Plant-pollinator Relationships at Two Altitudes in the Andes of Mendoza, Argentina

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Abstract

The assemblages of visitors to angiosperms flowering at a montane and at a high alpine site in the Andes of Mendoza, Argentina (33–34°S) were described and the plant-flower visitor matrices were analyzed and compared to other systems, in particular those located at a similar latitude on the western slope of the Andes. In the low-altitude (montane) habitat, 23 plant species had a total of 126 interactions with 71 taxa of insects and one hummingbird, and at the higher site 21 plants and 45 insect species had 83 interactions. Connectances of the visitor matrices were 7.6 and 8.7, respectively. Diptera and Hymenoptera dominated the visitor assemblages at both sites without change of proportions with altitude, while Lepidoptera significantly increased at the higher site. Flies were more species-rich than expected at the sites' latitude and more constant across altitudes than is usually observed. Lack of a significant decrease with altitude of (1) the frequency of Hymenoptera and (2) the number of interactions per plant were the main differences with a comparable gradient in the Chilean Andes. The proportion of self-compatible species increased with altitude; however, use of phylogenetically-independent contrasts showed that the prevalence of selfers at higher altitudes does not reflect a generalized reaction pattern but results from two speciose families (Asteraceae and Fabaceae) showing more self-compatibility at high altitudes.

Introduction

Many plants engage in specialized relationships with their pollinators (Faegri and van der Pijl, 1971; Proctor et al., 1996; Endress, 1998). However, plant-pollinator mutualisms are more commonly opportunistic and flexible (Jordano, 1987; Waser et al., 1996; Ollerton, 1998; Thompson, 1998; Hingston and McQuillan, 2000), i.e., most plant species have several pollinators and most pollinators visit more than one species (Proctor et al., 1996; Kearns et al., 1998). Therefore, as a rule a community approach will produce a more realistic picture of pollination relationships than autoecological studies. The difficulties inherent to the description of complete pollination webs have kept the number of such studies low (Jordano, 1987; Elberling and Olesen, 1999), and more information is needed to make more valid generalizations, e.g., on latitudinal and altitudinal patterns of variation of the structure of pollination webs (Elberling and Olesen, 1999). Community-level pollination studies are important for several research areas, including evolution of mutualisms and restoring of damaged ecosystems (Waser et al., 1996; Memmott, 1999).

The environmental conditions in alpine habitats (low temperatures, short growing seasons, and strong winds) may reduce the possibilities of cross pollination and are believed to represent important driving forces in the evolution of self-pollination at high altitudes and high latitudes (Savile, 1972; Bell and Bliss, 1980; Molau, 1993; Sandvik et al., 1999). In the mid-latitude Andes of Chile, however, the prediction of increased self-compatibility at higher altitudes has been questioned (Arroyo et al., 1985). A joint examination of plant-pollinator interactions and plant breeding systems along a comparable altitudinal gradient would reveal in which way both patterns are related.

Pollination studies at community scale are still few in southern South America, and we know only one paper that approaches a description of an entire pollination web in the region (Arroyo et al., 1982). The present paper reports on a study at two sites located at different altitudes in the central Andes of Mendoza, Argentina. In studying the pollination biology of a number of co-occurring plant species there are many aspects that could be considered. We focused on the structure of the plant-flower visitor interaction matrix of each community, asking about the effects of altitude on (1) the composition of visitor assemblages and (2) the proportion of self-compatible species in the plant community. We specifically tested the prediction that the degree of self-compatibility increases with altitude and compared our results with information available for other systems, especially those at the western slope of the Andes. The selection of the study sites at the opposite side of a biogeographic barrier like the Andes provides an opportunity to compare the responses of two related biotas to a similar range of physical environmental variation.

Materials and Methods

The study was carried out in the province of Mendoza, Argentina. The Laguna Diamante (LD) site was located at 34°10′S, 69°42′W at 3300 m a.s.l., and consisted of a 100 m × 200 m plot on the western shore of the Diamante lake, comprising low to very low, sparse vegetation on sandy soil near the shoreline and on rocky inland soils. The Río Blanco (RB) site was located at 33°00′S 69°17′W at an altitude of 1900 m a.s.l., and consisted of a 100 m × 250 m plot on the lower course of the Río Blanco, including woody riverine vegetation and scrub developed on the

drier adjacent terrain. Long-term climatic data for these sites are not available. Mendoza sites located at altitudes comparable to those of LD and RB have mean annual temperatures of −1.5 and 11.2°C, and mean annual precipitations of 700 and 300 mm, respectively (Capitanelli, 1972). Field work was conducted from 14 to 20 January 1995 at LD and from 11 to 17 December 1996 at RB. These dates were selected because pollinator activity tends to be highest at early flowering in alpine habitats (Arroyo et al., 1985; Inouye and Pyke, 1988; Totland, 1993).

Air temperature, relative humidity, and wind speed were recorded with hand-held instruments. We observed flower visitors by sampling along transects across the plot, trying to sample on each plant species at different times of the day and on different days in order to record visitor profiles as completely as possible. Twenty plant species that received no visits were left out of the study. We spent on average 5 h of observation and sampling on each plant species. Hummingbirds were identified visually, insects were caught and pinned, and plants were pressed. At LD 66% and at RB 56.9% of the visitor taxa could be identified to species or genus. When identifications to species were not available the material was morphotyped (in several cases with the assistance of specialists). All collected material is deposited at our department or (in the case of some insects) in the collections of assisting entomologists. The number of sampled (or observed) flower-visiting individuals of a given visitor species was used as a measure of its overall abundance. Flower rewards were identified by dissection of 10 flowers per species in the field. Breeding systems were estimated using pollen:ovule (p:o) ratios according to Cruden (1977). Pollen and ovule counts were averaged from a minimum of three flowers per species, using unopened buds fixed in FAA in the field. Ovules were counted under a dissecting microscope and pollen grain numbers were calculated extrapolating from haemocytomer counts. In four cases (species 6, 14, 16, and 23; for specific codes see Table 2) the fixed material proved to be inadequate and additional buds were obtained fom herbarium vouchers (label data available on request). Two heterostylous species (species 29 and 30) were scored as obligate xenogamous in spite of their p:o ratio predicting other breeding systems.

