


## RESEARCH PAPER

# Macroscale analysis of mistletoe host ranges in the Andean-Patagonian forest

G. C. Amico<sup>1</sup> , D. L. Nickrent<sup>2</sup>  & R. Vidal-Russell<sup>1</sup> <sup>1</sup> Laboratorio Ecotono, INIBIOMA CONICET, Universidad Nacional del Comahue, Bariloche, Río Negro, Argentina<sup>2</sup> Department of Plant Biology, Southern Illinois University, Carbondale, IL, USA**Keywords**

Andes; competitive exclusion; host specificity; parasitic plants; South America.

**Correspondence**

G. C. Amico, Laboratorio Ecotono, INIBIOMA CONICET, Universidad Nacional del Comahue, Quintral 1250, Bariloche, Río Negro, Argentina.

E-mail: guillermo.amico@comahue-conicet.gov.ar

**Editor**

D. Byers

Received: 14 June 2018; Accepted: 12 August 2018

doi:10.1111/plb.12900

**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 utilised 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 leads 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 rain forest biomes,

**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 at 55 °S, contains 12 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. Although 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 specialised mistletoes.

whereas significantly fewer occur in the southern South American bioregion. The temperate Andean-Patagonian forest (Bosque Andino Patagónico) is located between 35 and 55 °S 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 represent 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, 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

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

species	northern limit (s)	southern limit (s)	altitudinal range (m)	latitudinal range (°)	no. hosts	no. genera	no. families	no. orders	no. records	K <sub>Q</sub> species	K <sub>Q</sub> 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 punctulatum</i>	36° 31'	55° 02'	0–1700	18.02	6	1	1	1	101	0.06	0.01
<i>Misodendrum quadriflorum</i>	36° 30'	54° 04'	0–1500	17.55	3	1	1	1	34	0.09	0.03
Loranthaceae											
<i>Tristerix corymbosus</i> <sup>b</sup>	33° 30' <sup>a</sup>	42° 25'	0–2400	8.91	22	21	19	17	167	0.15	0.14
<i>Notanthera heterophylla</i> <sup>b</sup>	34° 26' <sup>a</sup>	42° 25'	0–1500	8.07	8	8	5	4	34	0.30	0.30
<i>Desmaria mutabilis</i>	35° 20'	41° 20'	0–1800	5.98	5	2	2	2	28	0.21	0.07

<sup>a</sup>Northern limit in the temperate forest.

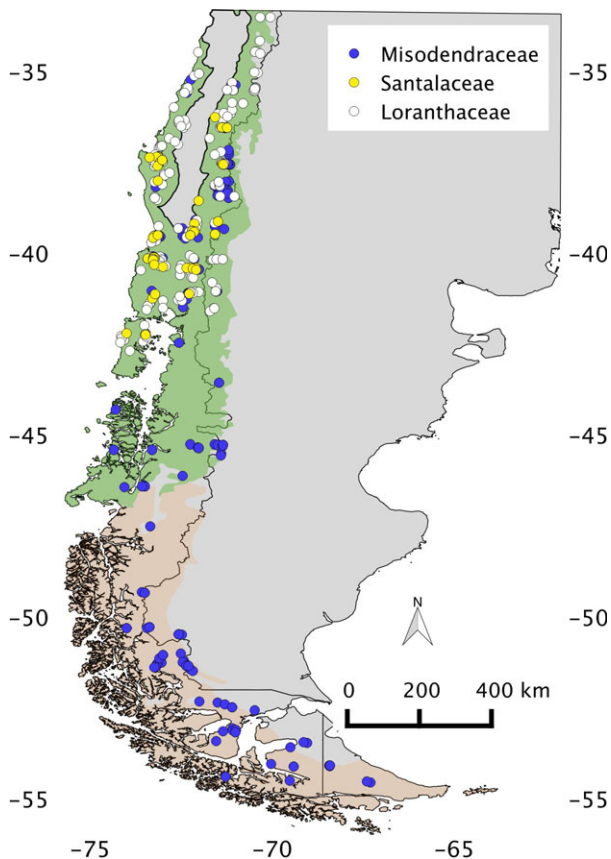
<sup>b</sup>Species that occur in the Chilean matorral, *Tristerix corymbosus* at 30°9' S and *Notanthera heterophylla* at 32°19' S.

