

# Patterns of species turnover in plant-pollinator communities along a precipitation gradient in Patagonia (Argentina)

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**Abstract** Recent studies have assessed the influence of different types of gradients (e.g. altitudinal, latitudinal and temporal, among others) on the structure and function of community-level plant-pollinator webs. Although the importance of humidity as a major driver of species-richness gradients worldwide has been stressed by recent reviews, no studies have been specifically designed to address the influence of precipitation gradients on pollination webs. In the present paper we describe for the first time the turnover of species of plants and their associated flower visitors between eight communities located along a steep precipitation gradient in north-west Patagonia, Argentina. Our results show that: (i) there is a high spatial turnover of plant communities and their associated pollinators; (ii) this turnover is strongly related to precipitation changes across the region; and (iii) the turnover rate is similar for plants and pollinators. Our results support the view that the precipitation gradient is a significant factor associated with the regional turnover of plants and their pollinators in the temperate forests of southern South America.

**Key words:** community, mutualism, precipitation gradient, spatial turnover, web.

## INTRODUCTION

Understanding the relationship between the distribution of plants and animals and the factors that govern them has traditionally been a key question in ecological research (Whittaker 1967). Many studies have used gradient analysis to explore the effect of environmental variables on the distribution of plants (e.g. Nilsson & Wilson 1991; Austrheim 2002) and animals (e.g. Blake & Loiselle 2000; Colville *et al.* 2002; Kaspari *et al.* 2003; Pfeiffer *et al.* 2003; Eatough Jones & Paine 2006). Analyzing communities along a well-defined and continuous variation in an environmental factor may provide an insight into understanding how that factor controls ecosystem structure and function and, ultimately, how it influences species distributions (Koch *et al.* 1995).

Understanding the relationship between species distribution and environmental factors is crucial in light of the evidence of anthropogenic changes in climate across the globe (McCarty 2001; Walther *et al.* 2005; Shoo *et al.* 2006; Brooker *et al.* 2007). Among several adverse effects, climate change has been predicted to disrupt ecological interactions between species,

including those between plants and their pollinators, by shifting species' phenological patterns and geographical distributions (Luig *et al.* 2005; Devoto *et al.* 2007; Memmott *et al.* 2007; Tylianakis *et al.* 2008). In a given gradient, if the effect of the main environmental factor on one of the interacting guilds (e.g. either plants or pollinators) is stronger than on the other, then the potential for disruption of interactions in a climate change scenario is higher than if both groups respond similarly. Thus, understanding the way the composition of communities of plants and their partners respond to environmental variables is essential for predicting the possible effects of climate change on ecological communities.

To our knowledge, only two previous studies have dealt with compositional changes of communities of plants and their partners along a gradient (Arroyo *et al.* 1985; Colville *et al.* 2002); the evidence from these studies is contrasting. An altitudinal gradient that included three plant-pollinator communities in the temperate Andes of central Chile (Arroyo *et al.* 1982) showed that plant turnover rate (measured as average Sorensen distance in community composition between sites, and calculated from the species list available at Interaction Web Database [<http://www.nceas.ucsb.edu/interactionweb>]) doubled that of pollinators. A precipitation gradient encompassing

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three communities of monkey beetles (Scarabaeidae: Hopliini) and their associated flora in the Namaqualand region of South Africa (Colville *et al.* 2002) showed no difference in turnover rates for beetles and plants. These contrasting results could be a result of the studies dealing with different environmental factors and comprising different spatial scales (a few kilometres in Chile *vs.* several hundreds of kilometres in South Africa). The lack of additional comparable studies makes it difficult to extract a general pattern.

