwoody, thin-stemmed climbing plants that are more frequently found at forest edges and forest understory. Species were also classified into functional groups based on their climbing mechanism according to Durigon *et al*. (2014a), who considered a combination of previous classifications presented by Darwin (1865), Acevedo-Rodríguez (2005), and Isnard & Silk (2009). Species were therefore classified as twiners, tendril-bearers, scramblers, hook-climbers, climbers with tendril-like branches, root-climbers, or leaf-climbers. Although some species can often display more than one mechanism, only the main one was considered, specifically the one present from the beginning of the plant's search for a support.

Conservation status of climbing species at the state level were obtained from the Rio Grande do Sul Endangered Plant Species List (Rio Grande do Sul 2014), based on the IUCN (2012) classification.

Results

The occurrence of 448 climbing plant species in the state of Rio Grande do Sul was confirmed and documented by voucher specimens. The species are distributed in 164 genera and 54 families, with 43 being eudicots, nine being monocotyledons, and one each being gymnosperms and ferns. The climbing flora of the state is composed primarily of herbaceous (57 %) and twining species (53 %), and nearly 40 % of the species have both attributes (i.e., are herbaceous twining plants). The second most species-rich morphological/functional group consists of herbaceous climbers with tendrils, which corresponds to approximately 15 % of species.

The most speciose families were Fabaceae (58 species) and Apocynaceae (56), together accounting for approximately 25 % of all species. Along with Asteraceae (48), Convolvulaceae (38), Cucurbitaceae (26), Bignoniaceae (24), Malpighiaceae (21), Sapindaceae (19), Passifloraceae (18), and Dioscoreaceae (13), these 10 families account for 321 species, which represents more than 70 % of the climbing species occurring in the state (Fig. 2). The other 127 confirmed species are included in the remaining 44 botanical families. Among the genera, *Mikania* (33 species), *Ipomoea* (25), *Oxypetalum* (19), *Passiflora* (18), *Dioscorea* (13), and *Cayaponia* (10) are the most diverse in the study area (i.e., genera with ten or more species). A complete list of useful references for species taxonomic identification by genera is available in the Supplementary Material (Tab. S1 in supplementary material).

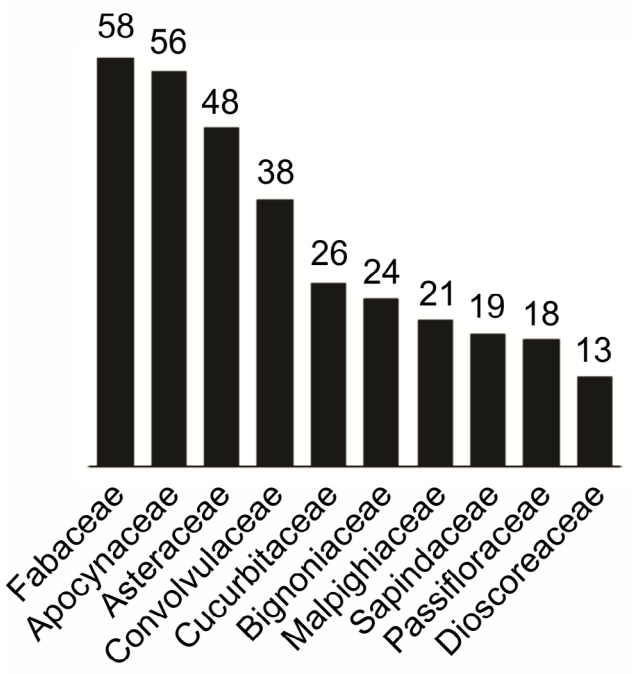

Figure 2. Species richness in the ten most-diversified families of climbing plants in Rio Grande do Sul state, Brazil. The numbers above the bars represent the number of species.

Species distribution

Species richness is unevenly distributed between the Mata Atlântica (predominantly forested) and Pampa

(predominantly non-forested) biomes. The Mata Atlântica biome comprises Dense Ombrophilous Forest (DOF), Central Seasonal Forest (CSF), *Araucaria* Forest-Grassland Mosaics (FGM), and Western Seasonal Forest (WSF), encompassing 232 climbing species (52 % of the total) which occurs exclusively in this biome, in at least one of the vegetation types. The Pampa biome comprises the Low Altitude Temperate Grasslands (LTG), Temperate Shrubland (TES), Subtropical/Temperate Coastal Scrub (SCS), and Temperate Savanna (TMS), including only 23 climbing species which are exclusive (5 % of the total).