Appropriate statistical testing of the prediction that self-compatibility (SC) increases with altitude requires accounting satisfactorily for taxonomical effects. To this end we applied a method based on phylogenetically independent contrasts (PICs, Burt, 1989). Phylogenetically independent contrasts were obtained using the phylogenetic arrangement proposed by Soltis et al. (2000). Species (or groups of species) were chosen that differed in origin (lower or higher site) such that each pair would constitute an independent contrast of pollen:ovule ratios. When more than one species was present in a given member of a pair, p:o ratios were averaged over all species included in that pair member. The values for each comparison were included in one overall paired t-test (for similar approaches, see Herrera et al. [1998] and Roulston and Buchmann [2000]). Since each breeding system corresponds to a range of p:o ratios, in some cases comparing p:o ratios can be misleading (because species with different p:o ratios may have the same breeding system). Therefore, a more conservative analysis was performed in which each p:o ratio was replaced by the corresponding breeding system. For calculations, breeding systems were given numerical values as follows: facultative autogamy = 1, facultative xenogamy = 2, and obligate xenogamy = 3.

Visitation records were used to construct plant-visitor matrices, which in turn were employed to draw qualitative plant-visitor webs (Memmott, 1999), and to analyze plant-visitor interactions, including calculation of connectance values. Calculations and most statistical analyses were performed with Microsoft Excel 97 and Statistica 4. The distributions of mutualist interactions were compared with Brandt-Snedecor tests (Sachs, 1978).

Results

SYSTEM CHARACTERISTICS

As expected because of the 1400 m difference in altitude, the LD site was colder and more windy than the RB site (Table 1). At LD, temperatures fell below zero every night and a snow storm took place on 16 January. Including both sites, a total of 359 animal visitors pertaining to 117 taxa visited 43 plant species. At LD, 45 insect species visited 21 of the 40 species potentially attracting visitors. At RB, 71 species of insects and one species of hummingbird visited 23 of the 24 plants surveyed. The system characteristics are summarized in Table 1. Traits related with the plant hosts are presented in the Table 2, and animal visitors are listed in Table 3. Both plant-visitor webs are graphically presented in Figure 1.

MUTUALIST COMMUNITIES

The number of plant species with visitors were nearly equal, but their composition was almost entirely different at the species level (there was only one shared plant species). Five genera (14% of total) and eight families (38%) were present both at LD and RB. Only four families (Asteraceae, Fabaceae, Portulacaceae, and Cactaceae) were represented with more than one species at the same site. Plant life forms were unequally distributed between sites (Table 1). Perennial herbs were more common at LD than at RB (N = 17 vs. 14), and shrubs were more abundant at RB (N = 9 vs. 4). Most plants offered nectar as a reward (N = 18), followed by species offering nectar and pollen (N = 15) and those with pollen only (N = 8). Only one species (*Jaborosa laciniata*) lacked rewards at all, their flowers being visited by deceit (Table 2). Half of the flowers were white or yellow, the remainder split among seven other colors. The relative abundance of flower reward types did not significantly differ between sites (Chi-square tests, $P \geq 0.51$), nor did that of flower colors (Chi-square tests, $P \geq 0.28$).

The animal communities differed between sites both in size and composition. The visitor assemblage at RB was 1.6 times greater than it was at LD, and the corresponding values at familial and ordinal level were 1.3 and 1.4. No animal species was shared between sites, but a large proportion of the families were (41%). Diptera dominated both insect communities in number of species and individuals, followed by Hymenoptera and (depending on site) Coleoptera and Lepidoptera (Table 4). Accordingly, the more species-rich families belonged to the first two orders (Syrphidae: 13 spp., Apidae: 8 spp., Tachinidae: 7 spp., Megachilidae: 7 spp., Bombyliidae: 6 spp., Andrenidae: 6 spp., both sites considered). The proportions of the visitor orders did not differ significantly between sites (Chi-square tests, $P \geq 0.19$), with the exception of Lepidoptera, which was more species-rich at LD (Chi-square = 7.54, df = 1, P = 0.006).

PLANT-ANIMAL INTERACTIONS

There were strong among-species differences in the number of interactions. At LD two plant species exceeded by far the mean number of interactions (*Discaria nana,* 20 interactions; *Azorella monanthos,* 12), and at RB *Grindelia chiloensis* showed

TABLE 1

Physical data and structure of the plant-pollinator system at two sites in the Andes of Mendoza, Argentina, and relevant comparative figures for equivalent sites at Cordón del Cepo, Chile (33°17'S, 70°16'W)[a]

	Mendoza		Cordón del Cepo	
	Laguna Diamante	Rio Blanco	Subnival area	Subandean scrub
Altitude (m)	3300	1900	3200–3600	2200–2600
Maximal daytime temperature (mean ± SE) (°C)	21.2 ± 1.2	22.5 ± 2.3		
Minimal daytime temperature (mean ± SE) (°C)	3.8 ± 0.7	13.3 ± 1.5		
Maximal windspeed (mean ± SE) (m s^{-1})	6.3 ± 1.2	4.9 ± 0.6		
Number of animal orders	5	7		
Number of animal families	24	31		
Number of plant families	14	15		
Number of animal species (a)	45	72	43	112
Total number of plant species	40	24		
Number of plant species visited (p)	21	23	38	86
System size (M = ap)	945	1656	1634	9632
Total number of interactions between species (I)	83	126	84	379
Connectance (C = I/M%)	8.78	7.60	5.1	3.9
Number of species interactions (mean ± SD [skewness])				
Per animal species	1.84 ± 1.24	1.75 ± 1.31	1.95	3.37
	[2.24 ± 0.35]	[3.18 ± 0.28]		
Per plant species	3.95 ± 4.57	5.59 ± 8.64	2.21 ± 1.74	4.40 ± 4.57
	[2.57 ± 0.5]	[2.70 ± 0.49]	[1.47 ± 0.38]	[2.33 ± 0.26]

[a] Data taken or calculated from Fig. 2 and Appendix II of Arroyo et al. (1982); only visited plants considered.

