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Macroscale Analysis of Mistletoe Host Ranges in the Andean-Patagonian Forest

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ABSTRACT

- The number of host species infected by a mistletoe (host range) is critical in that it influences prevalence, virulence and overall distribution of the parasite; however, macroecological analyses of this life history feature are lacking for many regions.
- The Andean-Patagonian forest, found along the southern Andes from 35°S to Tierra del Fuego 55°S, contains twelve mistletoe species in three families (Loranthaceae, Misodendraceae and Santalaceae). By tabulating herbarium records, the host ranges and geographical distributions of these mistletoes were explored.
- Our results show that these parasites occur on 43 plant species in 24 families but with varying degrees of specificity. All *Misodendrum* species and *Desmaria mutabilis* (Loranthaceae) are specialists that use *Nothofagus* as their primary hosts. *Tristerix* and *Notanthera* (Loranthaceae) and *Antidaphne* and *Lepidoceras* (Santalaceae) are generalists parasitizing more than six host species from several genera and families. Even though many of the mistletoe species are sympatric, there is low overlap in host use.
- Our data show that in the southern South American bioregion, generalist mistletoes have smaller geographic ranges than specialists. This contrast with a previous hypothesis that predicted mistletoes with large geographic ranges would also have large host ranges, and conversely less diverse regions would have more specialized mistletoes.

KEYWORDS: Andes, competitive exclusion, host specificity, parasitic plants, South America

INTRODUCTION

Parasitic angiosperms constitute over 4700 species in 277 genera and this nutritional mode has evolved independently 12 times (Nickrent 1997 onwards). These heterotrophic plants exhibit many different growth habits including annual or perennial herbs, shrubs and trees (Kuijt, 1969). All

parasitic plants connect to conductive tissues in the host's stems or roots through modified roots called haustoria (Kuijt, 1969; Press *et al.*, 1999); however, the degree of host dependence and number of hosts utilized varies considerably among species. Santalales is the largest clade of parasitic plants with 179 genera and over 2400 species. Within this clade are parasites that occur on host branches and these are generally referred to as mistletoes (Mathiasen *et al.*, 2008). A total of 87 genera and at least 1670 mistletoe species have been named and these are classified by Nickrent *et al.* (2010) in five families: Amphorogynaceae, Loranthaceae, Misodendraceae, Santalaceae in part (the former Eremolepidaceae) and Viscaceae. The vast majority of mistletoe species reside in two families, Loranthaceae (76 genera/1044 species) and Viscaceae (7/570). Previous studies estimated that aerial parasitism in the order evolved ca. 80 mya in the lineage that lead to Misodendraceae, followed by Viscaceae (72 mya), eremolepidaceous mistletoes in Santalaceae (53 mya) and most recently in Loranthaceae (50 mya) (Vidal-Russell & Nickrent, 2008b; Liu *et al.*, 2018).

Mistletoes are present on all continents with the exception of Antarctica. In South America, hundreds of mistletoe species occur in tropical seasonal and tropical rainforest biomes whereas significantly fewer occur in the southern South American bioregion. The temperate Andean-Patagonian forest (Bosque Andino Patagónico) is located between 35°S and 55°S latitude on both sides of the Andes mountain range in Argentina and Chile, and the dominant trees are members of the genus *Nothofagus* Blume. It is composed of two main ecoregions: the Magellanic and the Valdivian forests (Moreira-Muñoz, 2011). The latter of which is more biodiverse. Armesto *et al.* (1996) have proposed that this forest represents a biogeographic island because of its isolation from other continental forests. The flora of this ecoregion shows greater affinity with those in New Zealand than with others in the Neotropical biogeographic realm (Wardle *et al.*, 2001). It is composed of 185 woody species that represents a mixture of austral, boreal, endemic (24%), neotropical and tropical lineages (Aizen & Ezcurra, 1998). Most species are shrubs (57%), followed by trees (22%), climbing plants (15%) and 6% are aerial parasites (Aizen & Ezcurra, 1998; Aizen & Ezcurra, 2008).