Central Seasonal Forest (CSF) includes the largest number of species (283), followed by FGM (263), DOF (242), WSF (215), LTG (124), TES (132), SCS (116), and TMS (31). When area is taken into account, however, DOF stands out as having the highest species-area relationship (0.07081 species/km^2), followed by TMS (0.02188 species/km^2). According to the classification considered, DOF and TMS have the smallest areas, corresponding to 1.28 % and 0.53 % of the total state area, respectively. In contrast, LTG, which represents approximately 33 % of the state territory, is the vegetation type with the lowest species-area relationship (Tab. 1).

Table 1. Species-area relationship by vegetation type, ordered from highest to lowest. Areas are in km^2 and densities in species/km^2. DOF: Dense Ombrophilous Forest; TMS: Temperate Savanna; WSF: Western Seasonal Forest; CSF: Central Seasonal Forest; SCS: Subtropical/Temperate Coastal Scrub; FGM: *Araucaria* Forest-Grassland Mosaics; TES: Temperate Shrubland; LTG: Low Altitude Temperate Grasslands.

Vegetation type	Species-area	Species nº	Area	% of State area
DOF	0.07081	242	3,417.53	1.28
TMS	0.02188	31	1,416.99	0.53
WSF	0.00972	215	22,129.05	8.31
CSF	0.00952	283	29,734.20	11.17
SCS	0.00525	116	22,089.12	8.30
FGM	0.00410	263	64,165.48	24.10
TES	0.00364	132	36,250.26	13.62
LTG	0.00142	124	87,026.14	32.69

Most of the climbing species (c.a. 70 %) occur in more than one type of vegetation. Only 14 species, however, are largely distributed across all vegetations types. This number increases to 29 species when the TMS, which comprises a small area on the western border of the state with a particular flora, is not considered. Conversely, c.a. 30 % of climbers are exclusive or endemic (i.e., climbing species that were found only in one type of vegetation in the state). FGM includes the largest number of exclusive species (33), followed by predominantly forest physiognomies, such as DOF, WSF, and CSF, which contain 29, 25, and 20 exclusive species, respectively. The vegetation types in the southern half of the state (predominantly non-forest) exhibit a smaller number of exclusive species: LTG contained ten species, TMS contained four, SCS contained three, and TES contained only one exclusive species.

Observing the list of climbing species for each vegetation type, a shift in the richest families can be observed (Fig. 3). Asteraceae appears among the two richest families in all vegetation types of the Mata Atlântica biome, whereas Apocynaceae and Fabaceae are the most diversified families in almost the entire Pampa biome. These two families are also important in specific vegetation types of Mata Atlântica: Apocynaceae in DOF and WSF; Fabaceae in FGM and CSF.

Figure 3. Richest families in each vegetation type of the Rio Grande do Sul state. DOF: Dense Ombrophilous Forest; CSF: Central Seasonal Forest; FGM: *Araucaria* Forest-Grassland Mosaics; WSF: Western Seasonal Forest; TES: Temperate Shrubland; SCS: Subtropical/Temperate Coastal Scrub; LTG: Low Altitude Temperate Grasslands; TMS: Temperate Savanna.

The cluster analysis concerning floristic composition of the vegetation types had strong support for up to five groups (Fig. 4). Temperate Savanna (TMS) is the most dissimilar vegetation type, followed by one group of units from the Mata Atlântica biome and another group composed of the remaining units of the Pampa biome. Low Altitude Temperate Grasslands (LTG) and Temperate Shrubland (TES) are the closest vegetation types within the Pampa biome, whereas *Araucaria* Forest-Grassland Mosaics (FGM), Central Seasonal Forest (CSF), and Dense Ombrophilous Forest (DOF) form a single group, apart from the Western Seasonal Forest (WSF).

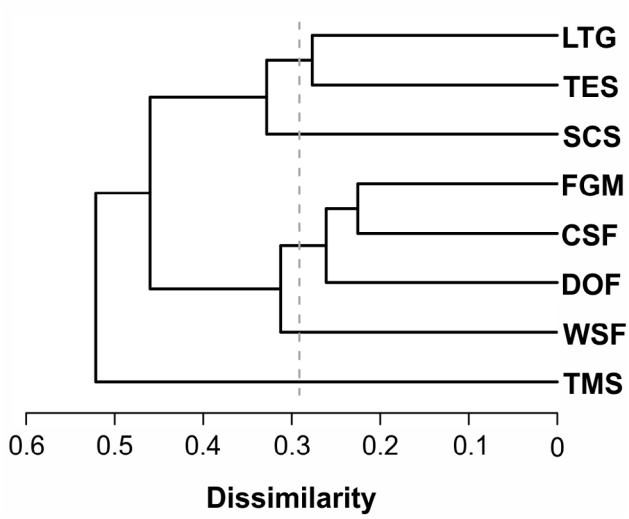

Figure 4. Groups of vegetation types, according to climbing species composition (presence/absence data). Gray line represents the maximum number of groups recognized by the group partition sharpness analysis. DOF: Dense Ombrophilous Forest; CSF: Central Seasonal Forest; FGM: *Araucaria* Forest-Grassland Mosaics; WSF: Western Seasonal Forest; TES: Temperate Shrubland; SCS: Subtropical/Temperate Coastal Scrub; LTG: Low Altitude Temperate Grasslands; TMS: Temperate Savanna.