In this context, an already published dataset (Devoto *et al.* 2005) was re-analyzed focusing on a so far unexplored aspect: the turnover that occurs *at the level of species* in plant-pollinator communities along a precipitation gradient. This dataset comprises eight plant-pollinator communities, which range from humid *Nothofagus*-dominated forests (close to the Valdivian rainforests of Chile) to the easternmost outskirts of *Austrocedrus*-dominated dry forests on the border of the grass-shrub Patagonian steppe. The mentioned gradient occurs in western Patagonia, from 40° to 55° S, where the Andes mountain range imposes a barrier to the wet air masses from the Pacific Ocean and generates a steep precipitation decay towards the east (Paruelo *et al.* 1998a; Steffen *et al.* 1999). Although several studies have shown that precipitation is the overriding climatic factor influencing the distribution of vegetation in the region (Cabrera & Willink 1973; Roig 1998; Steffen *et al.* 1999; Páez *et al.* 2001), to our knowledge, the changes in the animal component have been somewhat neglected (but see Cabrera & Willink 1973). In addition, although several aspects of the pollination ecology of this region have been studied (e.g. Riveros *et al.* 1991; Fraga *et al.* 1997; Vázquez & Simberloff 2002, 2003, 2004; Smith-Ramírez *et al.* 2005) no studies have addressed the influence of the regional precipitation gradient on the composition of both plant and pollinator communities.

The objectives of the present study are: (i) to describe the compositional changes between communities of plants and their pollinators along a precipitation gradient; and (ii) to test whether either plants or pollinators are the guild most influenced by the gradient. Regarding the second objective, there are three alternative results: (i) the compositions of plant and pollinator communities are equally affected by the rainfall gradient (i.e. the turnover rate between communities of both guilds is similar); (ii) plants are more influenced by the gradient than pollinators (i.e. plants' turnover rate is higher than that of pollinators), and (iii) pollinators are more influenced by the gradient than plants (i.e. pollinators' turnover rate is higher). We expect plants to be more influenced by the gradient than pollinators, given that pollinators' mobility might enable them to use resources outside the portion of the gradient in which they breed, whereas plants are more

restricted to their breeding climatic envelope. Thus, *a priori*, we expect the mobility of insects to blur the effect of the gradient on their distribution and, as a result, we expect their turnover rate to be lower than that of plants.

## MATERIAL AND METHODS

### Study site

The study was carried out in north-west Patagonia on the eastern slope of the Andes (Argentina) within the temperate forests biome and its transition to a grass-shrub steppe. Eight sites encompassing a 3.8-fold change in mean annual precipitation (700 to 2700 mm, Table 1), with only minor variations in altitude (~0.5-fold; 727 to 1000 m a.s.l.) and mean annual temperature (a 0.25-fold westward decrease; ~10°C to ~8°C), were selected (Fig. 1). All sites showed little evidence of human disturbance (e.g. heavy cattle grazing, recent logging activity). Previous studies have described the general ecology of the region (Veblen *et al.* 1996) and the distribution of vegetation throughout it (Roig 1998; Eskuche 1999).

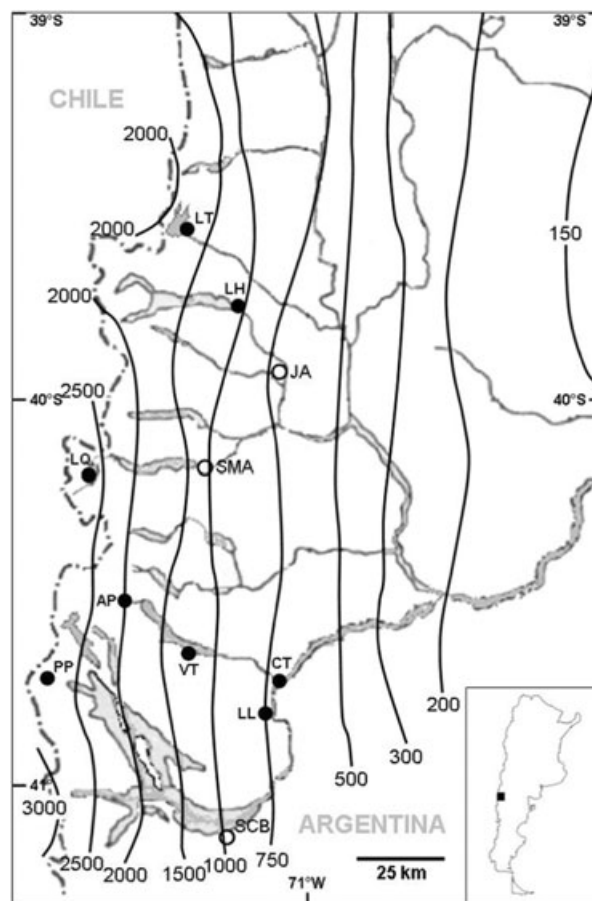
Mean annual precipitation of each site was estimated from the best available precipitation charts for the region (Movia *et al.* 1982). A graphical interpolation that assumed a linear increase in precipitation between each pair of contiguous isohyets was used. The use of this simple procedure instead of more complex interpolation algorithms (McCuen 1998) was possible because isohyets in the study region run roughly parallel in a general north-south direction (Movia *et al.* 1982; Paruelo *et al.* 1998a; Fig. 1). The difference in precipitation estimated for the Paso Puyehue site between Devoto *et al.* (2005) and the present study is a result of the recent correction of an interpolation error (note: correction of this error does not change, but rather reinforces, the conclusions of Devoto *et al.* 2005).