embedded within *Santalaceae sensu stricta*. The 'remolepidaceous' 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, 2014; Amico *et al.* 2007; Amico & Nickrent 2009); however, only one species, *T. corymbosus* (L.) Kuijt, has a range extending south into this bioregion. *Misodendraceae*, with a single genus *Misodendrum* DC, contains eight 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 entanglement 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 *et al.* (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, 1996); however, such rankings do not measure the frequency with which a host species is parasitized. The mistletoe host range diversity statistic (K<sub>Q</sub>) 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 summarised, 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 hypothesise that mistletoes in diverse regions tend to be host generalists, whereas mistletoes in depauperate regions tend to be host specialists (Barlow & Wiens 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



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

addition, we predict, that those Patagonian mistletoes with larger geographic ranges will also have larger host ranges (*i.e.* generalists).

**MATERIAL AND 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*

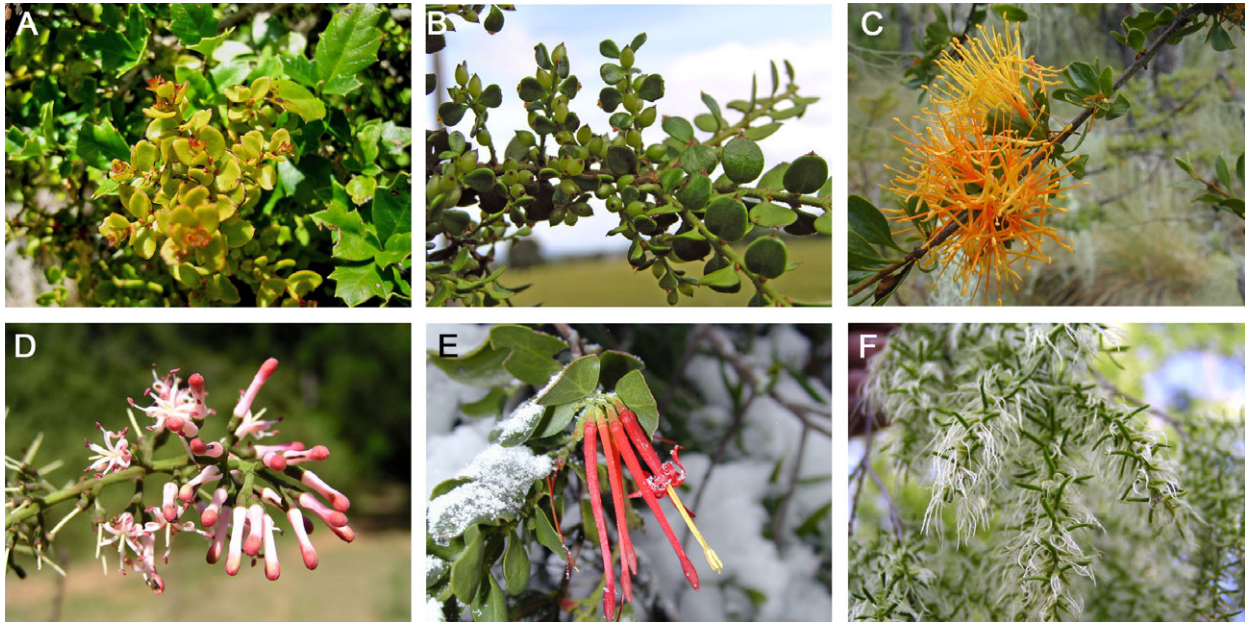
*heterophylla* Ruiz & Pav. G.Don) only the specimens collected within the temperate forest were considered for analysis. It is known that biases associated with herbarium data exist, *e.g.* collector bias (Garcillán & Ezcurra 2011); however, herbarium data can be used as a good approximation for general patterns and as a first approximation for a geographic 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  $\beta$  is host range and  $\alpha$  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 recorded 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 (R Core Team 2017).

**RESULTS**

We found that mistletoes parasitize 43 host plant species in 34 genera and 24 families in the Andean-Patagonian forest (Tables 1, 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, *M. brachystachyum* DC on *Caldecluvia paniculata* D.Don (*Cunoniaceae*) and *D. 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). *T. 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 *T. corymbosus*, and *T. corymbosus* parasitizing *D. mutabilis*. In northwest Patagonia, *M. brachystachyum* was the only species in the genus parasitizing exotic hosts: *Cytisus scoparius* (L.) Link (*Fabaceae*) and *Castanea sativa* Mill. (*Fagaceae*). *T. corymbosus* was found to parasitize more than ten exotic species (Table S2), the most frequent being *Populus* L. and *Salix* L. (*Salicaceae*).