Ecological characteristics and conservation status

Regarding functional groups, twiners and tendril-bearers correspond to 80 % of climbing species in all vegetation types. Tendril-bearers are the most expressive in the TES, corresponding to nearly 35 % of the climbing flora. This vegetation type also stands out by having the greatest proportion of leaf-climbers (5 %) in comparison to other types of vegetation (1–3 %). Another striking difference concerning species climbing mechanisms is the presence of root-climbers only in ombrophilous or otherwise humid forests, and the absence of tendril-like branches climbers in most non-forest physiognomies (Fig. 5).

According to the species list of threatened flora for the state of Rio Grande do Sul, approximately 20 % of climbing plant species are under some degree of threat. In terms of threat levels, most species (29) are classified in the "Endangered" category, followed by "Critically Endangered" (23), "Vulnerable" (21), "Least Concern" (six), "Regionally Extinct" (four), "Nearly Threatened (three), and "Extinct" (one species). A further seven climbing species are considered "Data Deficient". The majority of the endangered species (45 %) occurs in only one type of vegetation in the state, particularly in DOF and FGM. Moreover, approximately

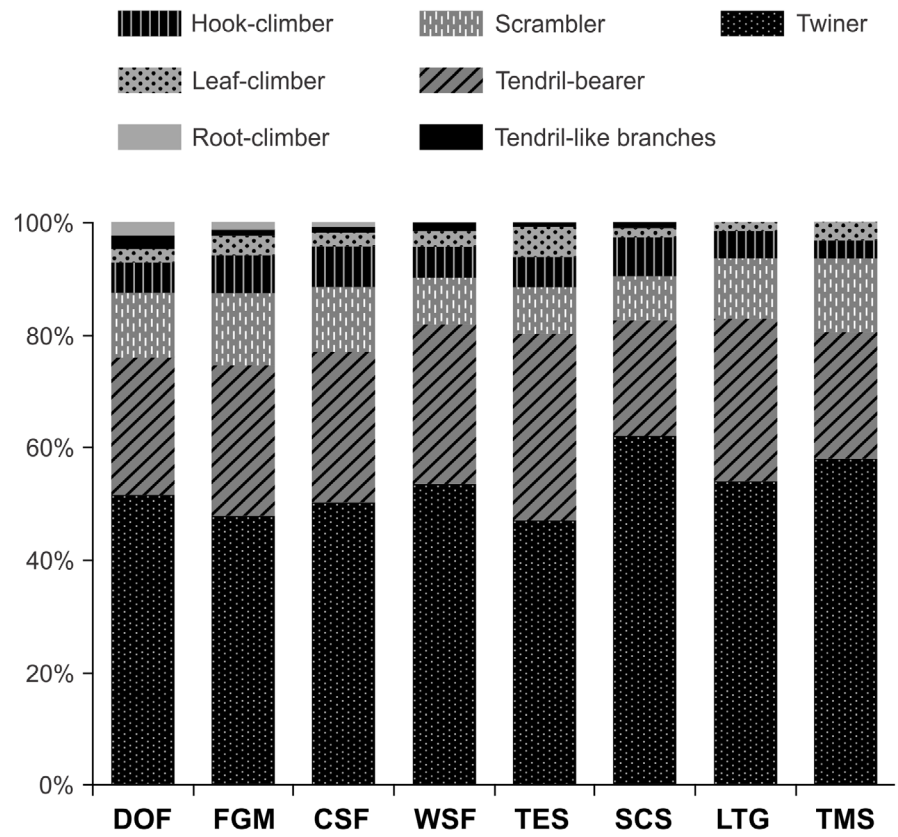

Figure 5. Percentage of species presenting a given climbing mechanism in each vegetation type. DOF: Dense Ombrophilous Forest; CSF: Central Seasonal Forest; FGM: *Araucaria* Forest-Grassland Mosaics; WSF: Western Seasonal Forest; TES: Temperate Shrubland; SCS: Subtropical/Temperate Coastal Scrub; LTG: Low Altitude Temperate Grasslands; TMS: Temperate Savanna.