The Andean-Patagonian forests harbour 12 mistletoe species, some of which are sympatric in the northern area (Table 1, Fig. 1). These mistletoes belong to three families: Loranthaceae, Misodendraceae and Santalaceae (Fig. 2). Santalaceae, as defined in Nickrent *et al.* (2010), is composed of 11 genera of neotropical root and stem parasites but only three are mistletoes: *Antidaphne* Poepp. & Endl., *Lepidoceras* Hook.f., and *Eubrachion* Hook.f. The first two genera are present in the Andean-Patagonian temperate forests. These three genera have previously been considered a distinct family, Eremolepidaceae (Kuijt & Hansen, 2015), however, molecular data show they are embedded within Santalaceae s. str. The “eremolepidaceous” mistletoes were shown to be monophyletic by Der & Nickrent (2008). For Loranthaceae, only three species in three genera are found in the Andean-Patagonian temperate forests: *Desmaria* Tiegh., *Notanthera* G.Don and *Tristerix* Mart.. *Desmaria* and *Notanthera* are monospecific and endemic to Chile (Barlow & Wiens, 1973; Kuijt, 1985; Vidal-Russell & Nickrent, 2008a). *Tristerix* has 13 species distributed along the Andes and the central Sierra in Argentina (Kuijt, 1988; Amico *et al.*, 2007; Amico & Nickrent, 2009; Kuijt, 2014), however, only one species, *T. corymbosus* (L.) Kuijt, has a range extending south into this bioregion. Misodendraceae with a single genus *Misodendrum* DC, contains 8 species (Vidal-Russell & Nickrent, 2007) all of which are endemic to the Andean-Patagonian forest. Most mistletoes have fleshy fruits and sticky viscin on their seeds that facilitates attachment to host branches after dispersal (Mathiasen *et al.*, 2008). In contrast, *Misodendrum* species have dry fruits provided with long feathery staminodes. These achenes are dispersed by wind and, after entangling on tree branches, germinate and parasitize the host.

The relationship between mistletoe species and their hosts has been examined from many perspectives and from these have emerged various terms such as host range, choice, susceptibility, preference, selectivity and specificity. As discussed by Watson (2017), host range (the number of host species infected by a particular parasite) is crucial when examining life history factors for parasites in that it influences prevalence, virulence and overall distribution, but comparative approaches to determine the underlying causes for host range differences are impeded by sampling artefacts. The majority of the literature dealing with host-mistletoe relationships report lists of various combinations

but lack quantitative data. For example, detailed lists of host-mistletoe combinations have been reported for dwarf mistletoes (*Arceuthobium* M.Bieb.) where hosts are classified as principal, secondary, occasional, rare and immune (Hawksworth & Wiens, 1972; Hawksworth & Wiens, 1996); however, such rankings do not measure the frequency with which a host species is parasitized. The mistletoe host range diversity statistic (K_Q) introduced by Kavanagh & Burns (2012) incorporates information on host range (species richness) as well as sampling effort and this metric can provide a measure of host generality and specificity.

The host ranges of the 12 mistletoe species occurring within the Andean-Patagonian forest have not been previously summarized and this study will provide macroecological data useful in filling that void. In addition, we will examine whether the latitudinal range and number of collection vouchers from different mistletoe species are associated with the total host number for each species. Previous studies hypothesize that mistletoes in diverse regions tend to be host generalists, whereas mistletoes in depauperate regions tend to be host specialists (Barlow, 1977; Norton & Carpenter, 1998). We expect that in the Andean-Patagonian forest mistletoes will tend to be host specialists (i.e., with small host ranges). In addition, we predict, that those Patagonian mistletoes with larger geographic ranges will also have larger host ranges (i.e., are generalists).

METHODS

Several herbaria were visited to record the host ranges of all mistletoe species that grow in the Andean-Patagonian forest: BCRU (Bariloche, Argentina), CONC (Concepción, Chile), CTES (Corrientes, Argentina), CORD (Córdoba, Argentina), MA (Madrid, Spain), MO (Saint Louis, USA) and SI (Buenos Aires, Argentina). Each voucher was examined and identified to species level. The host species was registered if this information was available on the label or if the host was collected together with the mistletoe. A data matrix was constructed with the information present on the voucher label (i.e. species, host, collector, date, locality, altitude and geographic coordinates when available). Duplicate specimens were excluded from the matrix; however, records from the same

locality were included. One of the eight species of *Misodendrum* (*M. macrolepis* Phil.) had only a few and very old collections (before 1870), thus this species was excluded from this study. Ten of the 12 mistletoe species found in the Andean-Patagonian forest are endemic; for the two that are not (*Tristerix corymbosus* and *Notanthera heterophylla* (Ruiz & Pav. G.Don), only the specimens collected within the temperate forest were considered for analysis. It is known that biases associated with herbarium data exist, e.g., collector bias (Garcillán & Ezcurra, 2011); however, herbarium data can be used as a good approximation for general patterns and as a first approximation for a geographical region. This approach has been used in other mistletoe studies (Downey, 1998; Norton & De Lange, 1999).

