

Patterns of interaction between plants and pollinators along an environmental gradient

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Patterns of variation in plant–pollinator (p–p) systems in response to environmental variables have been the focus of much recent attention. We analyzed species diversity and generalization of interactions of flower visitors belonging to eight p–p networks along a steep rainfall gradient in NW Patagonia, Argentina. To our knowledge, this is the first published study that applies a humidity – gradient approach to p–p networks analysis. Throughout the gradient, we recorded 1232 interactions between 413 different animal species and 111 plant species. We found that (a) specialization measures showed no clear pattern of variation throughout the rainfall gradient, (b) the diversity of flower-visiting insects does not consistently respond to rainfall gradients along the gradient, and (c) as we predicted, flies dominated the wetter end of the gradient, while at the drier end bees prevailed. The lack of differences in diversity could be explained by the repeated cycles of species extinctions undergone in the past by the southern temperate forests, which dominate the wetter end of the gradient. A logistic model that related the flies' dominance of the visitor assemblage with latitude was good predictor of the average fly composition of the entire region, although we found major between-site variations in response to local environmental conditions. The replacement of flies by bees towards the drier end of the gradient seemed to repeat a worldwide pattern where flies dominate humid regions while bees attain their greatest abundance in xeric regions. Regional patterns in the structure of our p–p systems (composition of the visitor fauna) were better explained by altitudinal differences, while function (percentage of interactions established by each taxon) seemed to be more influenced by precipitation.

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Plant–animal mutualistic interactions have a pervasive influence on community dynamics and diversity. Since Darwin (1859), biologists have been increasingly aware of the importance and complexity of pollination interactions in communities (Kearns and Inouye 1997, Kearns et al. 1998, Traveset 1999), posing questions that have been addressed both on evolutionary and ecological grounds (Proctor et al. 1996, Waser et al. 1996, Thompson 1998, Jordano et al. 2003).

Patterns of variation in plant–pollinator (p–p) systems along environmental gradients have been add-

ressed in a variety of ecological and spatial scales. Published papers include examples of search for patterns in response to variations in altitude (Moldenke 1975, 1979a, b, Kearns 1992, Totland 1993, Malo and Baonza 2002, Medan et al. 2002), latitude (Ollerton and Cranmer 2002), insularity (Ollerton and Cranmer 2002, Jordano et al. 2003), landscape complexity (Steffan-Dewenter and Tschardtke 1999, Steffan-Dewenter et al. 2001, 2002, Tschardtke and Brandl 2004) and successional stage following disturbance (Potts et al. 2001, 2003). These studies, at the same time, reveal the difficulty

inherent to gathering this type of data, which poses a constant trade off between spatial resolution (from local to worldwide), taxonomic scope (from single species to whole community) and sampling effort (from a few days to years). This trade off is evidenced in that studies which gathered data on several sites only focus on a single species (Malo and Baonza 2002), whereas studies that focused on whole communities are often based on few contrasting study sites (e.g. two sites in Medan et al. 2002 and Totland 1993, three sites in Arroyo et al. 1982). In addition, studies that search for worldwide patterns have no choice other than revise pre-existing data to answer questions for which such data was not primarily collected, thus suffering from statistical flaws (as the authors themselves notice; Ollerton and Cranmer 2002, Jordano et al. 2003). However, some of the available studies successfully test the impact of gradients on entire p-p systems using specifically designed replicated experiments (Steffan-Dewenter and Tscharrntke 1999, Steffan-Dewenter et al. 2001, 2002, Potts et al. 2001, 2003). In spite of the considerable attention that this topic has received, to our knowledge, there are no available community-level surveys specifically planned to address the influence of regional scale humidity gradients on patterns of interaction between plants and pollinators.