60 % of the endangered species were vines (56) instead of lianas (38).

The families with the largest numbers of endangered species correspond nearly entirely to the most speciose ones. In Apocynaceae, roughly 45 % of the climbing species are endangered, especially those belonging to *Oxypetalum*. As for Asteraceae, this percentage is not as high (33 %), but all the threatened species belong to *Mikania*. In Fabaceae, however, the 17 % of climbing species that are endangered belong to a greater variety of genera, such as *Lathyrus* and *Vicia*. The complete list of species with corresponding voucher indications, climbing mechanisms, growth forms, and conservation status is available in the Table S2 in supplementary material.

Discussion

The importance of climbing plants, already long recognized for tropical forests, is also beginning to be highlighted for extratropical regions. In southern South America, lianas are important components of forest vegetation types, such as those located in biogeographic and climatic transition regions in southern Brazil (Durigon & Waechter 2011) and temperate forests in Chile (Gianoli *et al*. 2010; Marticorena *et al*. 2010), whereas vines appear to have successfully diversified and occupied more opened vegetation types, assuming a greater importance in multiple non-forest physiognomies (Durigon *et al*. 2014a).

This update to the list of climbing species from Rio Grande do Sul, in addition to revealing a greater number of species than that found in a previous study (Durigon *et al*. 2014b), contributes to a re-evaluation of the importance that is given to climbers in extratropical regions. The state's climbing diversity has been shown to be similar to that registered for trees; there are 533 tree species known for the state (Sobral *et al*. 2013), whereas climbers stand at 448 species.

The two families containing the highest number of climbing genera and species in the flora of Rio Grande do Sul — Apocynaceae and Fabaceae — are also cited amongst the most important families in terms of species number at other geographical sites, including tropical ones (Gentry 1991; Gallagher 2016). Nonetheless, most of the woody species in these families, frequently found in tropical forests, are not so frequent in the study area. In Rio Grande do Sul, these families include predominantly herbaceous climbers, which correspond to approximately 80 % of their climbing species. In the case of Apocynaceae, many genera are derived from the Asclepiadoideae subfamily, amongst which the herbaceous habit is frequent. As for Fabaceae, the findings in this study concur with notes made by Gentry (1991), in which he pointed out the greater prominence of leguminous species in extratropical climbers' floristic compositions, with most of the species belonging to genera different from those commonly found in the tropics (Durigon *et al*. 2014b). Notably, other families known to possess great climbing plant representatives, such as Bignoniaceae, Sapindaceae, and Malpighiaceae, and renowned for supporting a high diversity of woody climbers in tropical regions are not overly representative in the study area. In local scale floristic surveys, however, Seger & Hartz (2014) found that Bignoniaceae and Sapindaceae richness is increased in seasonal sites.

The expressive success of herbaceous twiners and tendril-bearers, which represent more than half of Rio Grande do Sul climbing flora, can be related to the significant variety of more opened ecosystems (grasslands, shrublands, and forest-grassland mosaics) that correspond to more than 60 % of the state's territory. In the Pampa biome, which covers the southernmost part of Rio Grande do Sul, the entire territory of Uruguay, and part of Argentina, herbaceous twining species in the genera *Centrosema*, *Convolvulus*, *Ipomoea*, and *Oxypetalum* are highly frequent (Miotto 1987a; b; Ferreira & Miotto 2009; 2011), as are tendril-bearers belonging to *Lathyrus* and *Vicia* (Bastos & Miotto 1996; Neubert & Miotto 2001). The establishment of herbaceous climbers in more open conditions is favored, considering their production of many small seeds with high abiotic dispersal ability (Grime 2001).

In the case of herbaceous tendril-bearers, stem twiners, or leaf-climbers, their high proportion in extratropical climbing flora, or in some more opened vegetation types, as in the case of TES, can also be attributed to the great abundance of small-diameter supports available (Durigon *et al*. 2014a). In general, these groups of climbers have limitations concerning the upper limit of trunk diameter they can use, with twiners being able to make use of higher diameter supports than tendril-bearers (Putz & Holbrook 1991). Additionally, because leaf-climbers and tendril-bearers climb by using smaller and more specialized structures than those of twiners, who use their stems, they circumvent the need for their stems to coil, an issue which may restrain these plants from inhabiting greater diameter supports, both in relation to stem twiners (Teramura 1991) and in general.