For each mistletoe species we calculated host range (richness) as the number of host species reported. To detect methodological bias associated with herbarium vouchers, we analysed the relationship between host range and the number of herbarium records for all mistletoe species in the forest. We also analysed the relationship between host range and maximum latitudinal range for all mistletoe species. These analyses, together with host ranges, will determine mistletoe specificity. In addition, we calculated the K_Q proposed by Kavanagh & Burns (2012) to take into consideration sample effort differences between species. The K_Q value, equivalent to other measures of host diversity (e.g. the Shannon index), incorporates information on relative abundances and species richness. We obtained K_Q for the species and genus level with this formula: $K_Q = \beta / (\alpha + 1)$, where β is host range and α is redundant collection records. When the number of recorded host species is high and the number of redundant collection records is low, K_Q will take high values, indicative of host generality and an even distribution among host species (Kavanagh & Burns, 2012). The analyses were restricted to native host species; however, we registered when exotic hosts were mentioned on herbarium labels. All variables were log transformed and the data were fit to a simple regression model as carried out in R (RCoreTeam, 2017).

RESULTS

We found that mistletoes parasitize 43 host plant species in 34 genera and 24 families in the Andean-Patagonian forest (Table 1, Table S1). These mistletoe species parasitize a wide range of families spanning 21 orders of angiosperms and gymnosperms. Host range differed among mistletoe species. Eight mistletoe species are specialists, parasitizing mainly one plant genus, while the remaining four species are generalists. All *Misodendrum* species and *Desmaria mutabilis* Tiegh. mainly parasitize *Nothofagus* species (Nothofagaceae) and thus are considered specialists; however, two rare host combinations were found, *Misodendrum brachystachyum* DC on *Caldcluvia paniculata* D.Don (Cunoniaceae) and *Desmaria mutabilis* on *Weinmannia trichosperma* Cav. (Cunoniaceae). *Tristerix*, *Notanthera*, *Antidaphne* and *Lepidoceras* are all generalist mistletoes that parasitize more than six host species from several genera and families (Table 1). *Tristerix corymbosus* (Loranthaceae) is a highly generalist species parasitizing a total of 22 species in 21 genera and 18 families just within the study region.

Among Patagonian mistletoes, there are two cases of epiparasitism: *Lepidoceras chilense* (Molina) Kuijt parasitizing *Tristerix corymbosus*, and *T. corymbosus* parasitizing *Desmaria mutabilis*. In northwest Patagonia, *Misodendrum brachystachyum* was the only species in the genus parasitizing exotic hosts: *Cytisus scoparius* (L.) Link (Fabaceae) and *Castanea sativa* Mill. (Fagaceae). *Tristerix corymbosus* was found to parasitize more than 10 exotic species (Table S2), the most frequent being *Populus* L. and *Salix* L. (Salicaceae).

The latitudinal geographic ranges between Patagonian mistletoes are different. *Misodendrum* species have a wide (more than 8 degrees latitude) distributional range and primarily parasitize few species (Table 1). Except for *T. corymbosus*, species within Loranthaceae and Santalaceae have narrower distributional ranges and the number of host species parasitized per mistletoe species is similar to that of *Misodendrum*. The geographic distribution was negatively associated with host range but not significant (Fig. 3a, $R^2 = 0.233$, $P = 0.273$). At the genus level, the geographic distribution was significantly negative (Fig. 3b, $R^2 = 0.396$, $P = 0.033$).

Three mistletoe species, *Misodendrum punctulatum* Banks ex DC., *M. linearifolium* DC. and *Tristerix corymbosus* were frequently collected (>50 specimens) whereas *Desmaria mutabilis*, *Antidaphne punctulata* (Clos) Kuijt, *Lepidoceras chilense* and the remaining *Misodendrum* species were the least collected with less than 35 specimens each (Table 1). The number of voucher specimens was not associated with parasite host range (Fig. 3c, $R^2 = 0.307$, $P = 0.061$). The vouchers for each of the mistletoe species show that most use less than 10 host species. *Tristerix corymbosus* can be considered an exception since it uses a large number of host species and has been frequently collected. K_Q of the Patagonian mistletoe to species level varies from 0.06 to 2.0, the lowest were for the two most frequent *Misodendrum* species (*M. punctulatum* and *M. linearifolium*) and the highest also to a *Misodendrum*, *M. gayanum* Tiegh. (Table 1). K_Q at the genus level varies from 0.01 to 0.78, the lowest being *M. punctulatum* and *M. linearifolium* and the highest *Antidaphne punctulata*.