### Data collection

At each site, four to five trained observers recorded flower visitors and their host plants in mid-December. Additionally, a reduced team of one to two observers re-sampled most sites in mid-January or mid-December of a later year. At each site, samplings were spread over approximately 10 ha around the base camp. A rather intensive sampling protocol with the main efforts concentrated in 7–8 days of December was used. This method is particularly appropriate for the study sites given the seasonal reproductive phenology of the communities studied, which results in many

**Table 1.** Characteristics of eight complete plant-pollinator communities located in north-west Patagonia, Argentina

Site (abbreviation)	Paso Puyehue (PP)	Lago Queñi (LQ)	Lago Tromeñ (LT)	Arroyo Pedregoso (AP)	Villa Traful (VT)	Lago Huechulafquen (LH)	La Lipela (LL)	Confluencia Traful (CT)
Geographic coordinates	S 40° 44' W 71° 53'	S 40° 09' W 71° 43'	S 39° 34' W 71° 26'	S 40° 37' W 71° 35'	S 40° 39' W 71° 21'	S 39° 48' W 71° 12'	S 40° 48' W 71° 6'	S 40° 43' W 71° 05'
Mean annual precipitation (mm)	2700	2550	1750	1700	1250	1050	750	700
Altitude (m a.s.l.)	950	800	1000	872	900	780	735	727
No. pollinators	38	113	108	48	80	102	117	113
No. plants	17	23	23	16	28	29	33	21

**Fig. 1.** Location of study sites in north-west Patagonia, Argentina AP, Arroyo Pedregoso; CT, Confluencia Traful; LH, Lago Huechulafquen; LL, La Lipela; LT, Lago Tromeñ; LQ, Lago Queñi; PP, Paso Puyehue; VT, Villa Traful. The main three cities in the region are also indicated: San Carlos de Bariloche (SCB), San Martín de los Andes (SMA), and Junin de los Andes (JA). Main hydrographical features are also included. Isohyets are redrawn from Movia *et al.* (1982).

plants and pollinators being markedly active in December and, to a lesser extent, in January (Riveros & Smith-Ramírez 1996).

Each plant species was repeatedly sampled at different times of the day (between 09.00 and 18.00 hours) and on different days in order to record visitor profiles as completely as possible. An insect was recorded as a legitimate flower visitor when it worked in such a way that pollen removal from anthers or pollen deposition on stigma was possible. Although visitation not always results in effective pollination (Cayenne Engel & Irwin 2003), the terms 'pollinator' and 'flower visitor' are used interchangeably in the text for simplicity. All individuals were captured, except for the common species that could be unequivocally identified on the wing (e.g. *Bombus dahlbomii*). Plant species that received no visits and animal species that visited no plants were left out of the study. On particular species (*Discaria* spp.,

*Escallonia virgata*, *Fabiana imbricata*, *Junellia succulentifolia*, *Mulinum spinosum* and *Oenothera stricta* ssp. *altissima*) nocturnal pollinator observations were also done (between 21.30 and 23.00 hours on at least two days). These plant species were chosen for nocturnal sampling because insect activity had been observed after nightfall on their flowers at an earlier stage in fieldwork.