Species distribution

The distribution of climbing species richness in the state is characterized by a high number of species in northern forest physiognomies, with some points of species concentration in small distinctive areas, and a relatively homogeneous dilution of the diversity between the physiognomies in the southern half of the territory. In a more generalist first analysis, this pattern is an expression of the latitudinal gradient of diversity (Willig *et al*. 2003; Schnitzer 2005), but at a smaller scale. Apart from that, the convergence of different floristic elements and the occurrence of many taxa more widely distributed to the north, both of which characterize the forests of the Brazilian southern region

as a transitional area, can explain why they include most of the climbing diversity (Durigon & Waechter 2011). The most striking example is that which occurs in DOF, where many species derived from the highly diverse Mata Atlântica reach their southern limit of distribution, resulting in a high number of species in a small area of the state.

In addition to the association with the latitudinal gradient of species richness and biogeographic factors, the low number of climbing species in predominantly non-forest vegetation types may also be related to small-scale climatic conditions. Although there is no climatic dry season in Rio Grande do Sul, in summer, most of the southern state is affected by low rainfall, particularly in areas with shallow soils (Mota *et al*. 1970). According to Gentry (1991), dry grassland or shrubland areas impose severe constraints for both woody and herbaceous climbers, especially those of tropical origin, an observation which also explained the decline of climber species towards middle-west and southwest migration routes of the state's flora (Durigon & Waechter 2011). Furthermore, in non-forest vegetation types, the requirement for support is likely to be a local environmental filter for some species, especially for woody climbers (Putz & Holbrook 1991; Durigon *et al*. 2014a).

Conversely, the climbing richness distributed across the vegetation types of the southern half of the state cannot be disregarded, considering that these heterogeneous vegetations encompass a distinctive part of both taxonomic and functional climbing diversity. Moreover, considering the scarcity of herbarium records and that no study focusing on this group of plants in native areas of the Pampa biome has been published, it is probable that the data on climbing richness in the different types of vegetation (TES, LTG, SCS and TMS) are underestimated.

As expected, the analysis of floristic similarity showed a clear differentiation between vegetation types of the Mata Atlântica and Pampa biomes. Nevertheless, considering the heterogeneity existing in each biome, there are some internal differences for the richest families and climbing species composition. In the case of the Pampa biome, Subtropical/Temperate Coastal Scrub (SCS) and Temperate Savanna (TMS) (which were isolated from the other units in the cluster analysis) have specific climatic and edaphic conditions which can limit the occurrence of many species. The first vegetation type is distributed along the coastal plain of the state and holds specific soil and salinity conditions. The second type is a small area of dry woodlands and savannas which extends to Argentina, showing a flora with unique characteristics in the state (Leite 2002). This difference may explain the significant dissimilarity of TMS in relation to all vegetation types. In the Mata Atlântica Biome, the cluster analysis separated the Western Seasonal Forest (WSF) from the other vegetation types, even though the richest families are similar. The climbing species composition of this seasonal forest is strongly influenced by the western migration route (Rambo1961), and therefore this diversity is diluted along other forest formations of the state, such as the *Araucaria* Forest-Grassland Mosaics (FGM), and converges with the eastern migration route, in the Central Seasonal Forest (CSF) (Jarenkow & Waechter 2001).

Species conservation status

Regarding the contribution of climbing species, particularly vines, to regional and global extratropical biodiversity and, as supported by the present study, the high number of endangered climbing species, Brazilian conservation policies and environmental impact evaluation studies cannot continue to ignore them. The high proportion of endangered vine species found in the state of Rio Grande do Sul may significantly increase in a short period of time because the Pampa biome is increasingly under threat due to the agricultural conversion of its native non-forest ecosystems (Overbeck *et al*. 2007; 2015), and more recently, due the pressure to explore mineral resources.

Climbers are already recognized as an important group for tropical biodiversity, playing a key role in ecosystem-level processes and providing resources for pollinators and dispersers (Schnitzer & Bongers 2002; Schnitzer 2018) and they are likely to play an important role in extratropical areas as well. It should be noted that the evidence regarding negative effects of climbers on tree growth and carbon storage in the tropics (Schnitzer& Carson 2010; Schnitzer & Bongers 2011; Heijden *et al*. 2015) do not invalidate the need to include them in conservation policies. The results of the present study reinforce this requirement, demonstrating that a large percentage of the species that occur in the state of Rio Grande do Sul are under some degree of threat.

To obtain a better comprehension of the floristic, ecological, and biogeographical patterns of climbing species — or even vegetation types as a whole — at a global scale, it is of the utmost importance that future studies include an increased number of subtropical and temperate sites and take vines and lianas alongside their specificities into account. Even though much remains to be learned regarding the climbing flora of extratropical regions, there is already sufficient information to suggest that they should no longer be neglected.