DISCUSSION

Among the 185 woody species available in the Andean-Patagonian forest, mistletoes parasitize 43 species in 23 families. Eight mistletoes (seven *Misodendrum* species and *Desmaria mutabilis*) were specialist, while the remaining four species (*Tristerix corymbosus*, *Notanthera heterophylla*, *Antidaphne punctulata* and *Lepidoceras chilense*) are generalists. Even though many of the mistletoe species are sympatric, there was low overlap in host use by these mistletoes. It has been proposed that temperate forests mistletoes are likely to be specific to one genus or few host species (Norton & Carpenter, 1998; Norton & De Lange, 1999; Okubamichael *et al.*, 2016). According to our results, this statement applies only to *Misodendrum* spp. and *Desmaria*, but not for the other mistletoe species. However; if each of the two ecoregions within the temperate forest are examined separately, then the less diverse Magellanic forest contains only specialist mistletoes. New Zealand mistletoes have a similar pattern as the one we report here, where some species have larger host ranges than others (Norton & De Lange, 1999). These authors evaluated the host specificity for the five loranthaceous species in New Zealand. They found that three species (*Alepis flavida* Tiegh, *Peraxilla*

colensoi (Hook.f.) Tiegh. and *P. tetrapetala* (L.f.) Tiegh.) are host specific and parasitize mainly species of *Nothofagus*, whereas *Tupeia antarctica* Cham. & Schltdl. and *Ileostylus micranthus* Tiegh. parasitize a wide range of host species.

It is interesting that the two host specialist mistletoes (*Misodendrum* and *Desmaria*) primarily parasitize *Nothofagus* spp. but for both genera, rare hosts are found in the same family, Cunoniaceae. The reason for this is unknown but may indicate that certain anatomical, physiological or biochemical properties required for mistletoe establishment that are met by both hosts, despite being from distantly related families. Misodendraceae includes those mistletoes with the widest latitudinal ranges in the Andean-Patagonian forest and these were the ones with the smallest host ranges, thus indicating specialization. These two mistletoe genera, that show restricted hosts, have different modes of dispersal: the fruits of *Misodendrum* are wind dispersed while those of *Desmaria* are animal dispersed.

Among the mistletoes that are host generalists in the Andean-Patagonian forest, none appear to parasitize hosts that share recent common ancestors. Interestingly, there is no overlap in host use between generalist and specialist mistletoes. This is surprising because *Nothofagus*, the host genus parasitized by the specialist mistletoes, is the dominant tree in the Andean-Patagonian forests. Moreover, *Tristerix corymbosus*, the most collected mistletoe species, is a host generalist that does not parasitize *Nothofagus* (or Cunoniaceae). These observations also support the fact that our results are not biased by sampling. All host generalist mistletoes are dispersed by animals and there appears to be no relationship between dispersal mode and host range.

The intensity of mistletoe parasitism has been explored for three species of the temperate forest. *Tristerix corymbosus*, a host generalist, showed less than 2 mistletoe infections per host tree at one site (García *et al.*, 2009). The mistletoe host specialist, *Misodendrum punctulatum* and *M. linearifolium*, were studied at three sites. These mistletoes showed higher numbers (from 3 to 8) of infections per host tree (Vidal-Russell & Premoli, 2015). According to these studies, host specialists have greater infection intensity than generalists.

