

High incidence of plant-animal mutualisms in the woody flora of the temperate forest of southern South America: biogeographical origin and present ecological significance

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Abstract. *The flora of the temperate forest of southern South America highly depends on animals for pollination and seed dispersal. This resembles more tropical settings and distinguishes it from other temperate floras. This high mutualism-dependency seems paradoxical and potentially “anachronic” in view of this flora’s present interaction with an impoverished fauna. We analyzed the frequency of biotic pollination and seed dispersal across woody genera classified according to growth form and biogeographical affiliation. We found that genera that probably originated in warm or tropical like environments of ancient Gondwana and the Neotropics, two of the main biogeographical sources of this flora, had high incidences of biotic pollination and dispersal. The rich endemic foristic element, mostly related phylogenetically to these two foristic sources, also exhibited a high frequency of mutualism-dependency. Many endemic and Neotropical genera showed distinctive reproductive traits associated with bird pollination, a type of mutualism nearly absent in taxa with other biogeographical affiliations. This suggests that many southern South American plant taxa may have evolved novel mutualistic associations in situ, probably before the onset of present cooler climatic conditions. We propose that, despite the current relictual status of many of these genera and their associated reproductive traits, dependence on mutualists is not necessarily “anachronic” in today’s cool climate and depauperate faunal environment. Our finding that the average southernmost distribution limit is similar both for genera that depend on mutualists for either pollination or dispersal and for those that do not support this view. The steep W-E rainfall gradient created by the rising of the Andes represents a more potent ecological filter than the N-S temperature gradient, sorting out forest plant taxa according to their dependence on hummingbirds for pollination and vertebrates for dispersal. Overall, we believe that plant-animal mutualisms in the temperate forest of southern South America are still well suited interactions, because they rely on animals that are abundant and show a high degree of residency despite being represented by a low number of species. However, present human-induced elevated rates of deforestation, fragmentation and habitat degradation may be particularly threatening for mutualist-dependent plants due to low redundancy in alternative animal partners.*

Introduction

One of the most striking features of the narrow temperate forest biome that extends from around 35°S to 55°S latitude over much of southern Chile and the eastern slopes of the Patagonian Andes in Argentina, is the presence of many plant taxa that depend on animal mutualists for either pollination or seed dispersal (Willson et al. 1996a). The prevalence of different types of plant-animal mutualisms in the relatively rich and highly endemic flora of this region is among the largest recorded for any temperate ecosystem and is, in some respects, similar to that found in more tropical latitudes (e.g., Willson et al. 1989, Willson 1991). This high incidence of mutualism-dependency is rather paradoxical, however, in view of the depauperate fauna with which plants interact (Vuilleumier 1985, Willson 1991, Armesto et al. 1987, 1996).

Today, the temperate forest of southern South America provides some of the most extreme examples of mutualistic systems in terms of a relatively high number of plant species interacting with a relatively low number of animal species (Armesto et al. 1996, see also Jordano 1987). For instance, the percentage of this southern flora that is bird-pollinated (i.e., ornithophily) is probably among the highest present in any biome worldwide. Even the absolute number of ornithophilous plant taxa found at particular sites is comparable to that of many species-rich tropical localities (Ruffini 1992, Smith-Ramirez 1993, Armesto et al. 1996, Fraga et al. 1997). Yet, only one species of hummingbird (*Sephanoides galeritus*) seems to be responsible for the pollination of nearly 20% of the woody taxa in this forest ecosystem. In contrast, ornithophilous plant assemblages of similar richness (10-20 species) in tropical America may be interacting locally with > 10 species of hummingbirds (Armesto et al. 1996) and even >30 in certain cloud forests of Ecuador and Colombia (P. Feinsinger, personal communication). A similar pattern occurs with other pollinators as the more temperate bumblebees. While it is usual to find > 5 and up to 15 species of bumblebees visiting flowers locally in many temperate forest sites of the northern hemisphere (e.g., Pleasants 1980, Bowers 1985, Rathcke 1988, Inoue and Kato 1992, Obeso 1992), only one species, the native *Bombus dahlbomii*, visits and pollinates the showy flowers of several plant species throughout southern South America (Riveros 1991, Riveros et al. 1991, Aizen 1997). The recent invasion, rapid expansion, and successful establishment of a second species, the European *Bombus ruderatus*, provides circumstantial evidence that “empty bumblebee niches” might exist in this temperate forest biome (Roig-Alsina and Aizen 1996).

A similar asymmetry is observed in seed dispersal. While about 50% of the woody species of the temperate forest of southern South America (and near 70% in the island of Chiloé) produces fleshy fruits (Armesto et al. 1987; Armesto and Rozzi 1989, Willson 1991, Willson et al. 1996a), there are only a handful of opportunistic frugivorous species, mostly birds, interacting with this diverse plant guild (Willson 1991, Armesto et al. 1996, Rozzi et al. 1996). Indeed, a summer immigrant from tropical latitudes, *Elaenia albiceps*, is responsible for the dispersal of many of the fleshy-fruited taxa occurring in this biome (Armesto et al. 1996).

Although this apparently ill-suited or “anachronic” high incidence of mutualism-dependency (cf. Janzen and Martin 1982) might, in part, reflect the fragmentary state of knowledge of plant-animal interactions in this biome, evidence suggests that an impoverished and highly endemic fauna has been the result of long-standing geographic isolation and repeated events of forest habitat contraction (Vuilleumier 1985, Armesto et al. 1987). The final uplift of the Andes during the Mid-to Late-Tertiary and the establishment of the cold Humboldt current determined the aridification of the regions north and east of the present forest range distribution, disrupting the continuity between this southern forest landmass and the neotropical forest region to the north (Markgraf et al. 1995, 1996, Villagrán and Hinojosa 1997). The “forest island” thus originated also suffered drastic reductions in area during the glaciations of the Pleistocene that could have led to much faunal extinction. However, Mid- to Late-Tertiary and Pleistocenic events, which appear to have caused not only many animal but also many plant extinctions (Villagrán and Hinojosa 1997), do not explain the origin of high mutualism-dependency in the first place.

Here we searched into the past to find clues to the present pattern of high dependence on animals for pollination and dispersal by the woody flora of the temperate forest of southern South America. We asked to what extent the present high incidence of plant-animal mutualisms might be a reflection of the complex biogeographical origin of this flora -with many taxa having evolved in ancient, tropical-like environments (Villagrán et al. 1986, Markgraf et al. 1995, Arroyo et al. 1996)- and what is the present ecological significance of these high levels of mutualism-dependency. We had the following specific objectives. First, because many plant reproductive traits may show substantial “phylogenetic inertia” and often be homogeneous at the generic and even familial taxonomic categories (Kochmer and Handel 1986, Mazer 1989, Herrera 1992a, Jordano 1995), we estimated levels of ancestral biotic pollination and dispersal in the different biogeographical sources that contributed to the assemblage of this southern flora from reproductive characteristics present in extant genera. Second, given the relative importance of hummingbird pollination, we investigated to what extent ornithophily was a pre-existing trait or, alternatively, one that evolved mostly “in situ”.

Third, given that mutualism-dependency might be ill-suited (or “anachronic” sensu Janzen and Martin 1982) to the forest climatic and biological present conditions, we examined whether dependence on animals for either pollination or seed dispersal might constrain plant distribution along gradients of decreasing temperature (N-S) and rainfall (W-E). Finally, we briefly discussed the implications of our findings for the conservation of this unique and threatened ecosystem.

Origin and development of the temperate forest flora of southern South America

The origin and development of the temperate flora of southern South America (outlined by Cabrera 1954, Raven and Axelrod 1974, 1975, Solbrig 1978, Simpson 1983, and more recently reviewed by Axelrod et al. 1991, Markgraf et al. 1995, 1996, Stuessy and Taylor 1995, Arroyo et al. 1996, Hinojosa and Villagrán 1997) are intrinsically linked to the major geological and paleoclimatic events that took place during the late Cretaceous and throughout the Tertiary (Parrish 1987, Pascual and Ortiz-Jaureguizar 1990, Taylor 1995). Here we synthesize the historical setting in which this temperate forest flora evolved to infer how remote biological and environmental episodes might relate to its current characteristics.