Acknowledgements

We thank CNPq for the PROTAX (Programa de Capacitação em Taxonomia, Edital MCT/CNPq/MEC/CAPES Nº 52/2010) grant, as well as PhD fellowships of PPA Ferreira and ELC Soares. We also thank Msc. Luiz Fernando Esser for assistance with the maps.

References

Acevedo-Rodríguez P. 2005. Vines and climbing plants of Puerto Rico and the Virgin Islands. Contributions from the United States National Herbarium 51: 1-483.

Alvares CA, Stape JL, Sentelhas PC, Moraes JLG, Sparovek G. 2013. Köppen's climate classification map for Brazil. MeteorologischeZeitschrift 22: 711-728.

Bastos NR, Miotto STS. 1996. O gênero *Vicia* L. (Leguminosae-Faboideae) no Brasil. Pesquisas, Botânica 46: 85-180.

Bhattarai KR, Veetas OR. 2003. Variation in plant species richness of different life forms along a subtropical elevation gradient in the Himalayas, east Nepal. Global Ecology and Biogeography 12: 327-340.

Boldrini II. 2009. A flora dos campos do Rio Grande do Sul. In: Pillar VP, Müller SC, Castilhos ZMS, Jacques AVA. (eds.) Campos Sulinos, conservação e uso sustentável da biodiversidade. Brasília, Ministério do Meio Ambiente. p. 63-77

Brazil Flora Group. 2015. Growing knowledge: an overview of seed plant diversity in Brazil. Rodriguésia 66: 1085-1113.

Citadini-Zanette V, Soares JJ, Martinello CM. 1997. Lianas de um remanescente florestal da microbacia do Rio Novo, Orleans, Santa Catarina. Insula 26: 45-63.

CRIA-Centro de Referência em Informação Ambiental. 2012. SpeciesLink. http://splink.cria.org.br/. 09 Apr. 2018.

Darwin C. 1865. On the movements and habits of climbing plants. Botanical Journal of the Linnean Society 9: 1-118.

Durigon J, Canto-Dorow TS, Eisinger SM. 2009. Composição florística de trepadeiras ocorrentes em fragmentos de floresta estacional, Santa Maria, Rio Grande do Sul, Brasil. Rodriguésia 60: 415-422.

Durigon J, Ferreira PPA, Seger GDS, Miotto STS. 2014b. Trepadeiras na Região Sul do Brasil. In: Villagra BLP, Melo MMRF, Neto SR, Barbosa LM. (eds.) Diversidade e conservação de trepadeiras: contribuição para a restauração de ecossistemas brasileiros. São Paulo, Instituto de Botânica. p. 71-103.

Durigon J, Miotto ST, Gianoli E. 2014a. Distribution and traits of climbing plants in subtropical and temperate South America. Journal of Vegetation Science 25: 1484-1492.

Durigon J, Waechter JL. 2011. Floristic composition and biogeographic relations of a subtropical assemblage of climbing plants. Biodiversity and Conservation 20: 1027-1044.

Ferreira PPA, Miotto STS. 2009. Sinopse das espécies de *Ipomoea* L. (Convolvulaceae) ocorrentes no Rio Grande do Sul, Brasil. Revista Brasileira de Biociências 7: 440-453.

Ferreira PPA, Miotto STS. 2011. Three new species of *Ipomoea* L. (Convolvulaceae) from Southern Brazil. Kew Bulletin 66: 1-6.

Flora do Brasil 2020 [em construção]. 2018. Flora do Brasil 2020 - algas, fungos e plantas. Jardim Botânico do Rio de Janeiro. http://floradobrasil.jbrj.gov.br. 09 Apr. 2018.

Forzza RC, Baumgratz JF, Bicudo CEM, *et al*. 2010. Catálogo de plantas e fungos do Brasil. Vol. I and II. 1st. edn. Rio de Janeiro, Andréa Jakobsson Estúdio/Instituto de Pesquisas do Jardim Botânico do Rio de Janeiro.

Gallagher RV. 2015. Climbing plant diversity in Australia: taxonomy, biogeography and functional traits. In: Schnitzer SA, Bongers F, Burnham RJ, Putz FE. (eds.) Ecology of lianas. Chichester, John Wiley & Sons, Ltd. p. 104-115.

Gallagher RV. 2016. Correlates of range size variation in the Australian seed-plant flora. Journal of Biogeography 43: 1287-1298.

Gallagher RV, Leishman MR, Moles AT. 2011. Traits and ecological strategies of Australian tropical and temperate climbing plants. Journal of Biogeography 38: 828-839.

Gallagher RV, Leishman MR. 2012. A global analysis of trait variation and evolution in climbing plants. Journal of Biogeography 39: 1757-1771.