The identification of insect species represented a major difficulty of this study given the diverse and under-studied fauna of the region (see also Smith-Ramírez *et al.* 2005). Identifications by specialists were possible for some taxonomic groups and bird species were identified on sight in the field. Twelve plant species could not be thoroughly identified due to unrecoverable deterioration of herbarium vouchers. The minor differences in the number of plant and pollinator species between this study and Devoto *et al.* (2005) are due to improved identification of some specimens, which resulted in the merger of formerly separated morphotypes. Details on the species composition of plant-pollinator communities of all eight sites are available at: <http://agro.uba.ar/~mdevoto/patagonia.xls>.

### Sampling effort

The sampling effort used lies within the range of studies that sampled more than one site (8–92 days, as estimated in Ollerton & Cranmer 2002). Inter-annual variation, which in plant-pollinator communities can be very significant between years (Williams *et al.* 2001), was partially accounted for by sampling most sites (five out of eight) in at least two different seasons. Due to logistical reasons three sites were sampled at only one season, making the sampling effort uneven between sites. As mentioned above (see 'Data collection'), observers avoided over-capturing abundant species and concentrated the efforts on finding so far unrecorded interactions. This resulted in a biased estimation of species' abundances that prevented the use of rarefaction as a means of compensating for the uneven sampling between sites. However, comparisons with similar studies in the region suggest this study recorded a high proportion of the diversity of species engaged in pollination interactions at each site (see Devoto *et al.* 2005 for details on the contribution to visitor diversity of successive samplings). This is particularly evident for some taxa such as butterflies: whereas this study recorded 61 species of Lepidoptera, other community-level studies in the region recorded figures that are remarkably lower (Riveros *et al.* 1991, two species; Smith-Ramírez *et al.* 2005, three spp.; Vázquez & Simberloff 2003, two spp.). Thus, although a sampling effort more evenly distributed across sites would have certainly benefited the study,

it is unlikely that it would have changed its main conclusions.

### Data analysis

To assess differences between sites in the composition of the plant-pollinator communities we used the Sørensen distance ( $DS_{\text{Sør}}$ ) calculated as  $DS_{\text{Sør}} = 1 - [2c/(a + b)]$ , where  $c$  is the number of species shared by two sites, and  $a$  and  $b$  are the specific diversities of each individual site. We calculated  $DS_{\text{Sør}}$  between all possible pairs of sites for plants and flower visitors separately, resulting in two sets of 28 comparisons.

We used a partial Mantel test (Smouse *et al.* 1986) to assess whether  $DS_{\text{Sør}}$  was correlated to the differences between sites in mean annual precipitation (in mm) while controlling for the effect of geographic distance between them (in km). The partial Mantel test was carried out with a significance value of  $P = 0.05$  and based on 10 000 permutations of the data. This analysis was done for plants and pollinators separately. In addition, the differences in altitude between sites were used as an alternative explanatory variable (as a surrogate for differences in temperature; see Paruelo *et al.* 1998a for a similar approach) instead of precipitation, but they had no significant correlation with compositional differences between sites (analysis not shown). The correlation between precipitation and altitude patterns in the region (Devoto *et al.* 2005) prevented the simultaneous inclusion of both variables in the analysis. Nevertheless the increase in precipitation is considerably larger than the associated increase in altitude (3.8 *vs.* 0.5 fold, Table 1), and the former is expected to explain most of the variation along the gradient (see Aizen & Ezcurra 1998 for a discussion on the influence of precipitation *vs.* temperature patterns in the region).

We also evaluated if the rate of species turnover, measured as the Sørensen distances between adjacent sites ( $DS_{\text{Sør,adj}}$ ) was different for plants and flower visitors. For this, we carried out a t-test between the subsets of seven  $DS_{\text{Sør,adj}}$  calculated for plants and pollinators. Sites were considered adjacent in terms of annual precipitation values (e.g. PP and LQ, LQ and LT, and so on; see Table 1). All of the above analyses were repeated but excluding from the dataset those species recorded in only one site as a way of reducing the noise introduced by rare species.