**Fig. 2.** Representative 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. F: *Misodendrum linearifolium* (Misodendraceae) shoots with fruits bearing plumose staminodes. Photo credits: A. Gerhard Glatzel, the remaining G. Amico.

The latitudinal geographic ranges between Patagonian mistletoes are different. *Misodendrum* species have a wide ( $>8^\circ$  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 this was not significant (Fig. 3A;  $R^2 = 0.233$ ,  $P = 0.273$ ). At the genus level, the geographic distribution was significantly negative (Fig. 3B;  $R^2 = 0.396$ ,  $P = 0.033$ ).

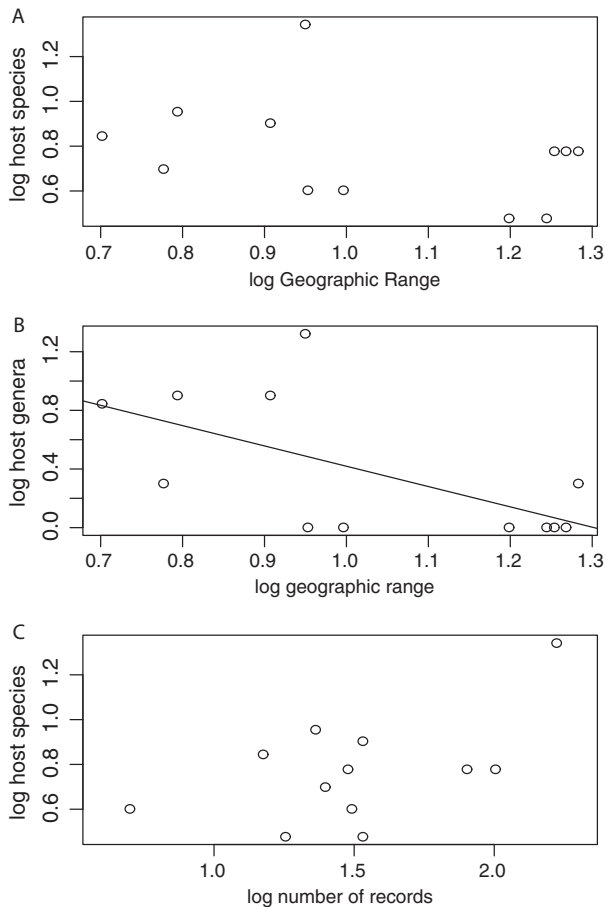
Three mistletoe species, *M. punctulatum* Banks ex DC., *M. linearifolium* DC. and *T. corymbosus* were frequently collected ( $>50$  specimens) whereas *Desmaria mutabilis*, *Antidaphne punctulata* (Clos) Kuijt, *Lepidoceras chilense* and the remaining *Misodendrum* species were the least collected, with  $<35$  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 ten host species. *T. 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  $K_Q$  were for the two most frequent *Misodendrum* species (*M. punctulatum* and *M. linearifolium*) and the highest also for 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 *A. 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 specialists, while the remaining four species (*Tristerix corymbosus*, *Notanthera heterophylla*, *Antidaphne punctulata* and *Lepidoceras chilense*) were generalists. Although many of the mistletoe species are sympatric, there was low overlap in host use by these mistletoes. It has been proposed that temperate forest mistletoes are likely to be specific to one genus or a 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 to 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 that reported 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. & Schltld. 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 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 specialisation. These two mistletoe genera that show restricted hosts have different



**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).

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, *T. 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. *T. corymbosus*, a host generalist, showed less than two mistletoe infections per host tree at one site (García *et al.* 2009). The mistletoe host specialists, *M. punctulatum* and *M. linearifolium*, were studied at three sites. These mistletoes showed higher numbers (from three to eight) 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 mistletoes (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*, which had 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, *M. 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 *T. 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 shows a 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° S, 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 & Wiens 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 host 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 *T. corymbosus* does not share hosts with *Misodendrum* species and *D. mutabilis*. We can, however, hypothesise 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 arms race leading to host specificity in *Misodendrum* and *Desmaria*. The interaction dynamics between potential host 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 the need for field studies to collect empirical data to directly address the causes of this observation.