During the Cretaceous period (144-65 m.y.a.) Antarctica appears to have been a center for the origin and dispersal of much of the flora of the temperate forests that are now disjunct in different southern continents, at that time united in Gondwana (Hill and Scriven 1995). In the Late Cretaceous, southern South America was still linked to Australia, Tasmania and New Zealand via Antarctica, a connection that remained until sometime in the Early Tertiary (Axelrod et al. 1991). The Late Cretaceous-Tertiary boundary (65 m.y.a.) was a time of general stability, climatic quiescence and warm global temperatures (Parrish 1987). By the end of the Cretaceous and Early Tertiary, most of the angiosperm families and the main modes of biotic pollination and dispersal that seed plants present today were already established and diversified (Tiffney 1984, Friis and Crepet 1987, Pellmyr 1992). The origin of austral genera now disjunct between different southern hemisphere continents (e.g., *Araucaria*, *Gevuina*, *Lomatia*, *Nothofagus*, among others; Arroyo et al. 1996) may in some cases be traced to the Cretaceous before the fragmentation of western Gondwana. The same can be inferred for many genera now endemic to the temperate forests of South America but with close relatives in other southern continents (e.g., *Austrocedrus*, *Lebethanthus*, *Laureliopsis*, etc.).

During the first part of the Tertiary (65-26 m.y.a.) the climate and vegetation of South America were generally tropical and essentially uniform. At that time, tropical wet forest covered most of what is now Patagonian steppe (Menéndez 1972, Romero 1993, Hinojosa and Villagrán 1997). The origin of Neotropical genera now disjunct between the tropical and subtropical regions of the New World and temperate areas of southern South America (e.g., *Azara*, *Chusquea*, *Crinodendron*, *Maytenus*, *Schinus* and others; Arroyo et al. 1996, Villagrán and Hinojosa 1997) probably can be traced to the first half of the Tertiary in which tropical and subtropical vegetation in South America used to form a continuous region that extended into high latitudes. The separation of Australia from Antarctica was completed at the end of the Eocene (ca. 38 m.y.a.), and a cycle of relatively cooler climate began (Hinojosa and Villagrán 1997).

During the second portion of the Tertiary (approx. 26-2 m.y.a.) the most important changes in the climate and geomorphology of South America took place. The separation of Antarctica and South America began in the early Miocene. The Middle Miocene (approx. 15 m.y.a.) marked the commencement of a major cycle of aridity, colder climate and larger environmental heterogeneity that had a profound effect on the flora of this region. By this time the separation from Antarctica culminated, and the circumpolar current was completed (Hinojosa and Villagrán 1997). This produced extensive ice in Antarctica, as well as a definite and very pronounced equator-to-pole thermal gradient (Simpson 1983). The modern wind and water current systems were developed, and the elevating Andes were high enough to cause some rainshadow effect.

During Pliocene and Pleistocene times (less than 10 m.y.a.) the Andes attained their highest elevation. The presence of Andean genera such as *Adesmia* and *Anarthrophyllum* in the southern temperate forest can probably be attributed to their diversification in the colder and more xeric

conditions created by the elevation of the Andes during the second half of the Tertiary. The existence of boreal genera such as *Berberis* and *Ribes* can be related to the connection of South America to North America produced at the end of the Tertiary. This connection coincided with the formation of the Andean corridor of cold, elevated areas that allowed the southern migration of cold-adapted taxa of the northern hemisphere to southern South America (Simpson 1983).

At the end of the Tertiary, the westerly winds on the Patagonian Andes produced a severe rainshadow effect. This probably resulted in a great reduction of the area formerly occupied by forests in this region. This reduction, together with isolation and a general trend to cooler climatic conditions due to the increased latitudinal thermal gradient, caused local extinction of many species of old tropical genera of Gondwanan and Neotropical affinities. Many of the taxa that appear in Tertiary floras of Patagonia (Menéndez 1972) are currently absent at these latitudes, although they are still found in subtropical and tropical South America (Villagrán and Hinojosa 1997). However, a wide array of phytogeographical elements that evolved under different climatic conditions (Arroyo et al. 1996) still characterize the forest of southern South America.

Methods

The data set

We compiled a list of the woody genera of the temperate forest of South America based on the floristic composition of the temperate rainforest of Chile (Arroyo et al. 1996). To these 82 genera, we added nine genera from floristic information on the southern forests from the eastern side of the Andes in Argentina (Dimitri 1972, 1974), which also include more xeric and cooler *Nothofagus* forests (Veblen et al. 1996). Therefore, the northern limits of the temperate forest of South America were established (following Arroyo et al. 1996) to coincide with the 16°C January isotherm at about 38°S latitude. The eastern limits were set approximately within the easternmost extension of the evergreen *Nothofagus* species, *N. dombeyi* and *N. betuloides*, which grossly coincides with the 1000 mm annual precipitation isohet. Nevertheless, this region also includes deciduous forest types at higher elevations, as well as at more xeric sites (e.g., Paez et al. 1994). All of the 91 genera listed in Appendix 1 include at least one species that is mostly restricted to the temperate forest environment. A few genera that occurred in more seasonal forest types in Chile between 35°S and 38°S were excluded because of insufficient information to judge whether they included species that were mostly restricted to the forest habitat.

We constructed a data base that included the following information for each genus: geographic distribution on a worldwide basis; southern latitudinal limit (in degrees S) within the temperate forest region; growth form (tree, shrub, epiphyte, vine or hemiparasite); pollination type (insect, bird or wind pollination); and dispersal mode (animal, wind, gravity, water or multiple dispersal). Information on geographic and latitudinal distributions were obtained from Correa et al. (1969-1988), Dimitri (1974), Moore (1983), Hoffmann (1991), Mabberley (1993), Donoso-Zegers (1994), Donoso-Zegers and Ramírez-García (1994), Rodríguez et al. (1995), and Arroyo et al. (1996). Here, the southernmost limit of a genus represents not only a measure of its southern extension, but also a good estimate of total latitudinal extent within the temperate forest region because almost all genera occur near the northern limit of this biome (Arroyo et al. 1996).

According to the current worldwide geographic distribution, we assigned each genus to one of the following distribution categories (see also Ulloa-Ulloa and Møller-Jørgensen 1993, Arroyo et al. 1996): Austral (present in temperate forest areas of South America and other continents from the southern hemisphere, e.g., New Zealand, Australia), Neotropical (in areas of tropical or subtropical America), Pantropical (in tropical America and tropical Africa and/or Asia), Andean-Patagonian (in the Andes and arid Patagonia), Cosmopolitan (in most continents), Endemic (restricted to the temperate forests of southern South America) and Boreal or Holarctic (that have their highest species diversity in temperate areas of the northern hemisphere, but sometimes extend through the cool areas of elevated mountains such as the Andes into the southern hemisphere).

We assume that these categories are related to the probable origin of a given taxon (e.g., Simpson and Todzia 1990, Armesto and Vidiella 1993, Ulloa-Ulloa and Moller-Jorgensen 1993, Arroyo et al. 1996, but see Morrone and Crisci 1995). We considered an Austral distribution as evidence of a probable remote Gondwanan origin, although for some particular genera an Austral distribution might result from relatively recent long-distance dispersal (e.g., *Sophora*; Arroyo et al. 1996). Similarly, we considered a distribution mostly restricted to the Neotropics as implying a probable tropical American origin, although the presence of a taxon at low latitudes today might be due to a range expansion northward for a genus of southern South American origin rather than viceversa (e.g., *Fuchsia*; Berry 1992). We think, however, that for most taxa our assumptions are correct (for some they are also supported by fossil and/or phylogenetic evidence), and that further refinement will not alter our basic conclusions.