Finally, compositional gradients were investigated using non-metric multidimensional scaling (NMS; Clarke 1993) as a method of ordination the eight sites. NMS was calculated with PC-ORD (McCune & Mefford 1999) both for plant and pollinator communities, and was based on Sørensen distances including all species.

## Results

A total of 2134 flower visitors belonging to 412 (morpho) species and five species of birds were recorded on flowers of 113 plant species. Sites had a mean (range) of 89.9 (38–117) species of flower visitors and 23.8 (16–33) plant species (Table 1). Most of the plants (~ 88%) were recorded in only one or two sites (72 and 28 species, respectively). Only four plant species (3.5%) were present in six or more sites, but no single plant species was recorded in all eight sites. Asteraceae (22 species), Fabaceae (13 spp.) and Scrophulariaceae (10 spp.) dominated the plant communities. Herbs were the dominant life-form (67 species), followed by bushes (33 spp.) and trees (four spp.). Eighteen plant species included in the study were adventitious.

Overall, Diptera was the richest order (156 species), followed by Hymenoptera (130 spp.), Lepidoptera (61 spp.) and Coleoptera (58 spp.). Tachinidae and Syrphidae accounted for half of the specific diversity among Diptera (40 spp., 25.6% and 35 spp., 22.4%, respectively). Several less-diverse families accounted for the rest of the flies: Bombyliidae (15 spp., 9.6%), Empididae (14 spp., 9.0%), Neme-strinidae (nine spp., 5.8%), Bibionidae and Muscidae (eight spp., 5.1%, each) and 11 additional families encompassing 27 species. Apoidea families dominated the hymenopterans: Halictidae (28 spp., 21.5%), Colletidae (22 spp., 16.9%), Apidae (19 spp., 14.6%), Megachilidae (14 spp., 10.8%) and Andrenidae (12 spp., 9.2%). Species in seven other families accounted for the remaining 26.9% of Hymenoptera. Geometridae and Nymphalidae were the most diverse families among Lepidoptera (17 spp., 27.9% and 13 spp., 21.3%, respectively), followed by Noctuidae (11 spp., 18.0%) and Hesperidae (six spp., 9.8%). Among Coleoptera the most diverse families were Melyridae (13 species representing 22.4% of all species of beetles), Buprestidae and Chrysomelidae (eight spp., 13.8% each), and Coccinellidae and Meloidae (six spp., 10.3% each), together with 17 additional species distributed in eight other families. Finally, six insect species belonging to three additional orders were recorded on flowers throughout the gradient: four Heteroptera, one Thysanoptera, and one Neuroptera. One species of Arachnida completed the arthropod visitors set. Among birds, we recorded five species (two Trochilidae, two Emberizidae and one Psittacidae), which represented 1.2% of the total pollinator community.

As mentioned in the introduction, a previous analysis of this dataset showed that while Hymenoptera dominated the drier end of the gradient, Diptera dominated the wetter sites (see Devoto *et al.* 2005) for further details). However, when the analysis of the

**Table 2.** Result of partial Mantel tests between Sørensen distances (DSør) and differences in precipitation between eight sites in north-west Patagonia (Argentina)

Guild for which DSør was calculated	Species used for DSør calculation	<i>r</i>	<i>P</i>
Pollinators	All species	0.607	0.001
	Rare species excluded	0.619	0.001
Plants	All species	0.537	0.003
	Rare species excluded	0.493	0.009