34 interactions, *Discaria trinervis* 28, and *Baccharis pingraea* 11 (Fig. 1). The flower visitors that showed the higher number of interactions were *Copestylum aricia* (9), *Megachile* sp1 (7), *Scaeva occidentalis* (6) and Bombyliidae sp1 (5) (Fig. 1).

The per-plant and per-animal average number of interactions varied with altitude (Table 1), but differences were nonsignificant (Mann-Whitney U = 234.5, P = 0.86 for plants, U = 1474.0, P = 0.41 for animals). As an effect of the unequal size of the interacting communities (Elberling and Olesen, 1999), plants had 2.14 as many interactions as animals at LD, and 3.25 as many interactions as animals at RB. The frequency distribution of plant interactions (Fig. 2) was not different from that of animal interactions (Fig. 3) at LD (Brandt-Snedecor Chi-square = 13.9, df = 7, P > 0.05) but they differed at RB (Brandt-Snedecor Chi-square = 21.7, df = 4, P < 0.01). Between-site differences were nonsignificant for plants and animals (P > 0.05, Brandt-Snedecor tests). Therefore, plants and visitors were equally generalized at both altitudes, but visitors were more generalized than hosts at the lower site. As a consequence of a few mutualists having many interactions and many mutalists having few interactions, most distributions departed from normality (Kolmogorov-Smirnov D = 0.272, P < 0.01 and D = 0.320, P < 0.01 for plant interactions at LD and RB, respectively; D = 0.236, P = 0.14 and D = 0.301, P < 0.05 for animal interactions at LD and RB, respectively).

At both sites, Diptera and Hymenoptera were slightly more overrepresented in the interaction web than expected according to their number of species (Fig. 1). This may be a consequence of their relatively high abundance as compared to other orders (Table 4). The mean number of interactions and the mean number of individuals were strongly correlated across the seven most species-rich families, six of which belonged to Diptera or Hymenoptera (Table 5; Spearman R = 0.99, P = 0.000015, both for LD and RB), indicating that the level of generalization was connected with each visitor's abundance in the community.

OUTCROSSING LEVEL AND ALTITUDE

Obligate outcrossers were significantly more common at RB than at LD (N = 15 vs. 6, Chi square = 9.05, P = 0.0026). Pollen: ovule ratios were on average 3.8 times higher at RB than at LD (mean ± SD = 10791.6 ± 22756.1 vs. 2824.6 ± 5125.1; Mann-Whitney U = 125.5, P = 0.006) (Table 1). This seems to confirm the prediction that self incompatibility decreases with altitude. But, is this result owed to a casual aggregation of high-p:o ratio species at RB and low-p:o ratio species at LD, or is there a generalized trend to increased SC with altitude across plant lineages? To provide an answer, 11 phylogenetically independent contrasts were constructed, which included 90% of all species (Table 6). Two PICs were within-genus (*Discaria* and *Oxalis*), five were within-family (Asteraceae, Fabaceae, Onagraceae, Brassicaceae, and Malvaceae), and the remaining contrasts involved species of different families. In 10 out of the 11 PICs the p:o ratio was lower in the LD-species (or species group) than in the corresponding RB-species or species group (paired t-test on log-transformed data: t = −3.89, df = 10, P = 0.003). This indicated that a phylogeny-independent, negative relationship exists between altitude and average pollen:ovule ratio. When we applied the more conservative approach of comparing the estimated breeding systems instead of p:o ratios (Table 6), we found that the LD species (or species group) of the pair had a more self-compatibility (SC) biased breeding system than its RB counterpart in four cases, a less SC-biased system in two cases, and the same breeding system in five cases. While self-compatibility was still numerically prevalent at LD, statistical significance was not reached (Wilcoxon matched paired test, T = 3.5, Z = 1.77, P = 0.075). Therefore, within our sample, plant lineages in general did not respond to environmental differences related to altitude with significant changes in the breeding system. Prevalence of self-compatibility at RB and self-incompatibility at LD was mainly due to two families in which self-compatibility increases with altitude (Asteraceae and Fabaceae) being rich in species at both sites.

Each plant's number of interactions and its pollen:ovule ra-

TABLE 2

Characteristics of plants included in two plant-pollinator systems in the Andes of Mendoza, Argentina[a]