For many decades, the use of natural gradients of various types and scales has been a common ecological tool for understanding the influence of environmental factors on structure and functioning of terrestrial ecosystems (Vitousek and Matson 1991, Hawkins et al. 2003). The gradient approach allows examination of variation in a single factor while many of the other environmental variables remain as constant as possible. Recently, this approach has also proved valuable for global change research (Steffen et al. 1999). An initiative of the International Geosphere-Biosphere Program (IGBP) identified a set of naturally occurring transects of climate and vegetation around the globe which represent an array of regional scale gradients on all continents that vary in major environmental variables (Steffen et al. 1999).

In the Patagonian region of South America, from 40° to 55° S, there is a strong longitudinal rainfall gradient, with a shift in vegetation in less than 150 km from xeric desert shrubland to grass-shrub steppe, leading to a low stature tree cover and finally closed canopy forest (Movia et al. 1982, Austin and Sala 2002). This rainfall gradient, identified as an IGBP transect, provides the opportunity to examine a wide range of p-p communities occurring in close proximity, encompassing a striking 3.6-fold change in mean annual rainfall with a minor 0.5-fold variation in altitude (pers. obs.) and a 0.25-fold change in mean annual temperature (Movia et al. 1982). There is strong evidence to expect that these minor variations in altitude and temperature do indeed

have little influence on the p-p systems included in this study and, conversely, to regard likely that the rainfall gradient is the major influence on the structure and function of these communities. In a recent review of available studies on plant and animal (including invertebrates) richness gradients, Hawkins et al. (2003) showed that over most of the earth (included temperate areas, such as the included in this study) the “water” variables (e.g. rainfall) were better predictors of species richness than “energy” or “water-energy” variables (e.g. temperature, evapotranspiration), especially in the southern hemisphere. Supporting this view, within the same region of our study Jobbágy et al. (1995) reported that along an E-W transect (42–44° S) the main floristic gradient was strongly correlated with total annual precipitation. In addition, a study of the pollination mechanisms in the forests that lie on the western side of the gradient suggested that an eastward decrease in the incidence of hummingbird-dependence among woody taxa is evidence of the influence of the rainfall gradient on pollination mutualisms (Aizen and Ezcurra 1998).

In this paper, we specifically seek to answer the following questions: (1) are interactions more specialized/generalized in wetter than in dryer environments? (2) Is the flower-visiting fauna more diverse in the more humid environment of the western end of the gradient? (3) Does any particular visitor taxon dominate the visitor assemblages towards either extreme of the gradient?

In contrast with the western end of the gradient, we expect the easternmost environments, which are dryer (Paruelo et al. 1998a) and less predictable (in terms of inter-annual rainfall variation, Jobbágy et al. 1995), to promote the existence of more opportunistic pollinators. Thus, a priori, we predicted an eastward increase in generalized interactions.

Elaborating our predictions regarding the second question is somewhat more difficult. The flower-visiting fauna of NW Patagonia reflects the long history and complex biogeographic origin of the region (Raven and Axelrod 1974, 1975, Aizen and Ezcurra 1998). The existence of relict, yet rather diversified taxa of bees (Michener 1979) and flies (Bernardi 1973) of Gondwanian origin are evidence of the extinctions and habitat contraction events that took place in South America since mid Tertiary (Hinojosa and Villagrán 1997, Aizen et al. 2002). At the same time, several bee taxa of Neotropical origin are abundant at the driest points of the gradient (Michener 1979). Moreover, the pollinator assemblage of the temperate forests within the region is reported as unexpectedly rich, as would be expected from the history of the region (Aizen et al. 2002). In summary, previous evidence does not lead to any obvious prediction regarding patterns of diversity of flower-visitors along the gradient. Thus, as a verifiable expectation, a null hypothesis of no change along the gradient seems suitable here.