Information on the three ecological traits (i.e., pollination, seed dispersal, and growth form) was compiled from Armesto and Rozzi (1989), Riveros (1991), Willson (1991), Cocucci (1991), Smith-Ramirez (1993), Smith-Ramirez and Armesto (1994), in combination with personal evaluations of the morphological characters described in the literature and our own field observations. Information on pollinator visitation was available for many of the genera listed in Appendix 1 (e.g., Riveros 1991, Riveros et al. 1991), and the actual pollinating role of hummingbirds has been corroborated for most of the taxa listed as ornithophilous (e.g., Riveros 1991, Ruffini 1992, Smith-Ramirez 1993). Less detailed information exists for seed dispersal. Vertebrates that ingest fruit, particularly birds, are the main biotic agents of dispersal in this biome. Ant-dispersal of forest species is practically unknown. Therefore, we categorized taxa producing fleshy fruits or with arilated seeds (e.g., *Maytenus*) as dependent solely on animals for dispersal (see also Willson 1991).

Finally, we considered the floristic composition of the temperate forest at five sites at approximately the same latitude (40–42°S) but at different geographic longitudes to represent the west-east variation in precipitation and, to a lesser extent, temperature. The sites from west to east were the Cordillera of Piuchué in Chiloé (hereafter Chiloé), Chile (Armesto and Rozzi 1989, Smith-Ramirez and Armesto 1994); Antillanca, Chile (Riveros 1991, Riveros et al. 1996); Puerto Blest, Argentina (Brian et al. 1988); Llao Llao, Argentina (J. Puntieri, personal communication); and Bariloche, Argentina (Naumann 1987, Grigera et al. 1996). Precipitation from west to east is -2500 mm (Chiloé), -4000 mm (Antillanca), -3000 mm (Puerto Blest), -1800 mm (Llao Llao), and -1000mm (Bariloche). Despite lower average annual precipitation at the Chiloé site than at Antillanca and Puerto Blest, air humidity is very high (>80%) all year around because of its proximity to the Pacific Ocean (Smith-Ramirez and Armesto 1994). Winter temperatures are more moderate (mean July temperature -5°C) at the lower Chilean sites (200–600 m) than at the Argentine sites (mean July temperature -2°C), which are at a higher elevation (800–900 m).

Data analysis

Most genera were uniform with respect to life form, pollination and dispersal mode and, with a few exceptions, we considered genera as the units of analysis. Five genera, however, were heterogeneous and included species that differed in one or more of the ecological characteristics described above. In those few cases, we assigned species sharing similar characteristics to different subgroups (e.g., *Escallonia*₁ and *Escallonia*₂) and estimated the southernmost latitude for each subgroup separately. Including those few genera as split entities in our analyses, or just as one entity characterized by the prevailing trait in the genera (e.g., Herrera 1992b), left our main conclusions unchanged. A different issue of much recent debate, however, is the statistical legitimacy of making comparisons across genera, or any other taxonomical category, by considering them as independent data points (as we do here) vs. making comparisons within a phylogenetic framework (reviewed in Ricklefs 1996a). However, even if we were able to count on a phylogeny including all lineages of this southern flora, which we can not, it has been argued (Ricklefs 1996b) that phylogenetic analysis is unlikely to alter conclusions when applied to data as taxonomically diverse as ours (see Appendix 1).

We assessed pairwise associations between biogeographical affiliation, growth form, and mutualism-dependency by using G-tests. In these analyses, we tested for associations between the first two variables with the following types of pollination and seed dispersal: (1) biotic (insect + hummingbird) pollination vs. abiotic pollination; (2) hummingbird vs. other pollination; (3) insect vs. other pollination; and (4) biotic (animal) vs. abiotic (all other) dispersal. To conduct these analyses, we grouped some biogeographical and growth-form categories that included a low number of taxa (see Sokal and Rohlf 1981). The Holarctic, Andean, and Cosmopolitan taxa were pooled into a single wide “temperate” biogeographical category; and the hemiparasites, vines, and true epiphytes were pooled into a wide “epiphytic” category. We tested for associations with growth form because this trait is often related to different reproductive characteristics (e.g., Bawa et al. 1985, Bullock 1985, Fox 1985, Mazer 1989). Therefore, we felt it was important to discard the possibility that variation in the incidence of different types of mutualisms across biogeographical components could be the indirect product of associations between growth form and biogeographical affiliation (see Westoby et al. 1990).

We used one-way ANOVAs to evaluate possible effects of presumed biogeographical origin (all seven categories), growth form (all five categories), and pollinator- and dispersal-dependency (three and two categories, respectively) on the southern latitudinal limit of genera. We also tested for an “independent” effect of each of these main factors (i.e., after accounting for all the variation explained by all the other factors) by means of a multiway ANOVA that used the type III Sums of Squares to establish significance levels (PROC GLM, SAS 1988; see also Mazer 1989).

Longitudinal trends in the incidence of biogeographical affiliation, growth form, and pollination and dispersal modes along the W-E transect were assessed by linear regression analysis for categorical data (PROC CATMOD, SAS 1988). Sites were numbered 1-5 from west to east and those values used to represent the independent variable. This ordinal variable gave almost identical results as the distance to the Pacific Ocean, but it seemed to better characterize the nonlinear nature of the W-E gradient, with the steepest changes occurring on the eastern side of the Andes where three of the five sites were situated.

Results

Occurrence of mutualism-dependency in relation to biogeographical origin and growth form

Genera of Endemic, Neotropical, and Austral distributions were the main floristic components of the woody forest flora of southern South America (about 33%, 25% and 22% of all the taxa listed in Appendix 1, respectively). Genera of Pantropical distribution represented 7 % of the flora, while taxa whose origin seems unequivocally associated with cool-temperate conditions represented only a minor component of this flora (Boreal, 5%; and Andean, 4%); only three Cosmopolitan genera (3 %) were native to this biome.

Overall, 85% of the genera were pollinated by animals. Biotic pollination was high (>75%) and similar ($G_4=4.39$, $P=0.36$) in all of the biogeographical sources that contributed to the assemblage of this southern flora (Figure 1A). Analysis of different types of biotic pollination, however, revealed that bird-pollination was almost completely restricted to the Endemic and Neotropical components ($G_4=15.9$, $P<0.005$), with about 30% of the genera relying on hummingbirds for pollination (Figure 1A). Only one genus from a different biogeographical category, *Sophora*, was highly visited and (presumably) pollinated by hummingbirds (Hoffmann 1991). The trend for insect pollination complemented that of hummingbird pollination (Figure 1A), but the association with biogeographical affiliation was less strong ($G_4=10.2$, $P=0.04$).

Biotic dispersal was found in 53% of the genera. Although Neotropical and Pantropical genera tended to exhibit a higher incidence of this type of mutualism (~60%; Figure 1B), we did not detect a significant association between animal dispersal and biogeographical affiliation ($G_4=1.46$, $P=0.83$). Despite the absence of animal dispersal in the few taxa of Andean distribution, 50% of the genera in the pooled temperate category produced fleshy fruits.