C	Species	Family	Site	LF	FC	FR	p:o ratio	BS
1	*Adesmia haemisphaerica* Hauman	Fabaceae	LD	S	Y+O	N	1236.5	FX
2	*Adesmia retrofracta* Hook. et Arn.	Fabaceae	RB	PH	Y+O	N	14789	OX
3	*Arjona patagonica* Hombron & Jacquinot	Santalaceae	RB	PH	W	N	11667	OX
4	*Astragalus cruckshanksii* (Hook. et Arn.) Grisebach	Fabaceae	LD	PH	V	N	1003.1	FX
5	*Astragalus nivicola* Gómez-Sosa	Fabaceae	LD	PH	V	N	615.6	FX
6	*Azorella monanthos* Clos in Gay	Apiaceae	LD	CU	Y	N+P	21875	OX
7	*Baccharis pingraea* DC.	Asteraceae	RB	PH	W	N+P	12317.4	OX
8	*Calandrinia caespitosa* Gill. ex Arn.	Portulacaceae	LD	PH	R+Y	N+P	55.8	FA
9	*Cerastium arvense* L.	Caryophyllaceae	LD	PH	W	N+P	711.2	FX
10	*Discaria nana* (Clos.) Weberb.	Rhamnaceae	LD	CU	W	N+P	8161.8	OX
11	*Discaria trinervis* (Hook. et Arn.) Reiche	Rhamnaceae	RB	S	W	N+P	15970.1	OX
12	*Epilobium nivale* Meyen	Onagraceae	LD	PH	PI	N	32.5	A/FA
13	*Grindelia chiloensis* (Corn.) Cabrera	Asteraceae	RB	SS	Y	N+P	5542	OX
14	*Hypochoeris montana* (Phil.) Reiche	Asteraceae	LD	PH	Y	N+P	1805.5	FX
15	*Hysterionica jasionoides* Willd.	Asteraceae	RB	PH	Y	N+P	2600	OX
16	*Jaborosa laciniata* (Miers) A.T. Hunziker & G. Barboza	Solanaceae	LD	PH	B	WR	1605.2	FX
17	*Junellia* cf. *tonini* (Kuntze) Moldenke	Verbenaceae	RB	CU	V	N	2099	FX
18	*Larrea divaricata* Cav.	Zygophyllaceae	RB	S	Y	N	110563	OX
19	*Lathyrus* sp.	Fabaceae	RB	AH	BL	N	850	FX
20	*Lecanophora heterophylla* (Cav.) Krapovickas	Malvaceae	RB	PH	PI	P	6157	OX
21	*Leuceria candidissima* Don	Asteraceae	LD	PH	W/PI	N	1490	FX
22	*Loasa incurva* Crespo & Pérez-Moreau	Loasaceae	LD	PH	W+Y	N	10622.4	OX
23	*Menonvillea hookeri* Rollins	Brassicaceae	LD	PH	W+R	P	2360.4	OX
24	*Mimulus* sp.	Scrophulariaceae	RB	PH	Y	N	70	FA
25	*Montiopsis gilliesii* (Hook. et Arn.) Ford	Portulacaceae	LD	PH	W	N+P	79.7	FA
26	*Mutisia decurrens* Cav.	Asteraceae	RB	VI	O	N	6667	OX
27	*Oenothera mendocinensis* Gilles ex Hook. et Arn.	Onagraceae	RB	PH	Y	N	91	FA
28	*Opuntia corrugata* S-D.	Cactaceae	RB	S	R	P	1199	FX
29	*Oxalis* sp.	Oxalidaceae	RB	PH	Y	N	1705.1	OX
30	*Oxalis erythrorhiza* Gillies	Oxalidaceae	LD	PH	Y	N	1387.2	OX
31	*Perezia pilifera* (Don.) Hook. et Arn.	Asteraceae	LD	PH	CR	P	900	FX
32	*Phacelia* cf. *secunda* Gmelin	Hydrophyllaceae	LD, RB	PH	W/V	N	590.9	FX
33	*Polygala stenophylla* A. Gray	Polygalaceae	RB	PH	PI	N	1692	FX
34	*Pyrrhocactus* cf. *strausianum* (K. Schum.) Berger	Cactaceae	RB	S	Y	P	3409.6	OX
35	*Rapistrum rugosum* (L.) Allioni	Brassicaceae	RB	AH	Y	N+P	27445.1	OX
36	*Rosa rubiginosa* L.	Rosaceae	RB	S	PI	P	2945	OX
37	*Senecio filaginoides* DC.	Asteraceae	RB	S	W	N+P	6666	OX
38	*Senecio subulatus* Don ex Hook. & Arn.	Asteraceae	RB	S	Y	N+P	1687	FX
39	*Senecio tricephalus* OK.	Asteraceae	LD	SS	Y	N+P	496.8	FX
40	*Senecio looseri* Cabr.	Asteraceae	LD	PH	Y	N+P	314.6	FA/FX
41	*Sisyrinchium junceum* ssp. *junceum* E. Meyer ex Presl.	Iridaceae	LD	PH	PI	P	177.1	FA
42	*Tarasa humilis* (Gill.) Krapovickas	Malvaceae	LD	PH	PI	P	3795.5	OX
43	*Thelesperma megapotamicum* (Spreng.) O. Kuntze	Asteraceae	RB	PH	Y	N+P	11486	OX

[a] Abbreviations: A = autogamy, AH = annual herb, B = black, BL = blue, BS = expected breeding system, C = species code, CR = cream, CU = cushion, FA = facultative autogamy, FC = flower color, FR = flower reward, FX = facultative xenogamy, LD = Laguna Diamante, LF = life form, OX = obligate xenogamy, P = pollen, PH = perennial herb, PI = pink, R = red, RB = Rio Blanco, S = erect shrub, SS = subshrub, V = violet, VI = vine, W = white, WR = without reward, Y = yellow.

tio were positively correlated (Spearman $R = 0.44$, $P = 0.031$ at RB; $R = 0.50$, $P = 0.020$ at LD). Neither flower characteristics (color and type of reward) nor life forms significantly differed among plants showing numbers of interactions below and above the site's average (Chi-square tests, $P > 0.05$). As in the previous analysis, the correlation lost significance when estimated breeding systems were used instead of p:o ratios (Spearman $R = -0.19$, $P > 0.05$).

Discussion

This study investigated the plant-visitor web structure at two widely differing altitudes in the mid-latitude Andes of Ar-

gentina. To our knowledge this is the first study of this type to be carried out in Argentina.