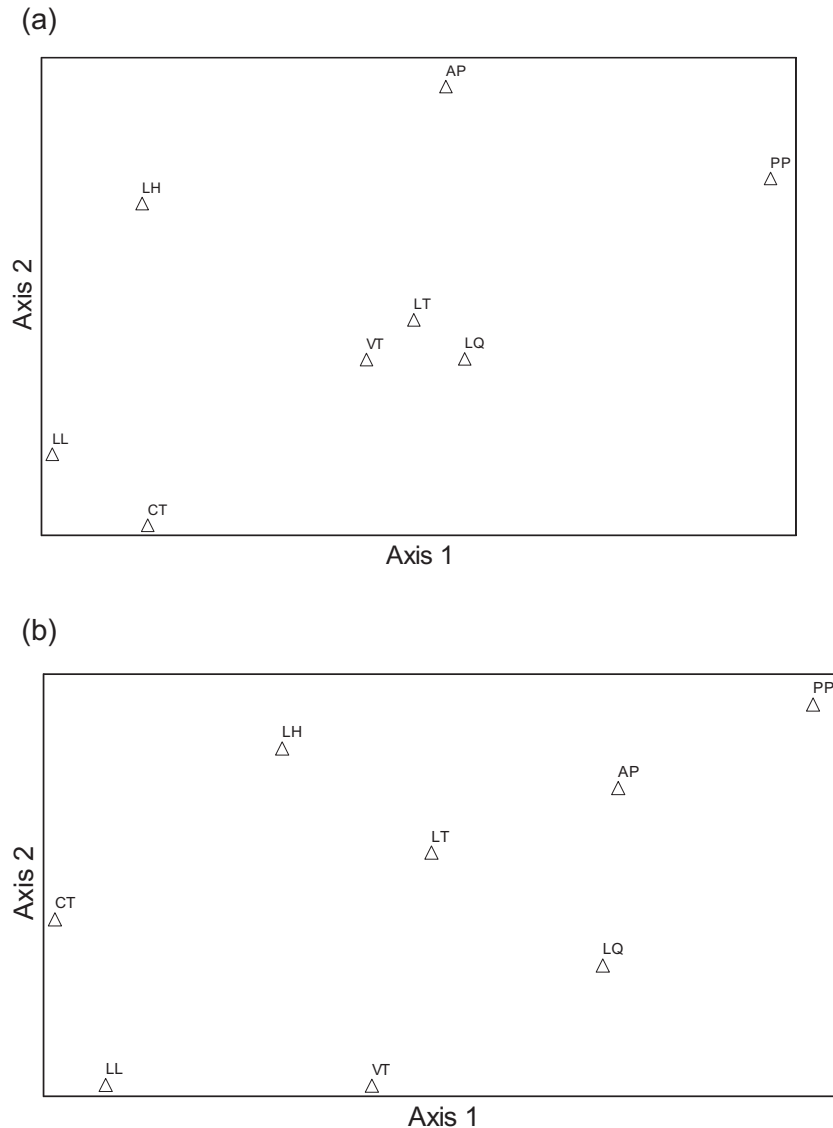
A matrix of geographic distances was used to account for spatial autocorrelation between sites. DSør was calculated between all possible pairs of sites. Tests were repeated excluding rare species (i.e. those recorded in only one site) from the dataset. The Pearson's correlation coefficient between variables (*r*) and its significance value (*P*) are shown.

west-east distribution of taxa was carried out at the level of families, the pattern was more complex. Although some families showed an evenly-distributed specific diversity across the gradient (e.g. Tachinidae, Halictidae, Geometridae and Hesperidae), other families were more diversified on the drier (e.g. Apidae, Bombyliidae, Megachilidae, Noctuidae) or the wetter portion of the gradient (e.g. Syrphidae, Buprestidae, Chrysomelidae).

Sørensen distances (DSør) were significantly correlated with differences in precipitation between sites for both plant and pollinator communities, and both with and without rare species (those recorded in only one site) in the dataset (Table 2). DSør between pollinator communities had a mean (range) of 0.76 (0.61–0.95) including all species and of 0.62 (0.38–0.91) after removal of rare species. DSør between plant communities had a mean (range) of 0.78 (0.60–0.92) including all species, and of 0.64 (0.33–0.83) after removal of rare species.

Differences in the turnover rate along the gradient (measured as Sørensen distances between adjacent sites; DSør<sub>Adj</sub>) of plants and pollinators were not statistically significant (all species,  $t = -0.959$ ; d.f. = 14;  $P = 0.354$ ; rare species removed,  $t = -0.736$ ; d.f. = 14;  $P = 0.474$ ). DSør<sub>Adj</sub> had a mean (range) of 0.69 (0.61–0.80) for pollinators and of 0.73 (0.60–0.86) for plants. After removing rare species from the dataset, DSør<sub>Adj</sub> had a mean of 0.51 (0.38–0.68) for pollinators and of 0.56 (0.36–0.79) for plants.