Concerning dominance of a given part of the gradient by any particular taxa, several factors need to be considered. Patterns of abundance of insect taxa have been reported to relate to plant diversity and abundance (Potts et al. 2001), diversity of habitat types (Steffan-Dewenter et al. 2002), soil preferences for nesting including moisture, sand and humus content, shadiness, exposure and slope (Kearns 1992, Potts and Willmer 1997, Michener 2000), and predation of larvae by ants (Michener 2000). Among these, moisture deserves special attention in light of (a) the evidence of its influence on world-scale patterns of invertebrate richness mentioned above (Hawkins et al. 2003) and particularly (b) because it has been proposed as a likely cause behind the worldwide pattern of abundance of the two major pollinator taxa: bees and flies. In general, solitary bees are more abundant in warm-temperate xeric (excluding extreme desert) regions (Michener 1979, 2000) while flies are commonly found in moist habitats (Kearns 1992). Nesting conditions might play an important role in shaping this pattern given the fact that bee groups that are more successful in humid areas are mostly those that no longer nest in the soil or that do not use simple cells excavated in it (Michener 2000). Thus, along our gradient we expect to observe a higher diversity of bees in the dryer extreme of the gradient coupled with domination by flies at the wetter sites. Answering these questions could be a valuable step towards understanding the influence of environmental variables in p–p interactions and mutualisms in general, both in a local and in a broader biogeographical context.

Material and methods

The study was carried out on the western part of the IGBP transect mentioned above which corresponds to a temperate forest and its transition to grass–shrub steppe (Patagonia, Argentina; Paruelo et al. 1998b). The southern South American temperate forests extend over a narrow strip from ca 35° S to 55° S latitude over much of southern Chile and the eastern slope of the Patagonian Andes in Argentina (Zegers 1993, Arroyo et al. 1996). Such distribution is explained by the north–south bounding of the Andes which impose an important barrier to the wet air masses from the Pacific Ocean (Paruelo et al. 1998a) generating an exponentially diminishing rainfall gradient from the Andes to the east. The distance from the Andes to the east explains 94% of the mean annual precipitation spatial variability (Paruelo et al. 1998a). Furthermore, as already mentioned, towards the drier end of the gradient inter-annual variation in rainfall increases markedly i.e. climate conditions become less predictable from one year to the next (Jobbágy et al. 1995).

Within the described area, we selected eight sites encompassing a mean annual precipitation (Pre) from 700 to 2550 mm (Table 1, Movia et al. 1982). We obtained mean annual precipitation values for each site from the best available precipitation charts (1:2 000 000; Movia et al. 1982). We used altitude (m a.s.l. measured in the field with a Garmin e-trex GPS) as a surrogate for temperature due to the inaccuracy associated to extrapolating from temperature charts of the region (Paruelo et al. 1998a for a similar approach).

To reflect “natural” communities as well as possible we selected sites with the least evidence of anthropic disturbance (heavy cattle grazing, recent logging activity, closeness to human settlements, etc.). At each site, 4–5 well trained observers collected data over a period of 7–8 days in mid-December. Additionally, a reduced team of 1–2 observers revisited most sites in mid-January and/or mid-December of a later year (Table 1) to further complete the plant–animal visitation web.

Throughout the field season, we observed flower visitors by sampling along transects in each site. We sampled on each plant species at different times of the day and on different days in order to record visitor profiles as completely as possible (see Table 1 and below for comments on estimates of sampling effort at each site). In all sites, a small proportion of the observations were performed using walking paths and watercourses as transects when vegetation was too dense to permit walking through it. Clearly, it is expected to find somewhat different plant–pollinator assemblages associated to watercourses as compared to the surrounding landscape matrix. However, we considered these watercourses (which are clearly more densely distributed towards the more humid sites; Movia et al. 1982) as an element of the landscape intimately associated to the amount of rainfall at each site, and thus being an inherent part of the typical habitats along the gradient. At worst, our occasional sampling along watercourses in all sites might reduce differences between sites, in which case our reported differences are conservative in this respect. An “interaction” was recorded when animals while foraging on a flower worked in such a way that pollen removal from anthers or deposition on stigma was possible. In all sites, we left out the study plant species that received no visits and sun-basking insects.