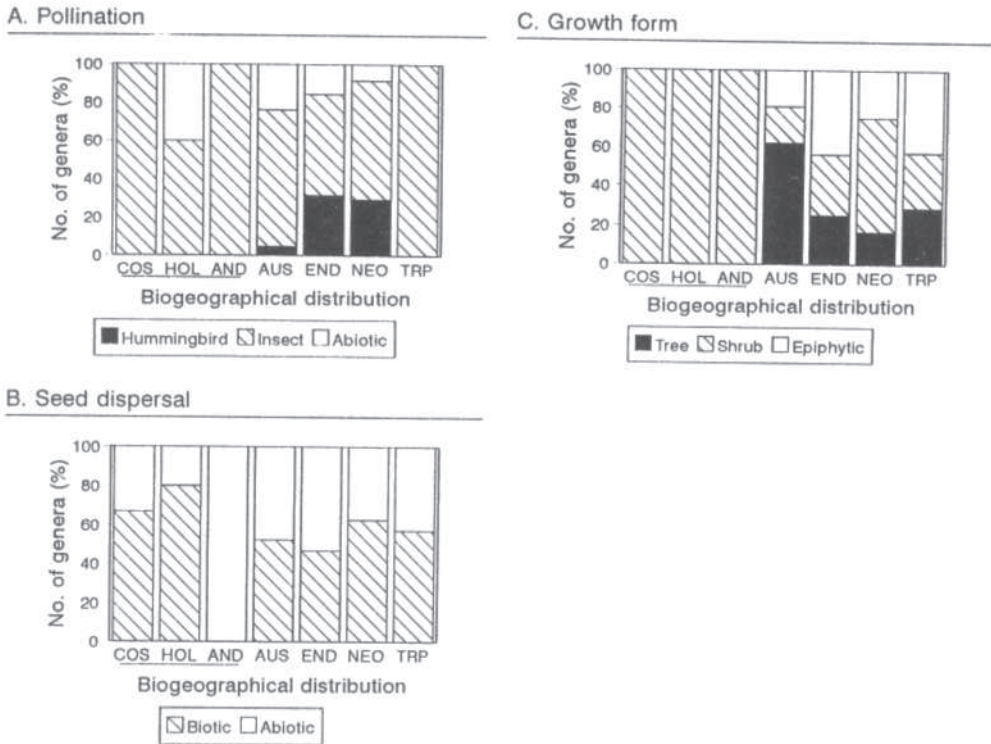


Figure 1. Incidence of different (A) pollination modes, (B) seed dispersal modes, and (C) growth forms across biogeographical affiliation categories. The epiphytic growth form includes true epiphytes, vines, and hemiparasites. Underlined biogeogeographical categories were grouped into a single Temperate distribution for the purpose of analysis. COS=Cosmopolitan (N=3), BOR=Boreal, (N=5), AND=Andean-Patagonian (N=4), AUS=Austral (N=21), END=Endemic (N=32), NEO=Neotropical (N=24), TRP=Pantropical (N=7).

The temperate forest of southern South America exhibits a diverse array of growth forms even within the woody component. We found that the incidence of trees, shrubs, vines, hemiparasites, and true epiphytes respectively accounted for 28%, 43%, 18%, 6% and 4% of the genera. Growth form and biogeographical affiliation were strongly associated ($G_8=37.7$, $P<0.0001$). The most striking pattern was the total absence of either trees or epiphytes (including hemiparasites, vines, and true epiphytes) among genera of a presumed Cosmopolitan, Boreal, or Andean origin (Figure 1C). The other biogeographical categories were characterized by a variety of growth forms, although the high occurrence of trees among Austral genera, shrubs among Neotropical genera, and of epiphytism (sensu lato) among Endemic genera was noticeable.

A significant association between biotic pollination and growth form ($G_2=6.27$, $P<0.05$) was due to a non-random distribution of ornithophily in relation to this factor ($G_2=10.7$, $P<0.005$). Entomophilous genera did not show evidence of an association with growth form ($G_2=2.44$, $P=0.30$). The highest incidence of hummingbird pollination was found in the epiphytic component (Figure 2A; 37% of genera), followed by shrubs (17%), and trees with only one ornithophilous genus (4%). Because the Neotropical and Endemic biogeographical categories were rich in both epiphytic (sensu lato) and ornithophilous genera (Figure 1), we asked whether the relationship between biogeographical affiliation and ornithophily still held when analyzed within growth forms

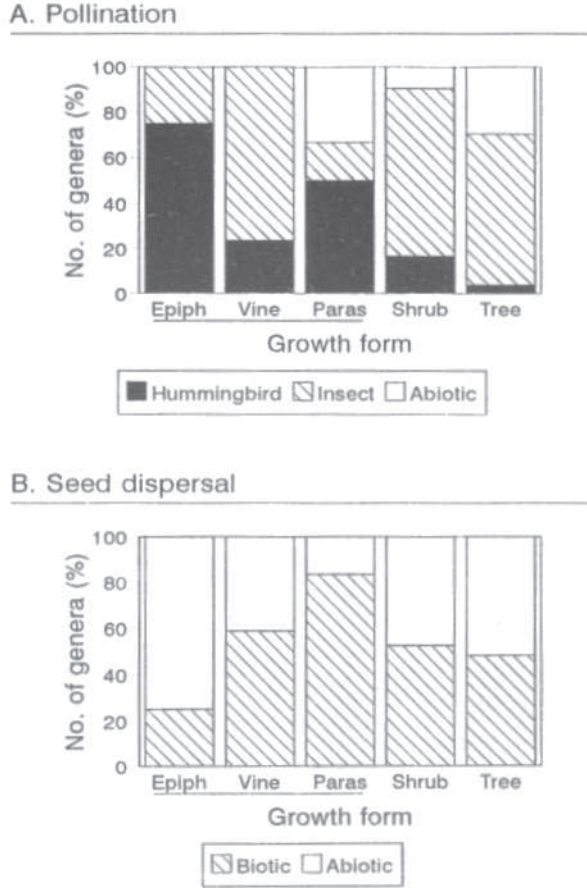


Figure 2. Incidence of different (A) pollination and (B) dispersal modes across growth forms. Underlined biogeographical categories were grouped into a single Epiphytic category for the purpose of analysis. Sample sizes are: true epiphytes (Epiph)=4, vines=17, hemiparasites (Paras)=6, shrubs =42, and trees =27.

(i.e., for the epiphytic and the shrub genera separately). We found that while 10 of the 20 epiphytic genera of either Endemic or Neotropical affiliation were ornithophilous, none of the 7 epiphytic genera with other biogeographical distributions had this pollination mode ($G_1=7.87, P=0.005$). A similar pattern was found among the shrubs: while 7 of the 24 Endemic or Neotropical genera were ornithophilous, none of the 18 shrub genera with other biogeographical affiliations had this pollination mode ($G_1=8.87, P<0.005$). We did not find evidence of any association between seed dispersal and growth form (Figure 213; $G_2=0.69, P=0.71$).

Occurrence of mutualism-dependency along N-S and W-E geographical gradients

The genera that depend on animals for either pollination (Figure 3A) or seed dispersal (Figure 3B) were not constrained in their latitudinal distribution when compared with the genera characterized by abiotic pollination or dispersal, respectively (Table 1). On the other hand, we found latitudinal trends in terms of growth form and biogeographical affiliation. Shrubs tended to reach higher southern latitudes than vines (Figure 3C), and Boreal genera extended to higher latitudes than