The K_Q values for mistletoes of the Andean-Patagonian forest are within the ranges of those reported for Australian mistletoe (Kavanagh & Burns, 2012). That study showed that K_Q ranged from 0 to 5.0 across all Australia. In the Andean-Patagonian forest, the values for K_Q are low, if we disregard the K_Q of 2.0 for *M. gayanum*, the highest value. Hence, the K_Q values give similar results on specificity; however, these numbers have to be considered with caution because they are affected by sample size (here number of herbarium records) and how the diversity of hosts is calculated. For example, *Misodendrum gayanum* parasitizes four different *Nothofagus* species, but only five records were seen. This inflates the K_Q value to 2.0 giving the false impression that this is the most generalist mistletoe in this study (Table 1). If one considers only the number of host genera, the value for *M. gayanum* drops by an order of magnitude and is more comparable to values seen in other species. Another undesirable aspect of the K_Q statistic is that high numbers of records push the K_Q value lower, despite comparatively high numbers of different hosts parasitized. This is best seen with *Tristerix corymbosus* that is clearly the most generalist parasite among the mistletoes studied, yet its K_Q value is in the range of the *Misodendrum* specialists. This artefact is not corrected by using host genera instead of species. The number of collections would have to be less than 47 for the K_Q value to surpass that of *Antidaphne*. Our study shows that the use of the K_Q index is subject to bias based on sample size. This statistic might be improved by incorporating stopping rules similar to those employed in field surveys of mistletoes (Watson *et al.*, 2017).

Mistletoe epiparasitism occurs worldwide; however, it is most common in the tropics and subtropics (Wilson & Calvin, 2016). Epiparasitism also occurs in the Andean-Patagonian forest. One of the cases we found in this study *Lepidoceras chilense* on *Tristerix corymbosus* has been previously reported (Wilson & Calvin, 2016), but the case of *T. corymbosus* parasitizing *Desmaria mutabilis* is a new record.

The geographic range width of Andean-Patagonian forest mistletoes show negative relationship with the number of host species and genera they parasitized. Specialist mistletoes were not the ones with restricted distributions as was predicted. The distributions of generalist mistletoes reach only up to 42° South, while the specialists (*Misodendrum*) have a larger distributional range. At least for the

southern South American bioregion, generalist mistletoes have smaller geographic ranges than specialists. In contrast to our results, host ranges of Australian mistletoes are not associated with their geographic ranges (Grenfell & Burns, 2009).

Mistletoes in floristically diverse regions tend to be host generalists whereas mistletoes in depauperate regions tend to be host specialists (Barlow, 1977; Norton & Carpenter, 1998). Kavanagh & Burns (2012) provided evidence supporting this hypothesis for several Australian mistletoes. Because the Andean-Patagonian forest is not very diverse, we expected to find specialist mistletoes; however, we found four generalist mistletoe species (two Santalaceae, two Loranthaceae). It appears that host specificity is not related only to the diversity of potential host species available but also to the interaction between potential hosts species with the mistletoe, and also with mistletoe competition.

In South Africa, mistletoe species rarely share the same primary host in a local area, especially if the species are from different families (Okubamichael *et al.*, 2016). The authors speculated that this could be an example of competitive exclusion, a process that contributes to a geographic mosaic of mistletoe-host interactions. Competitive exclusion has been implicated for other mistletoes such as *Arceuthobium* in North America (Hawksworth & Wiens, 1972; Jerome & Ford, 2002). For these dwarf mistletoes, there is overlap in host usage by at least two mistletoe species, thus suggesting that competition is currently taking place. In other mistletoes, such as the three sympatric species of Amazonian *Psittacanthus* studied by Fadini (2011), no overlap in host use was detected. In this case, one must assume that no competition is taking place, especially when artificially inoculated seeds fail to establish on such non-host trees. This appears to be the situation in the Andean-Patagonian forest where *Tristerix corymbosus* does not share hosts with *Misodendrum* species and *Desmaria mutabilis*. We can, however, hypothesize that competitive exclusion may have happened in the past and that a consequence of that process is that no host overlap exists today. This process could have acted as a reinforcement of a host-parasite coevolutionary arm race leading to host specificity in *Misodendrum* and *Desmaria*. The interaction dynamics between potential hosts species and several sympatric mistletoe species may lead to non-overlapping host use patterns as is currently seen with *Antidaphne*, *Tristerix* and *Lepidoceras* in the temperate forest. Even mistletoe species in the same family

(Loranthaceae) use different hosts in the same area. This lack of overlap suggests field studies to collect empirical data to directly address the causes of this observation.

The genus *Misodendrum* (with 8 species) that only parasitizes *Nothofagus* supports the concept that mistletoes in depauperate regions tend to be host specialists. This evolutionary outcome can be explained by the presence of selection favouring close physiological adaptations of the mistletoes to the predominant host species (Barlow, 1977; Dean *et al.*, 1994; Downey *et al.*, 1997). Features shared by *Nothofagus* forests of New Zealand, Chile and Argentina are that some mistletoe species are host specialists at the genus level (*Nothofagus*) whereas others parasitize multiple genera (Norton & De Lange, 1999). This observation may be evidence that for some mistletoes, strong physiological co-adaptation arose early in their evolutionary history whereas for others the host-mistletoe combination is of more recent origin. In these cases the mistletoes are not capable of parasitizing *Nothofagus* trees but instead parasitize other species from the community.