Gentry AH. 1991. The distribution and evolution of climbing plants. In: Putz FE, Mooney HA. (eds.) The Biology of Vines. Cambridge, Cambridge University Press. p. 3-49.

Gianoli E, Saldana A, Jiménez-Castillo M, Valladares F. 2010. Distribution and abundance of vines along the light gradient in a southern temperate rainforest. Journal of Vegetation Science 21: 66-73.

Grime JP. 2001. Plant strategies, vegetation processes, and ecosystem properties. 2nd. edn. Chichester, John Wiley & Sons.

Guerra E, Streher NS, Lüdtke R. 2015. Plantas trepadeiras do Horto Botânico Irmão Teodoro Luis, sul do Rio Grande do Sul, Brasil. Revista Brasileira de Biociências 13: 201-209.

Hasenack H, Weber E, Boldrini II, Trevisan R. 2010. Mapa de sistemas ecológicos da ecorregião das savanas uruguaias em escala 1:500. 000 ou superior e relatório técnico descrevendo insumos utilizados e metodologia de elaboração do mapa de sistemas ecológicos. http://www.ecologia.ufrgs.br/labgeo/arquivos/Publicacoes/Relatorios/2010/Relatorio_projeto_IB_CECOL_TNC_produto_4.pdf. 10 Apr. 2018.

Hegarty EE, Caballé G. 1991. Distribution and abundance of vines in forest communities. In: Putz FE, Mooney HA. (eds.) The Biology of Vines. Cambridge, Cambridge University Press. p. 313-335.

Heijden GMF, Powers SJ, Schnitzer SA. 2015. Lianas reduce carbon accumulation in tropical forests. Proceedings of the National Academy of Sciences of the United States of America 112: 13267-13271.

Hu L, Mingguang L, Zhen L. 2010. Geographical and environmental gradients of lianas and vines in China. Global Ecology and Biogeography 19: 554-561.

Iganci JRV, Heiden G, Miotto STS, Pennington TR. 2011. Campos de Cima da Serra: the Brazilian Subtropical Highland Grasslands show an unexpected level of plant endemism. Botanical Journal of the Linnean Society 167: 378-393.

Isnard S, Silk WK. 2009. Moving with climbing plants from Charles Darwin's time into the 21st century. American Journal of Botany 96: 1205-1221.

IUCN. 2012. The IUCN Red List of Threatened Species. version 2012.2. http://www.iucnredlist.org

Jarenkow JA, Waechter JL. 2001. Composição, estrutura e relações florísticas do componente arbóreo de uma floresta estacional no Rio Grande do Sul, Brasil. Brazilian Journal of Botany 24: 263-272.

Jiménez-Castillo M, Lusk CH. 2013. Vascular performance of woody plants in a temperate rain forest: lianas suffer higher levels of freeze-thaw embolism than associated trees. Functional Ecology 27: 403-412.

Jurinitz CF, Jarenkow JA. 2003. Estrutura do componente arbóreo de uma floresta estacional na Serra do Sudeste, Rio Grande do Sul, Brasil. Revista Brasileira de Botânica 26: 475-487.

Leite PF. 2002. Contribuição ao conhecimento fitoecológico do sul do Brasil. Ciência & Ambiente 24: 51-73.

Leite PF, Klein RM. 1990. Vegetação. In: Geografia do Brasil: Região Sul. Vol. 2. Rio de Janeiro, IBGE. p.113-150.

Marticorena A, Alarcon D, Abello L, Atala C. 2010. Plantas trepadoras, epífitas y parasitas nativas de Chile. 1st. edn. Concepción, Corporación Chilena de la Madera.

Miotto STS. 1987a. Os gêneros *Canavalia* DC. e *Dioclea* HBK (Leguminosae, Faboideae) no Rio Grande do Sul. Iheringia, Série Botânica 36: 41-55.

Miotto STS. 1987b. Os gêneros *Centrosema* (DC.) Benth. e *Clitoria* L. (Leguminosae, Faboideae) no Rio Grande do Sul. Iheringia, Série Botânica 36: 15-39.

Mota FS, Goedert CO, Lopes NF, Garcez JRB, Gomes AS. 1970. Balanço hídrico do Rio Grande do Sul. Pesquisa Agropecuária Brasileira 5: 1-27.

Neubert EE, Miotto STS. 2001. O gênero *Lathyrus* L. (Leguminosae-Faboideae) no Brasil. Iheringia, Série Botânica 56: 51-114.

Oliveira LC, Citadini-Zanette V, Durigon J, Padilha PT. 2016. As trepadeiras. In: Santos R, Citadini-Zanette V, Elias GA, Padilha PT. (eds.) Biodiversidade em Santa Catarina: Parque Estadual da Serra Furada. Criciúma, UNESC. p. 85-96.