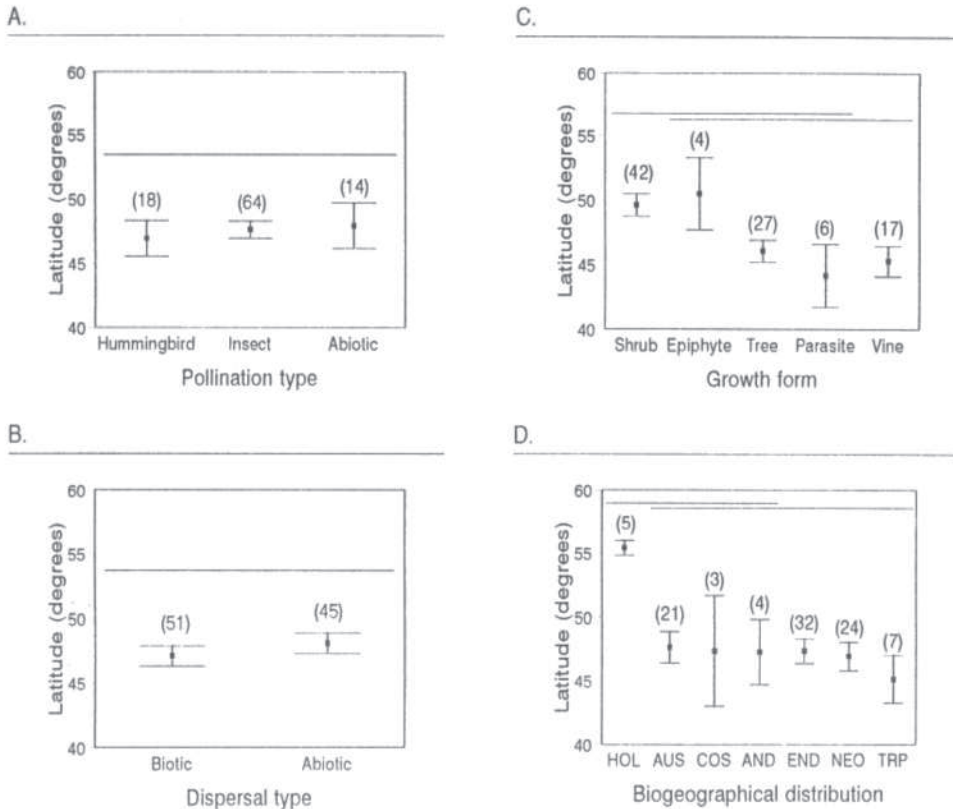


Figure 3. Means \pm 1 SE of southern latitudinal limits of genera classified according to (A) pollination mode, (B) dispersal mode, (C) growth form, and (D) biogeographical affiliation (BOR=Boreal, AUS=Austral, COS=Cosmopolitan, AND =Andean-Patagonian, END=Endemic, NEO=Neotropical, TRP=Pantropical). Sample sizes in parentheses. Means overtopped by the same bar do not differ statistically (Tukey test, $P > 0.05$).

Endemic, Neotropical, and other tropical genera, respectively (Figure 3D, Table 1). A multiway ANOVA showed, however, that the effect of biogeographical affiliation on southern latitudinal extent vanished after taking into account the effect of growth form (Table 1). More importantly, we did not find evidence of an association between either pollination or seed dispersal and southern latitudinal limit even after taking into account the effects of growth form and biogeographical affiliation (Table 1).

The incidence of biotic pollination did not vary significantly from west to east along the rainfall gradient ($\chi^2_1 = 0.64$, $P = 0.64$; Figure 4A). However, the incidence of hummingbird-pollination declined significantly ($\chi^2_1 = 6.55$, $P = 0.01$) from Chiloé, where about 25% of the genera were pollinated by hummingbirds, to Bariloche, where only 7% of the woody genera of the forest flora exhibited this pollination mode (Figure 4A). Interestingly, we did not find a significant complementary W-E increase in insect pollination ($\chi^2_1 = 1.43$, $P = 0.23$). Biotic dispersal decreased significantly from W to E ($\chi^2_1 = 4.47$, $P < 0.05$). While nearly 63% of the genera listed for the Chiloé site are animal-dispersed, this proportion decreased to 40% at the eastern limit of the forest near Bariloche (Figure 4B).

We also found a W-E pattern in the representation of genera with different growth forms (Figure 4C). While shrub, tree and epiphytic genera (sensu lato) were equally well-represented in

Table 1. Summary of F-statistics for ANOVAs testing the effects of pollination and dispersal modes, growth form, and biogeographical affiliation on the southern latitudinal extent of forest genera. Each factor was tested one at a time (one-way ANOVA) and after accounting for variation explained by all the other factors (multi-way ANOVA). Type III sums of squares were used to compute F-values for the main factor multi-way ANOVA (see Data analysis for details).

Source	One-way ANOVA		Multi-way ANOVA	
Pollination mode	$F_{2,93} = 0.14$	$P = 0.86$	$F_{2,82} = 0.16$	$P = 0.85$
Dispersal mode	$F_{1,94} = 0.72$	$P = 0.40$	$F_{1,82} = 0.97$	$P = 0.32$
Growth form	$F_{4,91} = 3.86$	$P < 0.01$	$F_{4,82} = 2.85$	$P < 0.05$
Biogeographical affiliation	$F_{6,89} = 2.06$	$P = 0.07$	$F_{6,82} = 1.63$	$P = 0.15$

the western extreme of the gradient, there were significant decreases in the presence of genera with these last two growth forms eastward ($\chi^2_2=14.7$, $P < 0.001$). For instance, while 27 % of the genera in Chiloé were characterized by epiphytic forms, only 13 % of the genera around Bariloche were epiphytic (Figure 4C). This eastward decrease in the incidence of the epiphytic component, which includes a large number of hummingbird plant genera (see above), could not explain the longitudinal, W-E decrease in the incidence of ornithophily. This trend was still observed when we restricted the analysis only to epiphytic (*sensu lato*) genera. We found that the proportion of hummingbird-pollinated genera with this growth form decreased from 41 % in Chiloé to 0 % in Bariloche ($\chi^2_1=24.7$, $P < 0.0001$).

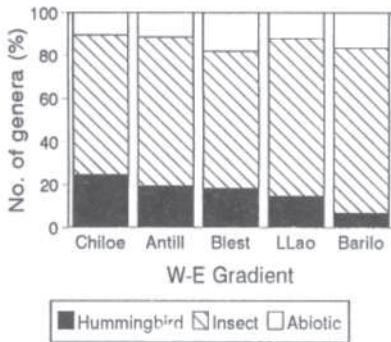
We also observed a W-E trend in the representation of genera with different biogeographical affiliations ($\chi^2_4=8.59$, $P=0.07$). Most notably, we found an eastward increase in the incidence of taxa of the pooled temperate biogeographical category (Figure 4D). Yet, we did not find a significant decline in the representation of genera with either an Endemic or Neotropical affiliation (both categories grouped together, $\chi^2_1=56$, $P=0.11$), which included nearly all of the hummingbird-pollinated genera.

Discussion

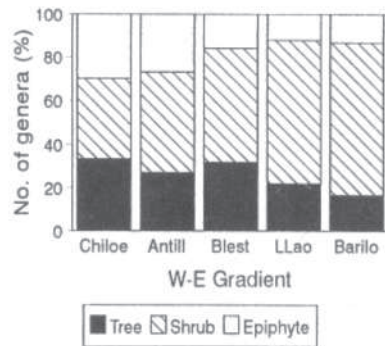
A historical perspective on the origin of a high incidence of mutualism-dependency

Plant-pollinator and plant-disperser interactions are ancient relationships that even precede the appearance of flowering plants on earth. However, the major evolutionary impact of these mutualisms was achieved during the impressive radiation of the angiosperms and the different invertebrate and vertebrate taxa associated with them by the Early- to Mid-Tertiary (Crepet and Friis 1987, Friis and Crepet 1987, Pellmyr 1992). Although the processes underlying this diversification are still poorly understood (Bawa 1995), they might have been fostered by warmer conditions that prevailed during the first half of the Tertiary. Today, fleshy fruits (i.e., those that contain seeds that are intimately associated with dispersal by vertebrates) are more common in tropical than in temperate families, and frugivory is more common among tropical than temperate bird and mammal families (Fleming 1991). Undoubtedly, these patterns underlie the high incidence of the “fleshy fruit syndrome” exhibited by many aseasonal tropical floras and its association with diverse frugivorous guilds (Willson 1991). In addition, the fact that these tropical vs. temperate ecological patterns may be interpreted as a consequence of a family-level phenomenon implies that present levels of plant-animal mutualisms might reflect substantial phylogenetic inertia (Herrera 1992a). Although similar geographic and taxonomic trends probably characterize plant-pollinator interactions, to our knowledge they have not been yet as comprehensively documented (but see Bawa 1990).