CONCLUSIONS

The Andean-Patagonian temperate forests show unique host utilization patterns among its component mistletoes. We provide evidence that contradicts a previous hypothesis that predicted mistletoes with large geographic ranges would also have large host ranges and conversely less diverse regions would have more specialized mistletoes. Host abundances and biogeographic history of hosts and parasites might be important factors to consider for understanding host range in this biome.

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FIGURE LEGENDS

Fig. 1. Distribution map of the three mistletoe families within the Andean-Patagonian temperate forest. Green shading represents the Valdivian forest and tan shading the Magellanic forest. Collections of *Notanthera heterophylla* and *Tristerix corymbosus* from outside the temperate forest (Chilean Matorral) are not shown (see text).

Fig. 2. Representatives of mistletoes from the Andean-Patagonian forest. A. *Antidaphne punctulata* (Santalaceae) prefloral shoots. B. *Lepidoceras chilense* (Santalaceae) with young fruits. C. *Desmaria mutabilis* (Loranthaceae) at anthesis. D. *Notanthera heterophylla* (Loranthaceae) inflorescence. E. *Tristerix corymbosus* (Loranthaceae), the quintral, in full flower with snow. E. *Misodendrum linearifolium* (Misodendraceae) shoots with fruits bearing plumose staminodes. Photo credits: A. Gerhard Glatzel, the remaining G. Amico.

Fig. 3. For the 12 mistletoe species of Andean temperate forest, relationships between geographic range size and the number of host species (A), geographic range size and host genera (B) and number of records and number of host species (C).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article

Table S1. Number of observations for each host species used by the 12 mistletoe species in the Andean temperate forests. Families and orders follows APG IV (2016).

Table S2. Exotics species used by *Tristerix corymbosus*.

Table 1. Mistletoe species present in Andean-Patagonian temperate forest

Species	Northern limit (S)	Southern limit (S)	Altitudinal range (m)	Latitudinal range (degrees)	No. hosts	No. genera	No. families	No. orders	No. records	K _Q species	K _Q genera
Santalaceae											
<i>Antidaphne punctulata</i>	37° 15'	42° 15'	0 - 1350	5.03	7	7	5	5	15	0.78	0.78
<i>Lepidoceras chilense</i>	36° 15'	42° 30'	0 - 2000	6.22	9	8	6	5	23	0.60	0.60
Misodendraceae											
<i>Misodendrum angulatum</i>	36° 32'	52° 21'	0 - 1350	15.80	3	1	1	1	18	0.19	0.06
<i>Misodendrum brachystachyum</i>	35° 21'	54° 32'	0 - 1500	19.19	6	2	2	2	30	0.24	0.07
<i>Misodendrum gayanum</i>	37° 25'	46° 23'	0 - 1300	8.97	4	1	1	1	5	2.00	0.20
<i>Misodendrum linearifolium</i>	35° 15'	52° 33'	0 - 2500	17.94	6	1	1	1	80	0.08	0.01
<i>Misodendrum oblongifolium</i>	35° 21'	45° 16'	0 - 2000	9.91	4	1	1	1	31	0.14	0.03
<i>Misodendrum</i>	36° 31'	55° 02'	0 - 1700	18.02	6	1	1	1	101	0.06	0.01

*punctulatum**Misodendrum
quadriflorum*

36° 30'	54° 04'	0 - 1500	17.55	3	1	1	1	34	0.09	0.03
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Loranthaceae*Tristerix
corymbosus**

33° 30'+	42° 25'	0 - 2400	8.91	22	21	19	17	167	0.15	0.14
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*Notanthera
heterophylla**

34° 26'+	42° 25'	0 - 1500	8.07	8	8	5	4	34	0.30	0.30
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*Desmaria
mutabilis*

35° 20'	41° 20'	0 - 1800	5.98	5	2	2	2	28	0.21	0.07
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+ Northern limit in the temperate forest

* Species that occur in the Chilean matorral, *Tristerix corymbosus* at to 30° 9' S and *Notanthera heterophylla* at to 32° 19' S