Overbeck GE, Müller SC, Fidelis A, *et al*. 2007. Brazil's neglected biome: The South Brazilian Campos. Perspectives in Plant Ecology, Evolution and Systematics 9: 101-116.

Overbeck GE, Vélez-Martin E, Scrano FR, *et al*. 2015. Conservation in Brazil needs to include non-forest ecosystems. Diversity and Distributions 21: 1455-1460.

Phillips OL, Martínez RV, Mendoza AM, Baker TR, Vargas PN. 2005. Large lianas as hyperdynamic elements of the tropical forest canopy. Ecology 86: 1250-1258.

Pillar VD. 1999. How sharp are classifications? Ecology 80: 2508-2516.

Pillar VD, Müller SC, Castilhos ZMS, Jacques AVA. 2009. Campos Sulinos, conservação e uso sustentável da biodiversidade. 1st. edn. Brasília, Ministério do Meio Ambiente.

Putz EF. 1984. The natural historyof lianas on Barro Colorado Island, Panama. Ecology 65: 1713-1724.

Putz FE, Holbrook NM. 1991. Biomechanical studies of vines. In: Putz FE, Mooney HA. (eds.) The biology of vines. Cambridge, Cambridge University Press. p. 73-98.

Putz FE, Mooney HA. 1991. The biology of vines. 1st. edn. Cambridge, Cambridge University Press.

R Development Core Team. 2018. R: A language and environment for statistical computing. Vienna, R Foundation for Statistical Computing. https://www.R-project.org

Rambo B. 1960. Die südgrenze des brasilianischen regenwaldes. Pesquisas 8: 5-41.

Rambo B. 1961. Migration routes of the South Brazilian rain forest. Pesquisas 12: 5-54.

Rio Grande do Sul. 2014. Lista de espécies da flora ameaçada de extinção no Rio Grande do Sul. https://secweb.procergs.com.br/livlof/?id_modulo=2&id_uf=23&ano=2013. 9 Apr. 2018.

Schnitzer SA. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. American Naturalist 166: 262-276.

Schnitzer SA. 2018. Testing ecological theory with lianas. New Phytologist 220: 366-380.

Schnitzer SA, Bongers F. 2002. The ecology of lianas and their role in forests. Trends in Ecology and Evolution 17: 223-230.

Schnitzer SA, Bongers F. 2011. Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. Ecology Letters 14: 397-406.

Schnitzer SA, Bongers F, Burnham RJ, Putz FE. 2015. Ecology of lianas. 1st. edn. Chinchester, John Wiley & Sons, Ltd.

Schnitzer SA, Carson WP. 2010. Lianas suppress tree regeneration and diversity in treefall gaps. Ecology Letters 13: 849-857.

Schnitzler A, Amigo J, Hale B, Schnitzler C. 2016. Patterns of climber distribution in temperate forests of the Americas. Journal of Plant Ecology 9: 724-733.

Seger GDS, Hartz SM. 2014. Checklist of climbing plants in an Araucaria forest of Rio Grande do Sul State, Brazil. Biota Neotropica 14: 1-12.

Seger GDS, Cappelatti L, Gonçalves LO, Becker FG, Melo AS, Duarte LDS. 2017. Phylogenetic and functional structure of climbing plant assemblages in woody patches advancing over Campos grassland. Journal of Vegetation Science 28: 1187-1197.

Sobral M, Jarenkow JA, Brack P, Irgang B, Larocca J, Rodrigues RS. 2013. Flora arbórea e arborescente do Rio Grande do Sul, Brasil. 2nd. edn. São Carlos, RiMa.

Teramura AH, Gold WG, Forseth IN. 1991. Physiological ecology of mesic, temperate woody vines. In: Putz FE, Mooney HA. (eds.) The biology of vines. Cambridge, Cambridge University Press. p. 245-285.

Thiers B. [continuously updated]. 2018. Index Herbariorum: A global directory of public herbaria and associated staff. New York, New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/science/ih/.

Villagrán C, Hinojosa LF. 1997. Historia de los bosques del sur de Sudamérica, II: Análisis fitogeográfico. Revista Chilena de Historia Natural 70: 241-267.

Willig MR, Kaufman DM, Stevens RD. 2003. Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. Annual Review of Ecology, Evolution, and Systematics 34: 273-309.

Zuloaga FO, Morrone O, Beltrano MJ. 2008. Catálogo de las plantas vasculares Del Cono Sur. Monographs in Systematic Botany from the Missouri Botanical Garden 107: 1-3486.