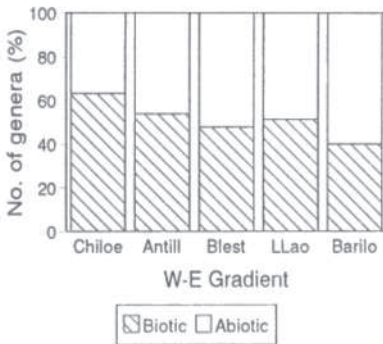
A. Pollination



C. Growth form



B. Seed dispersal



D. Biogeographical distribution

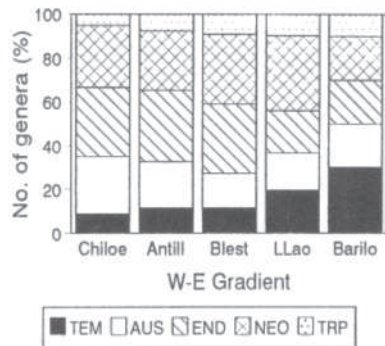


Figure 4. Incidence of different (A) pollination modes, (B) seed dispersal modes, (C) growth forms, and (D) biogeographical affiliation categories (TEM=Temperate, which groups Boreal, Andean-Patagonian, and Cosmopolitan; AUS=Austral; END=Endemic; NEO=Neotropical; TRP=Pantropical) among the woody genera present in five localities along the W-E rainfall gradient between 40° and 42°S. About 250 km separate the westernmost (Chiloé) from the easternmost site (Bariloche). Sample sizes are: Chiloé= 57, Antillanca=52, Puerto Blest=44, Llao Llao=41, Bariloche=30.

We propose that a high incidence of mutualism-dependency in the temperate forest flora of southern South America is, to a large extent, a pre-existing condition: one that still reflects the origin of most of these plant genera in the tropical-like environments of ancient Gondwana and in the Neotropics, the two main biogeographical sources from where the temperate flora of southern South America assembled (Arroyo et al. 1996). We found similar levels of biotic pollination and seed dispersal among genera with these biogeographical affiliations, suggesting that their high degree of mutualism-dependency were maintained as the climate became cooler in southern South America. This “biophylic” predisposition could also have been inherited by the many Endemic genera of Gondwanan and Neotropical affinities, which also showed high incidences of biotic

pollination and dispersal (Figure 1A,B). These similarities occurred despite differences in the growth forms associated with the different biogeographical components (Figure 1C).

If a much speculated tropical ancestry were the cause of “so much” present south-temperate mutualism, why is that the “true temperate” biogeographical element (i.e., Holarctic, Andean-Patagonian, and perhaps Cosmopolitan) also exhibit relatively high levels of mutualism-dependency? Two non-mutually exclusive possibilities are “random sampling” and “growth-form sorting”. Random sampling would explain this apparently high incidence as a consequence of large “sampling errors” associated with reduced sample sizes. After all, the few genera of true temperate biogeographical affiliation -which only represent about 10% of the forest flora of southern South America- just by chance might not necessarily reflect the levels of mutualism found in their respective biogeographical sources. For instance, the total absence of biotic dispersal among the four Andean genera probably underrepresents the true incidence of biotic dispersal in the Andean-Patagonian flora.

Growth-form sorting (cf. Herrera 1992b), on the other hand, provides an explanation based on the fact that the true temperate element was exclusively represented by shrubs in an otherwise physiognomically diverse flora. This might have introduced a bias in terms of the extent to which these genera represent the average mutualism levels found in their respective phytogeographical regions. For instance, while Holarctic floras are relatively poor in fleshy-fruited genera, a large proportion of the genera that possess this trait are shrubs (Willson 1991). An alternative view of the growth-form sorting hypothesis, however, would state that north-temperate shrubs could invade southern latitudes because the temperate South American forest environment favored biotically-dispersed taxa rather than favoring shrubs.

Ornithophily in the temperate forest flora

The arguments presented above could imply that reproductive traits associated with animal mutualists were maintained over time due to phylogenetic inertia despite much climatic change. Is there any evidence, however, that might suggest otherwise? The relatively high incidence of ornithophily in the Endemic and Neotropical components of the flora, and the near absence in all others, provides some evidence that novel plant-animal associations may have evolved “in situ” in southern South America. Ornithophily is usually associated with a distinctive set of characters or “syndrome”: red or orange tubular flowers that secrete copious amounts of diluted nectar (Grant and Grant 1968, Richards 1986). This ornithophilous syndrome commonly observed today in the woody flora of the temperate forest might reflect a long-standing relationship with bird pollinators, particularly hummingbirds.

The confinement of ornithophily to the South American biogeographical components (Endemic and Neotropical) also may provide an age estimate for the evolution of “novel” plant-animal associations in the woody flora of the southern temperate forest. Hummingbirds (Trochilidae), the most specialized mutualists of all nectarivorous birds, are a Neotropical group that appear to have had their origin in South America, where they are highly diversified, especially in tropical and premontane parts of the north Andean region (Gentry 1982). The relatively high percentage of ornithophily in genera of probable Neotropical origin in the southern temperate forest might relate to the selective pressure of hummingbirds. It has been suggested that hummingbirds radiated into the Andes beginning in mid-Miocene (Bleiweiss et al. 1994), about 20 m.y.a., but their presence and interactions with the flora of South America can be traced to even earlier in the Tertiary, probably at least to early Eocene (Bleiweiss et al. 1994, Feduccia 1996). It is also probable that bird-flower coevolution started earlier in the New World than elsewhere (Stiles 1981). Because some of the Endemic genera interacting today with hummingbirds (e.g., *Embothrium*, *Mitraria*) are related to ornithophilous genera in Australia or New Zealand (e.g., Smith-Ramírez and Armesto 1998), it could even be argued that ornithophily may have evolved in southern South America even before the final breakage of the Gondwanan link. In any event, it is likely that the evolution of ornithophily took place well before the climatic cooling and biogeographical isolation of the southern forest that occurred during the second half of the Tertiary.

Present ecological significance of high mutualism-dependency

There is some evidence indicating that the flora of the temperate forest of southern South America is characterized by a high degree of relictualism with a large representation of endemic, taxonomically isolated, monotypic genera (Arroyo et al. 1996). This is probably the result of low speciation and high extinction rates associated with long-standing biogeographical isolation, climatic cooling, and repeated cycles of habitat contraction that occurred since the Mid-Tertiary (Villagrán and Hincjosa 1997). Although present plant reproductive traits might also be interpreted as “relicts”, a reflection of the more benign climatic and probably richer faunal environment in which they originated, one may ask why traits that condition plants to rely on mutualists are still present. The answer might be that these traits prove not to be so “anachronistic” in the present environmental setting (see Howe 1985). The study of the distribution of plant-animal mutualisms along major temperature (N-S) and precipitation (W-E) gradients may provide some insights into the ecological significance of mutualism-dependency in today’s temperate forest environment. If a cooling trend rendered mutualism-maladaptive, then we should not expect those plant taxa that depend on animals to occur as far south as those that are less dependent. This was not the case. In this study, we found that the latitudinal ranges of genera that did and did not depend on animals for either pollination or dispersal had, on average, similar southern limits (Figure 3A, B).

As a contrast, our analysis of plant communities along a W-E transect suggests that plant-animal mutualisms might be influenced by the rainfall gradient created by the rise of the Andes. Our results imply that this gradient represents an ecological filter that has sorted out taxa based on their dependence on hummingbirds for pollination and vertebrates for seed dispersal (Figure 4A,B). We propose, however, that these patterns are better explained as a response of plants to abiotic conditions (i.e., lower water availability) rather than as a consequence of an eastward decrease in the abundance of potentially mutualistic fauna. First, *Sephanoides galeritus*, the sole hummingbird native to this biome, is most abundant but not restricted to the forest habitat (Ruffini 1992, Smith-Ramírez 1993, Rozzi et al. 1996, Fraga et al. 1997). Actually, this hummingbird shows a very opportunistic behavior, moving over long distances in search of nectar, which probably determines its partial migration from the south to north-central Chile during the winter (Ruffini 1992, Smith-Ramírez 1993, Fraga et al. 1997). This plasticity might have allowed it to colonize the oceanic and distant islands of Juan Fernandez (Colwell 1989). Consequently, it is unlikely that the eastward decrease in bird-pollinated taxa is due to an innate scarcity of hummingbirds. Second, birds in general have been found to be particularly abundant and diverse in the eastern ecotone between forest and steppe (Ralph 1985). Yet, water availability might constrain the secretion of the high nectar rewards required for hummingbird pollination, or production of fleshy fruits for bird dispersal. Indeed, correlations between frequency of fleshy-fruited species and precipitation have been noted in other biomes (see references in Willson 1991).