Diptera constituted the most abundant visitor group. With ca. 42% of the total visitor fauna, the proportion of flies exceeded the prediction of Elberling and Olesen (1999) for our sites' latitude (32%). However, flies did not significantly increase with altitude as could be expected from other studies. For instance, Diptera grow in importance as pollinators with increasing altitude in the European Alps (Müller, 1880), the Himalayas (Mani, 1962), British Columbia (Pojar, 1974), New Zealand (Primack, 1978, 1983), and Chile (Arroyo et al., 1982).

Arroyo et al. (1982) provided visitation profiles for three different levels of the Andes in Chile, of which the low- and

TABLE 3

Animal visitors in two plant-pollinator systems in the Andes of Mendoza, Argentina[a]

TABLE 3

Continued.

Code	Family	Order	Species	Site
a	Anthomyiidae	D	Anthomyiidae sp1	LD
b			Anthomyiidae sp2	RB
c	Bibionidae	D	Bibionidae sp1	RB
d			Bibionidae sp2	RB
e	Bombyliidae	D	Geron sp.	LD
f			Thyridanthrax sp1	LD
g			Thyridanthrax sp2	LD
h			Thyridanthrax sp3	LD
i			Thyridanthrax sp4	LD
j			Thyridanthrax sp5	RB
k	Calliphoridae	D	Chlorobrachycoma versicolor	LD
l			Compsomyiops fulvicrura	RB
m			Calliphoridae sp1	LD
n			Calliphoridae sp2	RB
o	Chironomidae		Chironomidae sp.	LD
p	Empididae	D	Empididae sp.	RB
q	Ephydridae	D	cf. Mosillus sp.	LD
r		D	cf. Notiphila sp.	RB
s			Ephydridae sp.	RB
t	Muscidae	D	Muscidae sp1	RB
u			Muscidae sp2	RB
v			Muscidae sp3	RB
w			Muscidae sp4	RB
x	Sarcophagidae	D	Microcerella rusca	LD
y			cf. Microcerella sp.	RB
z			Sarcophagidae sp.	RB
al	Syrphidae	D	Alipumilio sp.	RB
af			Carposcalis punctulata	RB
am			Carposcalis saltana	RB
aa			Copestylum aricia	RB
ab			Copestylum sp2	RB
ae			Dolichogyna sp.	LD
ad			Eristalis tenax	RB
ac			Eristalis bogotensis	RB
ak			Ocyptamus meridionalis	RB
ai			Scaeva occidentalis	RB
ag			cf. Toxomerus sp.	RB
ah			Tropidia notata	LD
aj			Syrphidae sp3	RB
an	Tabanidae	D	Dasybasis chillan	LD
ao	Tachinidae	D	Tachinidae sp1	LD
ap			Tachinidae sp2	LD
aq			Tachinidae sp3	LD
ar			Tachinidae sp4	RB
as			Tachinidae sp5	RB
at			Tachinidae sp6	RB
au			Tachinidae sp7	LD
av	Tephritidae	D	Tephritidae sp.	RB
aw	unidentified	D		LD
ax	Buprestidae	C	Buprestidae sp.	RB
ay	Cantharidae	C	Cantharidae sp.	RB
az	Coccinelidae	C	Coccinela anchoralis	LD
ba			Eriopis cf. conexa	RB
bb			Coccinelidae sp1	RB
bc			Coccinelidae sp2	RB
bd			Coccinelidae sp3	RB
be	Curculionidae	C	Curculionidae sp.	RB
bf	Meloidae	C	Epicauta sp.	RB
bg	Melyridae	C	Astylus sp.	LD
bh	Mordellidae	C	Mordellidae sp.	RB
bi	unidentified	HE	Hemiptera sp1	RB
bj			Hemiptera sp2	RB
bk	Andrenidae	HY	Arhysosage bifasciata	RB
bl			Callonychium mandibulare	RB
bm			Liphantus sp1	LD
bn			Liphantus sp2	LD
bo			Psaenythia rufipes	RB
bp			Spinoliella sp.	LD
bq	Apidae	HY	Alloscirtetica antarctica	LD
br			Alloscirtetica herbsti	RB
bs			Alloscirtetica sp.	LD
bt			Apis mellifera	RB
bu			Centris muralis	RB
bv			Centris sp.	RB
bw			Diadasia patagonica	RB
bx			Svastrides zebra	RB
by	Colletidae	HY	Chilimelissa farellones	LD
bz			Chilimelissa sp.	LD
ca			Colletes lycii	RB
cb	Crabronidae	HY	Podagritus sp.	LD
cc	Eumenidae	HY	Hypodinerus sp1	LD
cd			Hypodinerus sp2	LD
ce			Hypodinerus sp3	RB
cf			Eumenidae sp.	RB
cg	Halictidae	HY	Augochloropsis sp.	RB
ch			Caenohalictus sp1	RB
ci			Caenohalictus sp2	RB
cj			Dialictus sp1	RB
ck			Dialictus sp2	RB
cl	Ichneumonidae	HY	Ichneumonidae sp.	LD
cm	Megachilidae	HY	Anthidium chubuti	LD
cn			Anthidium rubriceps	RB
co			Chalepogenus caeruleus	RB
cp			Megachile sp1	LD
cq			Megachile sp2	LD
cr			Megachile sp3	RB
cs			Megachile sp4	RB
ct	Pompilidae	HY	cf. Entypus sp.	RB
cu	Sphecidae	HY	Ammophila sp.	RB
cv			Oxybelus sp.	RB
cw			Prionyx sp.	RB
cx			Sphecidae sp.	RB
cy	Geometridae	L	Geometridae sp.	RB
cz	Hesperiidae	L	Pyrgus cf. fides	LD
da	Noctuidae	L	Agrotis ipsilon	LD
db			Peridroma saucia	LD
dc			Pseudoleucania nobilis	LD
dd			Pseudoleucania sp.	LD
de			Tamseuxoa ingoufii	LD
df	Nymphalidae	L	Issoria lathonioides	LD
dg			Vanessa cf. cardui	RB
dh	Pieridae	L	Tatochila sp.	RB
di			Phulia sp1	LD
dj			Phulia sp2	LD
dk	unidentified	T	Thysanoptera sp1	LD
dl			Thysanoptera sp2	RB
dm	Trochilidae	TR	Sappho sparganura	RB