For each site, we constructed the plant–pollinator interaction web as a binary matrix where 1s represented observed visitations while 0s represented absence of interaction (Olesen and Jordano 2002). Based on these matrices, we calculated a set of descriptive parameters of the interaction webs: connectance (C, formula in Table 1), number of interactions, plant species and animal species (L, P and A, respectively). To assess the generalization level of the interactions, at each site we calculated mean number of interactions across animal and plant species (L_A and L_P , respectively; formula in

Table 1. Characteristics of eight complete plant–pollinator networks located in NW Patagonia, Argentina. Sampling effort was calculated as fieldwork days × no. of persons participating in fieldwork × no. of hours of observations per day.

| Site (abbreviation) | Lago Queñi (LQ) | Paso Puyehue (PP) | Lago Tromen (LT) | Arroyo Pedregoso (AP) | Villa Traful (VT) | Lago Huechulafquen (LH) | La Lipela (LL) | Confluencia Traful (CT) |
|--|------------------------|--------------------|------------------------|-------------------------------------|-------------------------------------|-------------------------|------------------------|-------------------------------------|
| Date of field observations | Dec. 1999 Jan. 2000 | Dec. 2001 | Dec. 1998 Dec. 2003 | Dec. 2001 Dec. 2002 Jan. 2003 | Dec. 2001 Dec. 2002 Jan. 2003 | Dec. 1997 Dec. 2003 | Dec. 2000 Jan. 2001 | Dec. 2001 Dec. 2002 Jan. 2003 |
| Geographic coordinates | S40°09' W71°43' | S40°44' W71°53' | S39°34' W71°26' | S40°37' W71°35' | S40°39' W71°21' | S39°48' W71°12' | S40°48' W71°06' | S40°43' W71°05' |
| Mean annual precipitation (Pre) (mm) | 2550 | 2000 | 1750 | 1700 | 1250 | 1050 | 750 | 700 |
| Altitude (m a.s.l.) | 800 | 950 | 1000 | 872 | 900 | 780 | 735 | 727 |
| Sampling effort (SE) (hours) | 304 | 48 | 180 | 68 | 92 | 232 | 320 | 92 |
| No. of flower visitors (A) | 116 | 38 | 113 | 48 | 122 | 101 | 122 | 117 |
| No. of plants (P) | 23 | 17 | 23 | 16 | 28 | 30 | 34 | 21 |
| System symmetry (A:P) | 5.04 | 2.24 | 4.91 | 3.00 | 2.93 | 3.37 | 3.59 | 5.57 |
| Total number of interactions (I) | 186 | 64 | 194 | 71 | 171 | 146 | 231 | 169 |
| Connectance (C = 100*I/(A*P)) | 7.0% | 9.9% | 7.5% | 9.4% | 7.4% | 4.8% | 5.6% | 6.9% |
| Mean number of interactions across plant species (I _p = I/P) | 8.09 | 3.76 | 8.43 | 4.44 | 6.11 | 4.87 | 6.79 | 8.05 |
| Mean number of interactions across animal species (I _a = I/A) | 1.60 | 1.68 | 1.72 | 1.51 | 2.09 | 1.45 | 1.89 | 1.44 |

Table 1). In addition, we calculated the importance of the main orders of flower visitors in the visitation webs both in terms of percentage of the total visitor fauna and in terms of percentage of the community interactions accumulated by each taxa. The influence of SE on these two measures was tested for the same taxa.

With this data, we constructed linear models to investigate the relationship across sites between the relative frequency (%) of Diptera and Hymenoptera as flower visitors, and precipitation and altitude as the independent variables. For each dependent variable, we compared the performance of both models in terms of the percentage of variation they explained. We additionally compared our data with the logistic model proposed by Elberling and Olesen (1999) which describes an increase of dominance of the visitor assemblage by flies towards higher latitudes according to the formula

$$\%Dip = \frac{e^{-2.15 + 0.0443lat}}{1 + e^{-2.15 + 0.0443lat}} \cdot 100$$

To further refine our results we performed a canonical correspondence analysis with Pre, Alt and SE as independent variables and total species richness and Diptera:Hymenoptera ratio (both in terms of species richness and interactions established) as dependent variables. Finally, to evaluate the validity of our conclusions, we compared our models with three other community-level surveys available within the same region (Riveros et al. 1991, Aizen et al. 2002, Vázquez and Simberloff 2003, 2004).