Plants and animals usually engage in diffuse mutualisms, where alternative mutualists may achieve similar goals (Feinsinger 1983, Jordano 1987, Waser et al. 1996). Specialization over evolutionary time may in part be prevented by different timescales of persistence of plants and animals, which expose plants to changing faunal assemblages. While angiosperm species last ~30 m.y. in the fossil record, vertebrates last about one order of magnitude less (Herrera 1984). In the specific case of the temperate forest of southern South America, higher animal turnover rates might explain why, unlike the flora, the forest avifauna is closely related to the one inhabiting the ecologically dissimilar Patagonian steppe (Vuilleumier 1985). Specialization in plants also may be prevented in ecological time because of unpredictable spatial-temporal fluctuations in animal populations. In this southern forest, fluctuations could be large, given the high rates of disturbances (vulcanism, fire, avalanches, etc.) that characterize this biome (Veblen et al. 1977, 1992, Kitzberger and Veblen 1997). This lack of specialization might in part have buffered mutualist-dependent taxa from much faunal change and depauperation. With the exception of ornithophily, the flora of southern South America exhibits quite unspecific mutualistic syndromes (Armesto and Rozzi 1989, Riveros 1991, Willson et al. 1996a).

Although much more empirical work is needed for a comparative assessment of the functional levels that characterize mutualistic interactions in different biomes, there are examples of highly

interactive plant-pollinator and plant-frugivore systems occurring in the temperate forest of southern South America (e.g., Riveros 1991, Ruffini 1992, Willson et al. 1996c, Aizen 1997, Smith-Ramírez and Armesto 1998). In this study, we could not find any evidence that relying on mutualism constrains plant distribution within the temperate forest region, at least from a latitudinal perspective. Why is it that plant-animal mutualisms apparently still thrive in the present cool-temperate and fauna-poor forest environment? On one hand, frequent small- and large-scale disturbances might have favored the maintenance of biotic mutualisms because of their benefits in terms of increased reproduction among relatively isolated individuals and recolonization of denuded areas (e.g., Villagrán et al. 1986). On the other hand, several traits of the local mutualistic animal assemblages might have compensated for their low richness. The first one is a high degree of mutualist reliability due to a low incidence of long-distant migrants in the southern South America avifauna (Willson 1991, Willson et al. 1996b, Rozzi et al. 1996). Despite the potential role of migratory *Elaenia albiceps* as a key disperser (Armesto et al. 1996), other opportunistic frugivorous birds are present in the forest all year-around (Rozzi et al. 1996). This high degree of residency might relate in turn to the more equable climate of southern South America in comparison to similar latitudes in the northern hemisphere (Arroyo et al. 1996). Associated with the continuous presence of frugivores, there is also a relatively high number of plants that bear fruit during the winter (Smith-Ramírez and Armesto 1994, Riveros and Smith-Ramírez 1996). Second, population densities of southern frugivores may be higher and thus compensate for their low species richness (Willson et al. 1996b). The same may be true for pollinator assemblages. Despite the predominance of self-incompatibility and dioecy in the woody forest flora of southern South America (i.e., breeding systems that obligate plants to rely on external pollination agents), reproductive success is high in comparison with other temperate and tropical forests (Riveros 1991, Riveros et al. 1996). Similar comparative data assessing removal and dispersal rates of fruits still are lacking.

Conservation implications

Our evidence indicates that dependence on animals for pollination and dispersal has been a resilient plant reproductive strategy in the forest of southern South America. Today the highly unique flora of this biome is threatened by probably the highest rates of habitat destruction, fragmentation and degradation ever experienced. How the forest biota will respond to these human-induced changes is an open question. Present low redundancy in species of mutualistic partners, however, leaves a sizable portion of this southern flora highly vulnerable to the loss of any particular one (Bond 1994, Waser et al. 1996, Naeem 1998). For instance, the disappearance of a single species like the hummingbird *Sephanoides galeritus* could be reflected in much reduced reproductive levels in a large proportion of the flora. Although most of the key animal mutualists may be relatively abundant at present, they might not be so in the near future. Even if their abundances were not much reduced by human activities, their very opportunistic nature, along with the sudden appearance of new, abundant, and accessible resources (e.g., the flowers of introduced *Eucalyptus* plantations) could induce them to leave the native flora unattended. The present low redundancy in alternative mutualistic partners may easily shift the outcome of relationships that involve many plants but only a few animal species.

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Appendix 1. Genera of woody plants of the flora of the temperate forest of southern South America. N: number of species present in the temperate forest. Biog.: biogeographical distribution category (AUS=Austral, END=Endemic, NEO=Neotropical, TRP=Pantropical, AND =Andean, BOR=Boreal, COS=Cosmopolitan). P: pollination type (I=insect, O=bird, W=wind). D: dispersal type (A=animal, G=gravity, H= water, M=multiple, W=wind). GF: growth form (T=tree, S=shrub, E=epiphyte, V=vine, P=hemiparasite). Lat.: southernmost latitudinal extension (in degrees S). Ch., An., Bl., Ll., Bar.: presence in Chiloé, Antillanca, Puerto Blest, Llao Llao, Bariloche, i.e., different locations along the W-E rainfall gradient at 40°-42° S (1= presence, 0 =absence).

Genus	N	Family	Biog.	P	D	GF	Lat.	Ch.	An.	Bl.	Ll.	Bar.
<i>Acrisione</i>	1	Compositae	END	I	W	S	43	0	0	0	0	0
<i>Adesmia</i>	1	Fabaceae	AND	I	M	S	53	0	0	0	1	1
<i>Aextoxicon</i>	1	Aextoxicaceae	END	I	A	T	43	1	1	0	0	0
<i>Amomyrtus</i>	2	Myrtaceae	END	I	A	T	48	1	1	1	0	0
<i>Anarthrophyllum</i>	1	Fabaceae	AND	I	G	S	44	0	0	0	0	1
<i>Antidaphne</i>	1	Loranthaceae	NEO	W	A	P	40	0	0	0	0	0
<i>Araucaria</i>	1	Araucariaceae	AUS	W	M	T	40	0	0	0	0	0
<i>Aristolelia</i>	1	Elaeocarpaceae	AUS	I	A	T	45	1	1	0	1	1
<i>Asteranthera</i>	1	Gesneriaceae	END	O	G	E	53	1	1	1	0	0
<i>Austrocedrus</i>	1	Cupressaceae	END	W	W	T	43	0	0	0	1	1
<i>Azara</i>	3	Flacourtiaceae	NEO	I	A	S	53	1	1	1	1	0
<i>Baccharis</i>	8	Compositae	BOR	I	W	S	56	1	1	1	1	1
<i>Balbisia</i>	1	Ledocarpaceae	AND	I	G	S	42	0	0	0	0	1
<i>Berberis</i>	11	Berberidaceae	BOR	I	A	S	56	1	1	1	1	1
<i>Blepharocalyx</i>	1	Myrtaceae	NEO	I	A	T	43	0	0	0	0	0
<i>Boquila</i>	1	Lardizabalaceae	END	I	A	V	43	1	0	0	0	0
<i>Buddleja</i>	1	Buddlejaceae	TRP	I	G	S	43	0	1	1	1	0
<i>Caldcluvia</i>	1	Cunoniaceae	AUS	I	W	T	47	1	1	0	0	0
<i>Campsidium</i>	1	Bignoniaceae	END	O	W	V	50	1	1	1	0	0
<i>Chiliotrichum</i>	2	Compositae	END	I	W	S	56	0	1	0	1	0
<i>Chusquea</i>	6	Poaceae	NEO	W	M	S	49	1	1	1	1	1
<i>Cissus</i>	1	Vitaceae	TRP	I	A	V	43	1	1	0	0	0
<i>Colletia</i>	1	Rhamnaceae	NEO	I	G	S	46	0	0	1	1	1
<i>Coriaria</i>	1	Coriariaceae	AUS	W	A	S	44	1	1	0	0	0
<i>Corynabutilon</i>	1	Malvaceae	END	I	G	S	43	0	1	0	0	0
<i>Crinodendron</i>	1	Elaeocarpaceae	NEO	O	M	S	43	1	0	0	0	0
<i>Cynanchum</i>	6	Asclepiadaceae	TRP	I	W	V	44	1	0	1	1	1
<i>Dasyphyllum</i>	1	Compositae	NEO	I	W	T	43	1	1	1	1	0
<i>Desfontainia</i>	1	Desfontainiaceae	NEO	O	A	S	53	1	1	1	1	0
<i>Desmaria</i>	1	Loranthaceae	END	O	A	P	40	0	0	0	0	0
<i>Discaria</i>	1	Rhamnaceae	AUS	I	G	S	55	0	0	0	1	1
<i>Dioscorea</i>	1	Dioscoreaceae	TRP	I	W	V	41	0	1	0	0	0
<i>Dioatea</i>	1	Verbenaceae	END	I	G	S	50	0	0	1	1	1
<i>Drimys</i> ₁	1	Winteraceae	NEO	I	A	T	56	1	1	0	0	0
<i>Drimys</i> ₂	1	Winteraceae	NEO	I	A	S	42	0	1	1	1	0
<i>Ecchremocarpus</i>	1	Bignoniaceae	NEO	O	W	V	42	0	0	0	0	0
<i>Elytropus</i>	1	Apocynaceae	END	I	W	V	43	1	1	0	0	0
<i>Embothrium</i>	1	Proteaceae	END	O	W	S	56	1	1	1	1	1
<i>Empetrum</i>	1	Empetraceae	BOR	W	A	S	56	1	1	1	0	0
<i>Ephedra</i>	1	Ephedraceae	BOR	W	A	S	53	0	0	0	1	1
<i>Ercilla</i>	2	Phytolaccaceae	END	I	A	V	43	1	1	0	0	0
<i>Escallonia</i> ₁	1	Escalloniaceae	NEO	O	G	S	51	1	1	1	1	0
<i>Escallonia</i> ₂	5	Escalloniaceae	NEO	I	G	S	56	0	1	1	1	1
<i>Eucryphia</i>	1	Eucryphiaceae	AUS	I	W	T	43	1	1	0	0	0
<i>Fabiana</i>	1	Solanaceae	AND	I	G	S	50	0	0	0	1	1
<i>Fitzroya</i>	1	Cupressaceae	END	W	W	T	43	0	0	1	0	0
<i>Fuchsia (Quelusia)</i>	1	Onagraceae	NEO	O	A	S	55	1	1	1	1	1
<i>Gaultheria</i>	8	Ericaceae	AUS	I	A	S	56	1	1	1	1	1
<i>Gevuina</i>	1	Proteaceae	AUS	I	A	T	44	1	0	0	0	0