[a] Abbreviations: C = Coleoptera, D = Diptera, HY = Hymenoptera, HE = Hemiptera, L = Lepidoptera, LD = Laguna Diamante, RB = Rio Blanco, T = Thysanoptera, TR = Trochiliformes.

high-altitude ones are comparable with ours (see Table 1). Instead of Diptera, at Arroyo et al.'s (1982) low-level Hymenoptera dominated (44.6%), decreasing sharply with altitude (13.9%) in favor of Diptera (58.1%) (Table 4). The increase of
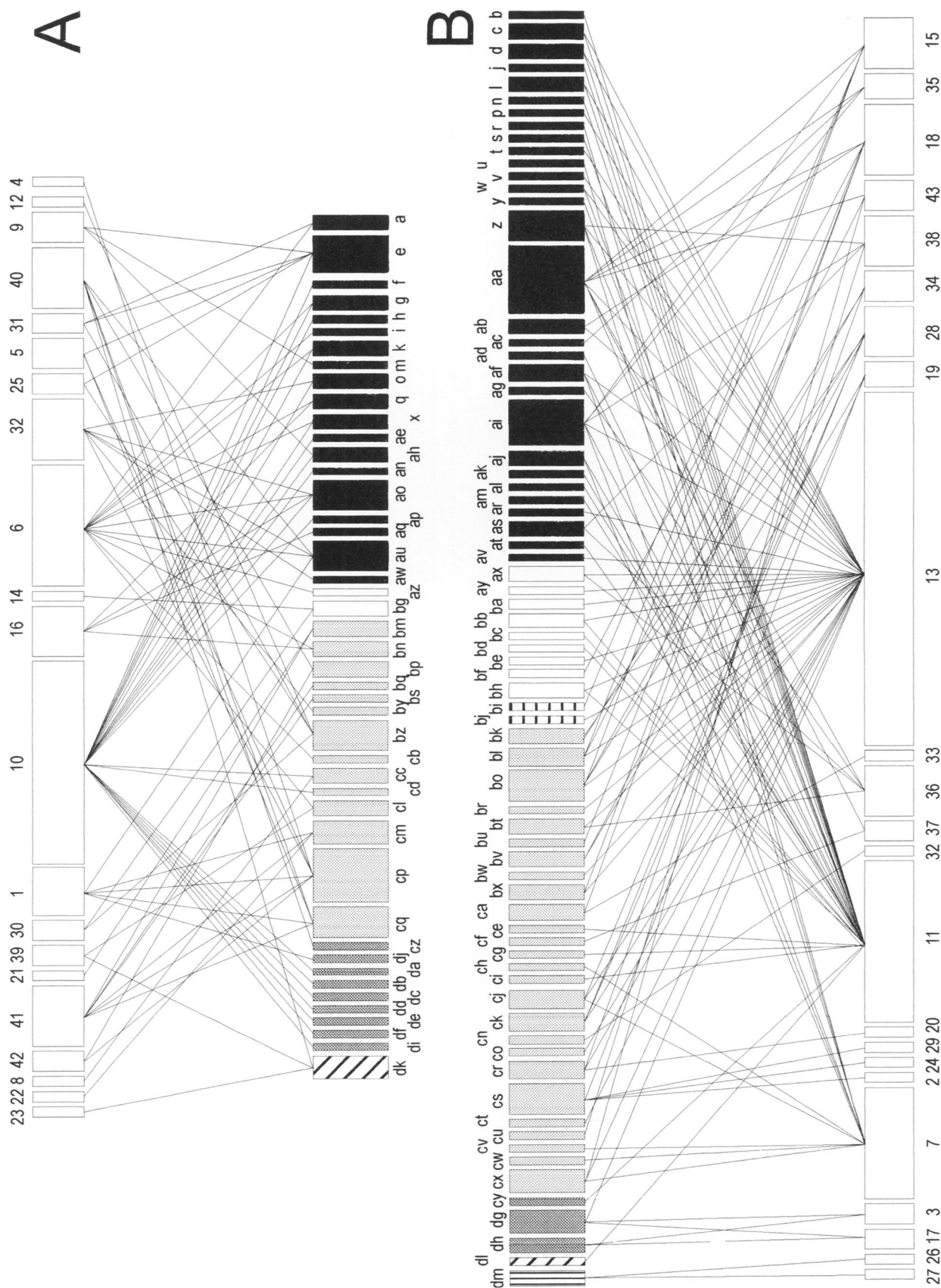
FIGURE 1. *Qualitative pollination webs for the Laguna Diamante site (A) and the Río Blanco site (B). Each box represents a species. For letter codes (animals) see Table 2, for numerical codes (plants) see Table 2, for letter codes (plants) see Table 3. Box width is proportional to the species' number of interactions. The specular web arrangement is intended to facilitate between-site comparison of the relative proportions of groups of animal mutualists (among these, black = Diptera, white = Coleoptera, horizontal hatching = Hemiptera, light gray = Hymenoptera, dark gray = Lepidoptera, diagonal hatching = Thysanoptera, vertical hatching = Trochiliformes).*
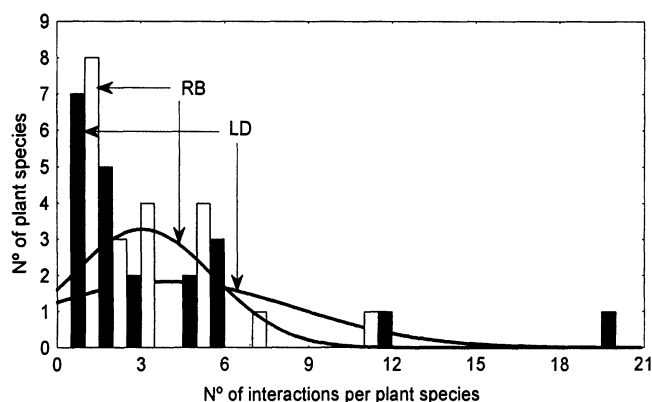
FIGURE 2. Frequency distribution of generalization level of plants at the Laguna Diamante and Río Blanco sites. A normal fit corresponding to sample values was inserted in the the histogram plot.
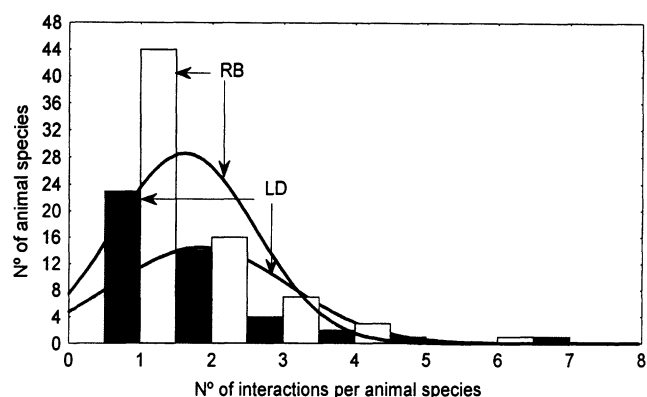