The NMS ordination based on the composition of flower-visitor and plant communities showed the first axis was strongly correlated with Pre (Pearson's correlation coefficient,  $r = 0.915$  for pollinators,  $r = 0.937$  for plants). Thus, both for plants and pollinators, sites result partially ordered according to their precipitation values (drier sites on the left and wetter sites on the right; Fig. 2a,b, respectively).



**Fig. 2.** Two-dimensional graphic solution to the non-metric multidimensional scaling (NMS) of (a) flower-visitor and (b) plant communities from eight sites in north-west Patagonia, Argentina. Pearson's correlation coefficients between main ordination axis and precipitation (secondary matrix in NMS) are 0.915 for pollinators and 0.937 for plants.

## DISCUSSION

Recent research has addressed variations in the structure and function of plant-pollinator webs along gradients, including variations in altitude (Kearns 1992; Ollerton *et al.* 2006), latitude (Ollerton & Cranmer 2002; Armbruster 2006), insularity (Olesen & Jordano 2002), landscape complexity (Steffan-Dewenter *et al.* 2002; Holzschuh *et al.* 2007) and successional stage following disturbance (Potts *et al.* 2003). However, until now no studies had specifically addressed the influence of regional variations in precipitation on the composition of plant-pollinator webs. In a previous paper that analyzed the same dataset used here, we

showed that strong precipitation changes along a gradient were associated with changes at the level of order in the composition of the pollinator community: flies dominated the wetter sites, while bees prevailed at the drier sites (Devoto *et al.* 2005). A likely cause for this pattern, which is also observed on a worldwide scale, is that many bee species need low moisture conditions to nest in the soil, whereas the larvae of many fly species live in bodies of standing water (Michener 1979, 2000; Kearns 1992).

In the present paper, a reanalysis of the original dataset of Devoto *et al.* (2005) described the species-level composition of eight communities of plants and their pollinators along a precipitation gradient in the

mid-latitude Andes of Argentina and revealed that: (i) there is a high spatial turnover of plant communities and their associated pollinators; (ii) this turnover is strongly related to precipitation changes across the region; and (iii) the turnover rate is similar for plants and pollinators.

### High spatial turnover of plants and pollinators

A high spatial turnover of pollinators at the landscape level has been reported in several studies worldwide (Minckley *et al.* 1999, p. 138, and references therein) and it thus seems to be a characteristic inherent to plant-pollinator systems, although the causes thereof are not clear. For north-west Patagonia, the average Sørensen distance between adjacent sites of 0.51 for pollinators and 0.56 for plants evidences a marked turnover of species along the precipitation gradient (rare species not considered). This means that, on average, roughly half of the visitor community on the one side and of the floral resources on the other are replaced from one site to the next one. This variation seems to continue on the Chilean side of the Andes: Smith-Ramírez *et al.* (2005) considered a species of *Eucryphia* and three species of Myrtaceae (none of which were recorded in the present study) as the pivotal plant species, of the temperate forest biome in the island of Chiloé. Under this view, the spatial turnover of plant-pollinator communities in the temperate forests of southern South America is much more complex than would be suggested by the changes in the group of dominant trees (several species of *Nothofagus*), which are less abrupt.

Regarding the factors causing this turnover, a significant relationship between precipitation differences and the composition of plant and visitor communities along the gradient was found. However, this does not mean that precipitation itself is the driver of the observed turnover of species. Rather, water availability can affect the distribution of plants and insects in many complex ways. Water availability can directly affect several key processes such as germination and establishment (Schutz *et al.* 2002), reproduction (Eckstein 2005), and nectar production (Leiss & Klinkhamer 2005) in plants, and nesting conditions (Okland *et al.* 2005) and survival (Knisley & Juliano 1988) in insects. For example, the diversity of Syrphidae, a family of Diptera that has aquatic larvae, was higher at the wettest sites of the gradient. This pattern is most likely explained by an increased availability of breeding sites in places with higher rainfall. In addition, water availability can indirectly affect insects via its effect on plant community composition, as insects may critically depend on various plant resources at different life stages (nesting, feeding, pupation, mate location; Dennis *et al.* 2007).