Genus	N	Family	Biog.	P	D	GF	Lat.	Ch.	An.	Bl.	Ll.	Bar.
<i>Griselinia</i>	4	Cornaceae	AUS	I	A	V	50	1	1	0	0	0
<i>Hebe</i>	2	Scrophulariaceae	AUS	I	G	S	56	0	0	0	0	0
<i>Hydrangea</i>	1	Hydrangeaceae	NEO	I	M	V	46	1	1	1	0	0
<i>Lapageria</i>	1	Philesiaceae	END	O	A	V	40	0	0	0	0	0
<i>Latua</i>	1	Solanaceae	END	O	A	S	43	0	0	0	0	0
<i>Laurelia</i>	1	Monimiaceae	AUS	I	W	T	42	0	0	0	0	0
<i>Laureliopsis</i>	1	Monimiaceae	END	I	W	T	47	1	1	1	0	0
<i>Lardizabala</i>	1	Lardizabalaceae	END	I	A	V	43	0	0	0	0	0
<i>Lebetanthus</i>	1	Epacridaceae	END	I	G	E	56	0	0	0	0	0
<i>Lepidoceras</i>	1	Loranthaceae	NEO	I	A	P	43	1	1	0	0	0
<i>Lomatia</i>	3	Proteaceae	AUS	I	W	T	50	1	1	1	1	1
<i>Luma₁</i>	1	Myrtaceae	END	I	A	T	45	1	1	1	1	0
<i>Luma₂</i>	1	Myrtaceae	END	I	A	S	43	0	0	0	0	0
<i>Luzuriaga</i>	3	Philesiaceae	AUS	I	A	V	56	1	1	1	0	0
<i>Maytenus₁</i>	1	Celastraceae	TRP	I	A	T	46	1	0	1	1	1
<i>Maytenus₂</i>	3	Celastraceae	TRP	I	A	S	56	0	1	1	1	1
<i>Misodendrum</i>	8	Misodendraceae	END	W	W	P	56	0	1	1	1	1
<i>Mitraria</i>	1	Gesneriaceae	END	O	A	E	50	1	1	1	0	0
<i>Muehlenbeckia</i>	1	Polygonaceae	AUS	I	A	V	44	0	0	0	1	1
<i>Mutisia</i>	2	Asteraceae	NEO	I	W	V	44	0	0	0	1	1
<i>Myoschilos</i>	1	Santalaceae	END	I	A	S	55	1	1	1	1	1
<i>Myrceugenia₁</i>	1	Myrtaceae	NEO	I	A	T	45	1	0	1	1	0
<i>Myrceugenia₂</i>	4	Myrtaceae	NEO	I	A	S	50	1	1	1	0	0
<i>Myrteola</i>	1	Myrtaceae	NEO	I	A	S	56	1	0	1	0	0
<i>Notanthera</i>	1	Loranthaceae	END	O	A	P	43	1	0	0	0	0
<i>Nothofagus</i>	7	Fagaceae	AUS	W	W	T	56	1	1	1	1	1
<i>Ovidia</i>	2	Thymelaeaceae	END	I	A	S	46	1	1	0	1	1
<i>Persea</i>	1	Lauraceae	TRP	I	A	T	43	0	0	0	0	0
<i>Philesia</i>	1	Philesiaceae	END	O	A	V	56	1	0	0	0	0
<i>Pilgerodendron</i>	1	Cupressaceae	END	W	W	T	56	0	0	1	0	0
<i>Podocarpus</i>	2	Podocarpaceae	AUS	W	A	T	50	1	0	1	0	0
<i>Prumnopitys</i>	1	Podocarpaceae	AUS	W	A	T	39	0	0	0	0	0
<i>Pseudopanax₁</i>	1	Araliaceae	AUS	I	A	T	50	1	1	1	1	0
<i>Pseudopanax₂</i>	1	Araliaceae	AUS	I	A	V	42	1	0	0	0	0
<i>Rhamnus</i>	1	Rhamnaceae	COS	I	A	S	43	0	0	0	0	0
<i>Rhaphithamnus</i>	1	Verbenaceae	NEO	O	A	S	40	1	1	1	1	0
<i>Ribes</i>	4	Grossulariaceae	BOR	I	A	S	56	1	1	1	1	1
<i>Sarmienta</i>	1	Gesneriaceae	END	O	W	E	43	1	1	0	0	0
<i>Saxegothaea</i>	1	Podocarpaceae	END	W	W	T	46	1	1	1	0	0
<i>Schinus</i>	1	Anacardiaceae	NEO	I	A	S	43	0	0	0	1	1
<i>Senecio</i>	1	Asteraceae	COS	I	W	S	56	0	1	1	1	1
<i>Solanum</i>	2	Solanaceae	COS	I	A	S	43	1	1	0	1	0
<i>Sophora (Edwardsia)</i>	1	Fabaceae	AUS	O	H	T	44	1	0	0	0	0
<i>Tepualia</i>	1	Myrtaceae	END	I	G	S	50	1	0	1	0	0
<i>Tristerix</i>	1	Loranthaceae	NEO	O	A	P	43	1	1	0	1	0
<i>Ugni</i>	2	Myrtaceae	NEO	I	A	S	44	1	0	0	0	0
<i>Weinmannia</i>	1	Cunoniaceae	AUS	I	W	T	49	1	1	1	0	0