FIGURE 3. Frequency distribution of generalization level of animals at the Laguna Diamante and Río Blanco sites. A normal fit corresponding to sample values was inserted in the the histogram plot.

Lepidoptera was comparable to that in our sites. The particular bias in the Chilean visitation pattern results from the unusually rich bee fauna in the lower Mediterranean sclerophyllous scrub adjacent to the Andes range (Arroyo et al., 1982), which explains the high proportion of hymenopterans at the lower montane level. Remarkably, the decrease of bees and wasps with altitude at our sites was much more moderate. At the higher level, in Mendoza there were more than twice the number of species than in Chile and hymenopterans still accounted for 31.1% of the pollinator assemblage. Presently we have no explanation for this transandean difference in abundance of Hymenoptera.

The connectance values we obtained for the RB and LD sites (7.6 and 8.7%, respectively) lie close to, or within, the known range for high latitude- and altitude systems (8.6–19, Elberling and Olesen, 1999). Arroyo et al.'s (1982) systems were 5.8–1.7 times larger than ours (lower and upper level, respectively; Table 1) and showed a stronger decrease in complexity with altitude than we recorded in Mendoza (Chi-square = 35.8, $P < 0.0001$, for the number of interactions at the upper vs. the lower sites; Table 1). Their (appreciably smaller) connectance values increased with altitude like ours. Lower connectance values may be a consequence of vegetation heterogeneity within each area sampled by Arroyo et al. (1982). Since these vegetation belts spanned 500 m in altitude, different, poorly connected plant-pollinator subsystems may have been included in each area, in contrast with our much smaller and more homogeneous

plots where all plant individuals lie within flight distance of most pollinators. Comparing both Andean slopes, plant's generalization level was similar within altitudes (Mann-Whitney $U = 944.5$, $P = 0.74$ for the lower level; $U = 303.0$, $P = 0.12$ for the upper level) but, unlike at the eastern slope, the decrease of per-plant interactions with altitude was significant at the Chilean side (Fig. 4, Mann-Whitney $U = 1120.0$, $P = 0.0053$) and plants were more generalized at the higher than at the lower level (Brandt-Snedecor test, Chi-square = 11.8, $P < 0.05$).

Self-compatible species become more frequent with altitude at our sites, in accordance with a prediction based on several studies (see Introduction). For instance, at comparable mid-latitude alpine sites, Moldenke (1979) found an increase of habitual or obligate selfers of 31 to 70% between 1700 and 3400 m, figures that are not distant from ours (3 and 62%). Therefore, the mid-latitude Andes are not exceptional as regards the increase of SC with altitude, contrary to the suggestion of Arroyo et al. (1985). However, using phylogenetically independent contrasts we showed that the prevalence of self-compatible species at higher altitudes does not result from a generalized reaction pattern, but from certain speciose families (Asteraceae and Fabaceae) showing more SC at high altitudes. The use of PICs may be a useful tool in studies of this type, to determine whether the increase of SC with altitude is restricted to altitude-sensitive lineages, or is a community-scale phenomenon.

The fact that the per-plant number of interactions did not

TABLE 4

Species richness and abundance of orders of flower visitors at two sites in the Andes of Mendoza, Argentina, and relevant comparative figures for equivalent sites at Cordón del Cepo, Chile

| | Mendoza | | | | | | | | Cordón del Cepo | | | |
| | Laguna Diamante | | | | Rio Blanco | | | | Subnival area | | Subandean scrub | |
	No. of species	%	No. of individuals	%	No. of species	%	No. of individuals	%	No. of species	%	No. of species	%
Diptera	19	42.2	49	43.7	30	41.7	115	46.5	25	58.1	45	40.1
Hymenoptera	14	31.1	38	33.9	26	36.1	92	37.2	6	13.9	50	44.6
Lepidoptera	9	20	13	11.6	3	4.2	9	3.6	9	20.9	12	10.7
Coleoptera	2	4.4	6	5.3	9	12.5	25	10.1	3[a]	6.9	5[a]	4.5
Hemiptera	0	0	0	0	2	2.7	2	0.8				
Thysanoptera	1	2.2	6	5.3	1	1.4	2	0.8				
Trochiliformes	0	0	0	0	1	1.4	2	0.8				

[a] All other visitors pooled.