The ordination procedure based on Sørensen distances between communities, in which sites resulted roughly ordinated on the first axis according to their relative differences in precipitation (Fig. 2), further supports the view that the precipitation gradient is a significant factor (although not the only one; see below) influencing the composition of plant-pollinator communities in this region (Cabrera & Willink 1973; Jobbágy *et al.* 1996; Paruelo *et al.* 1998b). This is in accordance with a recent review (Hawkins *et al.* 2003) on plant and animal (including invertebrates) richness gradients, which showed that over most of the earth's temperate areas (as the one considered in this study) the 'water' variables (e.g. precipitation) had a stronger influence on diversity gradients than 'energy' or 'water-energy' variables (e.g. temperature, evapotranspiration), especially in the southern hemisphere.

### Unexplained variation

In spite of the high correlation between precipitation and compositional patterns other non-exclusive factors may account for the remaining unexplained variation; whereas some of these might be owed to the sampling method used, others might reflect true ecological differences between sites. First, an unavoidable single-season sampling of some communities (see Methods) may have prevented us from recording the possible inter-annual variation in visitor composition at some sites, potentially leading to exaggerated between-site differences in community composition. Also, the sampling surface limited to approximately 10 ha at each site (see Methods) may have hampered the recording of some visitor species with patchy distributions across the landscape (Minckley *et al.* 1999) also inflating between-site differences. Second, although their effect is expected to be small compared with precipitation changes, small differences in altitude and latitude between sites (0.5-fold and less than two degrees, respectively; Table 1) may still contribute to explain some of the spatial variation observed among communities. Third, some visitor species may have been absent from a particular site simply because their regular floral resources were not present there. However, a detailed study of the distribution and floral associations of the species of tangle-veined flies (Nemestrinidae) across north-west Patagonia (Devoto & Medan 2006) suggests that only sometimes (in three out of nine species) the absence of putative plant partners can be a possible explanation for the absence of a given species of pollinator. Similarly, a general low spatial predictability of co-occurrence of floral visitors and their hosts has been reported for several systems (Herrera 1988). Finally, soil differences could also be responsible for some of the unexplained variation. In fact, there is a strong regional variation in soil

characteristics but it mainly occurs in a west–east direction, like rain and altitude (del Valle 1998). Remarkably, the arid soils on the eastern sites are substantially more varying over short distances in the surface or near-surface properties (leaching characteristics, salinity levels and moisture contents) than the soils on the western sites (del Valle 1998). However, at the driest environments, where the turnover of species should be more ‘chaotic’ in response to soil heterogeneity, the species replacement seems to be explained fairly well by precipitation differences among sites: drier sites were ordered according to their relative differences in mean annual precipitation (Fig. 2).

### Similar turnover rate of plants and pollinators

Overall, both plant and pollinator communities showed a similar turnover rate along the gradient. Against our initial expectation, the higher mobility of insects does not make them less dependent on regional-scale environmental patterns. As a result, the community composition of insects is as ‘tied’ to precipitation changes as that of plants. This result is consistent with the only available study of a community of plants and their flower visitors along a precipitation gradient, in which similar turnover rates were observed across three communities of Scarabaeid beetles and their associated flora in South Africa (Colville *et al.* 2002). Further studies are needed to confirm this apparent trend.

The similar turnover rate of plants and pollinators is relevant in the context of climate change studies. Previous studies have assumed a greater susceptibility of pollinators to shifts in precipitation patterns when modelling the potential for disruption of interactions in plant–pollinator webs under climate change scenarios for Patagonia (Devoto *et al.* 2007). Our results suggest that, should the predicted shifts in rainfall patterns take place, plants and their pollinators would, on average, respond similarly. This would significantly constrain the potential for disruption of interactions and it should thus be considered in the future when modelling the response of plant–pollinator webs to climate change (Devoto *et al.* 2007).

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