The genus *Misodendrum* (with eight 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 dominant host species (Barlow & Wiens 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 utilisation 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 specialised mistletoes. Host abundances and biogeographic history of hosts and parasites might be important factors to consider for understanding host range in this biome.

## ACKNOWLEDGEMENTS

We thank the curators of the various herbaria visited for their assistance in collecting the specimen data used in this paper. Special thanks to Javier Puntieri for comments. Authors GCA and RVR were supported by Consejo Nacional de investigaciones Científicas y Técnicas (CONICET).

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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

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

## REFERENCES

- Aizen M.A., Ezcurra C. (1998) High incidence of plant–animal mutualisms in the woody flora of the temperate forest of South America: biogeographical origin and present ecological significance. *Ecología Austral*, **8**, 217–236.
- Aizen M.A., Ezcurra C. (2008) Do leaf margins of the temperate forest flora of southern South America reflect a warmer past? *Global Ecology and Biogeography*, **17**, 164–174.
- Amico G.C., Nickrent D.L. (2009) First report of the mistletoe *Tristerix verticillatus* on *Schinus molle* from the Sierra de San Luis, Argentina. *Plant Disease*, **93**, 317–317.
- Amico G.C., Vidal-Russell R., Nickrent D. (2007) Phylogenetic relationships and ecological speciation in the mistletoe *Tristerix* (Loranthaceae): the influence of pollinators, dispersers, and hosts. *American Journal of Botany*, **94**, 558–567.
- Angiosperm Phylogeny Group (APG) (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society*, **181**, 1–20.
- Armesto J.J., León-Lobos P., Arroyo M.T.K. (1996) Los bosques templados del sur de Chile: una isla biogeográfica. In: Armesto J. J., Villagran C., Arroyo M. T. K. (Eds), *Ecología de los bosques nativos de Chile*. Editorial Universitaria, Santiago, Chile, pp. 23–28.
- Barlow B.A., Wiens D. (1973) The classification of the generic segregates of *Phrygilanthus* (= *Notanthera*) of the Loranthaceae. *Brittonia*, **25**, 26–39.
- Barlow B.A., Wiens D. (1977) Host–parasite resemblance in Australian mistletoes: the case for cryptic mimicry. *Evolution*, **31**, 69–84.
- Dean W.R.J., Midgley J.J., Stock W.D. (1994) The distribution of mistletoes in South Africa: patterns of species richness and host choice. *Journal of Biogeography*, **21**, 503–510.
- Der J.P., Nickrent D.L. (2008) A molecular phylogeny of Santalaceae (Santalales). *Systematic Botany*, **33**, 107–116.
- Downey P.O. (1998) An inventory of host species for each aerial mistletoe species (Loranthaceae and Viscaceae) in Australia. *Cunninghamia*, **5**, 685–720.
- Downey P.O., Gill A.M., Banks J.C. (1997) The influence of host attributes on mistletoe colonization: an example from Mulligan's Flat Nature Reserve, ACT. *Victorian Naturalist*, **114**, 105–111.
- Fadini R.F. (2011) Non-overlap of hosts used by three congeneric and sympatric loranthaceous mistletoe species in an Amazonian savanna: host generalization to extreme specialization. *Acta Botanica Brasiliense*, **25**, 337–345.
- García D., Rodríguez-Cabal M.A., Amico G.C. (2009) Seed dispersal by a frugivorous marsupial shapes the spatial scale of a mistletoe population. *Journal of Ecology*, **97**, 217–229.
- Garcillán P.P., Ezcurra E. (2011) Sampling procedures and species estimation: testing the effectiveness of herbarium data against vegetation sampling in an oceanic island. *Journal of Vegetation Science*, **22**, 273–280.
- Grenfell M., Burns K.C. (2009) Sampling effects and host ranges in Australian mistletoes. *Biotropica*, **41**, 656–658.
- Hawksworth F.G., Wiens D. (1972) *Biology and Classification of Dwarf Mistletoes (Arceuthobium)*. Forest Service, USDA, Washington, DC, USA, pp 234.
- Hawksworth F.G., Wiens D. (1996) *Dwarf Mistletoes: Biology, Pathology and Systematics*. USDA Forest Service, Washington, DC, USA, 410 pp.
- Jerome C.A., Ford B.A. (2002) The discovery of three genetic races of the dwarf mistletoe *Arceuthobium*