TABLE 5

Flower specialization among the most abundant insect families at two sites in the Andes of Mendoza, Argentina. Only families with 5 spp. or higher are included. Mean ± SD

Family (no. of spp.)	No. of plant species visited per insect sp. (generalization level)		No. of visiting individuals per insect sp. (abundance)	
	LD	RB	LD	RB
Syrphidae (13)	1.5 ± 0.7	2.54 ± 2.62	2.5 ± 2.12	5.45 ± 5.85
Apidae (8)	1.0 ± 0.0	1.5 ± 0.54	1.0 ± 1.0	4.0 ± 3.28
Tachinidae (7)	2.25 ± 1.5	1.33 ± 0.57	3.5 ± 3.31	4.0 ± 4.35
Megachilidae (7)	4.33 ± 2.3	2.25 ± 1.5	5.33 ± 1.52	3.75 ± 3.4
Bombyliidae (6)	2.0 ± 1.73	1.0 ± 0.0	3.4 ± 2.51	1.0 ± 0.0
Andrenidae (6)	2.0 ± 0.0	3.0 ± 1.0	2.66 ± 0.57	9.33 ± 7.5
Coccinelidae (5)	1.0 ± 0.0	1.25 ± 0.5	1.0 ± 0.0	2.25 ± 2.5

FIGURE 4. *Frequency distribution of generalization level of plants at two levels in the Cordón del Cepo, Chile (data from Arroyo et al. [1982], for details see text.) A normal fit corresponding to sample values was inserted in the the histogram plot.*

show a significant decrease with altitude does not imply that opportunities for outcrossing were similar at both altitudes, because the overall visitation rate was much lower at the higher site (Medan, pers. observation; also reflected in the values of insect abundance, Tables 4–5, and in the fact that no visits were recorded for many plants potentially attracting visitors at LD). A drastic impoverishment of the visitation web would be unexpected even if self-compatibility were more strongly prevalent, because visitors may be needed for efficient selfing (e.g., in *Saxifraga stellaris*, Sandvik et al., 1999).

The simultaneous occurrence within a system of a few plants with many interactions and many species with few interactions has been already observed (Moldenke, 1979; Memmott, 1999; Elberling and Olesen, 1999), which suggests that a non-normal distribution of the number of plant interactions is of common occurrence. Plants attracting a high proportion of the available animal mutualists may represent the main nectar and pollen source in the system, playing a crucial role in the community (cornucopia species, Moldenke and Lincoln, 1979; keystone species, Memmott, 1999; core species, Ne'eman et al., 2000). At both altitude levels we detected species falling into this category, all of which offered nectar and pollen as reward, but their actual importance cannot be assessed without further studies.

In our systems the plants with the most interactions had the highest p:o ratios, and the correlation was stronger at the high-
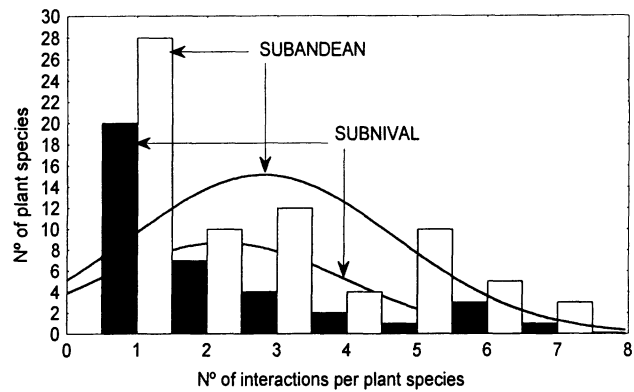
altitude site. Although a correlation between number of interactions and breeding system could not be demonstrated, the trend occurred at both sites and should be further explored. Competition for pollinator service has been shown to be one of the selective forces leading to autogamy (Wyatt, 1983); accordingly, under conditions of insufficient or unpredictable pollinator service, the less visited plants of a community are expected to include those having escaped competition by evolving selfing. The visitation pattern we found, especially at the higher site, may represent the outcome of such a process of disruptive selection on breeding systems. Disruptive selection is known to produce divergence and reproductive isolation in populations (Strickberger, 1996). An alternative way to escape competition (via a reduced overlap of flowering periods) is unexpected because in areas of high environmental stochasticity, directional selection for phenological displacement (Feinsinger, 1987) is probably weaker than selection for early flowering (see Totland, 1993).

Acknowledgments

TABLE 6

Phylogenetically independent contrasts (PICs) of pollen:ovule ratios and breeding system types between species (or species groups) occurring at two sites in the Andes of Mendoza, Argentina[a]

Level of PIC	Composition of pairs being compared		Sign of PIC	
	LD	RB	p:o ratio	breeding system
within genus	10	11	LD < RB	LD = RB
within genus	30	29	LD < RB	LD = RB
within family	1, 4, 5	2, 19	LD < RB	LD < RB
within family	14, 21, 31, 39, 40	7, 13, 15, 26, 37, 38, 43	LD < RB	LD < RB
within family	12	27	LD < RB	LD = RB
within family	23	35	LD < RB	LD = RB
within family	42	20	LD < RB	LD = RB
between families	6, 22	18, 33, 36	LD < RB	LD > RB
between families	8, 25	28, 34	LD < RB	LD < RB
between families	9	3	LD < RB	LD < RB
between families	16	17, 24	LD > RB	LD > RB

[a] For species encoding see Table 2.

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