- americanum* (Viscaceae) provides insight into the evolution of parasitic angiosperms. *Molecular Ecology*, **11**, 387–405.
- Kavanagh P.H., Burns K.C. (2012) Mistletoe macroecology: spatial patterns in species diversity and host use across Australia. *Biological Journal of the Linnean Society*, **106**, 459–468.
- Kuijt J. (1969) *The Biology of Parasitic Flowering Plants*. University of California Press, Berkeley, CA, USA, 246 pp.
- Kuijt J. (1985) Morphology, biology and systematic relationships of *Desmaria* (Loranthaceae). *Plant Systematics and Evolution*, **151**, 121–130.
- Kuijt J. (1988) Revision of *Tristerix* (Loranthaceae). *Systematic Botany Monographs*, **19**, 61.
- Kuijt J. (2014) Five new species, one new name, and transfers in neotropical mistletoes (Loranthaceae), miscellaneous notes, 61–68. *Novon*, **23**, 176–186.
- Kuijt J., Hansen B. (2015) Eremolepidaceae. In: Kuijt J., Hansen B. (Eds), *The Families and Genera of Vascular Plants: Flowering Plants, Eudicots*. Springer, Berlin, Germany, pp. 69–72.
- Liu B., Lea C., Barrette R., Nickrent D., Chena Z., Lua L., Vidal-Russell R. (2018) Historical biogeography of Loranthaceae (Santalales): diversification agrees with emergence of tropical forests and radiation of songbirds. *Molecular Phylogenetics and Evolution*, **124**, 199–212.
- Mathiasen R.L., Nickrent D.L., Shaw D.C., Watson D.M. (2008) Mistletoes: pathology, systematics, ecology, and management. *Plant Disease*, **92**, 988–1006.
- Moreira-Muñoz A. (2011) *Plant geography of Chile*. Springer Science & Business Media, Berlin, Germany.
- Nickrent D.L. (1997) onwards. The Parasitic Plant Connection. <http://www.parasiticplants.siu.edu>.
- Nickrent D.L., Malécot V., Vidal-Russell R., Der J.P. (2010) A revised classification of Santalales. *Taxon*, **59**, 538–558.
- Norton D.A., Carpenter M.A. (1998) Mistletoes as parasites: host specificity and speciation. *Trends in Ecology & Evolution*, **13**, 101–105.
- Norton D.A., De Lange P.J. (1999) Host specificity in parasitic mistletoes (Loranthaceae) in New Zealand. *Functional Ecology*, **13**, 552–559.
- Okubamichael D.Y., Griffiths M.E., Ward D. (2016) Host specificity in parasitic plants—perspectives from mistletoes. *AoB Plants*, **8**, pii: plw069.
- Press M., Scholes J., Watling J. (1999) Parasitic plants: physiological and ecological interactions with their hosts. In: Press M., Scholes J., Barker M. G. (Eds), *Physiological Plant Ecology*. Blackwell, Oxford, UK, pp 175–197.
- R Core Team (2017) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Vidal-Russell R., Nickrent D.L. (2007) A molecular phylogeny of the feathery mistletoe *Misodendrum*. *Systematic Botany*, **32**, 560–568.
- Vidal-Russell R., Nickrent D.L. (2008a) Evolutionary relationships in the showy mistletoe family (Loranthaceae). *American Journal of Botany*, **95**, 1015–1029.
- Vidal-Russell R., Nickrent D.L. (2008b) The first mistletoes: origins of aerial parasitism in Santalales. *Molecular Phylogenetics and Evolution*, **47**, 523–537.
- Vidal-Russell R., Premoli A.C. (2015) *Nothofagus* trees show genotype difference that influence infection by mistletoes, Misodendraceae. *Australian Journal of Botany*, **63**, 541–548.
- Wardle P., Ezcurra C., Ramírez C., Wagstaff S. (2001) Comparison of the flora and vegetation of the southern Andes and New Zealand. *New Zealand Journal of Botany*, **39**, 69–108.
- Watson D.M., Milner K.V., Leigh A. (2017) Novel application of species richness estimators to predict the host range of parasites. *International Journal for Parasitology*, **47**, 31–39.
- Wilson C.A., Calvin C.L. (2016) Metadata provide insights on patterns of epiparasitism in mistletoes (Santalales), an overlooked topic in forest biology. *Botany-Botanique*, **95**, 259–269.