Accounting for additional effects on system properties

Recent empirical studies (Elberling and Olesen 1999) and influential reviews (Olesen and Jordano 2002, Ollerton and Cranmer 2002) have stressed the influence that sampling effort (SE), system symmetry (A:P) and the potential number of interactions (M = A × P, also referred as “network size” in Olesen and Jordano 2002) can have on the properties of a p–p web.

We estimated sampling effort (SE) at each site as fieldwork days × no. of hours of observations per day × no. of persons participating in fieldwork (SE is thus expressed in hours). The eight sites included in our study varied considerably in sampling effort (Table 1). Consequently, we tested the effect of SE on A, P, I and C through one-way ANOVAs. In the cases this effect was significant, when assessing the response of A, P, I and C to Pre we accounted for it by including SE together with Pre as a complex of independent variables in a multiple regression analysis (see Ollerton and Cranmer 2002 for a similar approach).

System symmetry has been suggested to influence estimations of generalization levels in plants and animals when measured as I_A and I_P (Elberling and Olesen 1999). Differences in I_A and I_P between communities may be the result of their differences in A:P rather than due to other more complex ecological factors (Olesen and Jordano 2002). For example, an apparent trend for decreased plant generalization in island p-p webs compared to mainland ones was associated with island networks showing a markedly lower A:P ratio than mainland networks (Olesen and Jordano 2002). Consequently, when analyzing the dependency of I_A and I_P on Pre and Alt, we included A:P in the regression model to account for this effect.

The maximum number of interactions (M) may strongly influence estimations of C as in general, C decreases hyperbolically with increasing M (Jordano 1987, Olesen and Jordano 2002). We accounted for differences in M by incorporating this variable into a multiple regression when including Alt or Pre as independent variables (Olesen and Jordano 2002 for a similar approach).

Finally, even when differences in altitude (Alt) across our eight sites seem of little incidence as compared to the prevailing steep humidity gradient, we additionally explored the effect of Alt as a variable. However, we avoided including Pre and Alt together in the same regression model because they are correlated variables (Pearson's correlation coefficient: $r = 0.83$, $P < 0.05$) and would likely introduce multicollinearity-related flaws into our analysis. Nevertheless, as discussed above, the increase in Pre is considerably larger than the associated increase in Alt (3.6 vs 0.5 fold), and we expected the former to explain most of our variation along the gradient.

Quality of the data set

The quality of our data set should be evaluated in light of the scope and objectives of this study. We will address three concerns that could obscure the conclusions we draw upon our sampling procedures (a) seasonal variation, (b) interannual variation, and (c) the consequences of temporal aggregation of data, this third point being closely related to the first two. We used a rather intensive sampling protocol during a short time-span with the main efforts concentrated in 7–8 days of December to generate for each site a “snapshot” capturing the essence of the interaction structure of these communities (for a similar approach see Medan et al. 2002), regardless of seasonal variation. This method is particularly appropriate for our sampling sites given the unimodal and strongly seasonal reproductive phenology of the communities studied, where the activity of most plants and pollinators is markedly concentrated in December and,

to a lesser extent, in January (Smith-Ramírez and Armesto 1994). For example, Riveros and Smith-Ramírez (1996) reported for Puyehue National Park (79 km west of our PP site, 40°44'S; 72°49'W) a flowering peak from mid November to early December where 71.4% of the species were in bloom. A similar pattern has been described also for the steppe habitats on the driest sites of the gradient (Soriano et al. 1976). Certainly, such a short sampling window would be seriously questionable if applied to (other) year-long active systems (Petanidou 1991, Petanidou and Ellis 1993, Petanidou et al. 1995, Medan et al. 2005) where, unlike the present study, a significant non-overlap of phenologies and a continuous turnover of species in the reproductive stage are expected, unlike our own study.

To our knowledge, among more than forty available studies on complete plant–pollinator webs (most of these reviewed by Olesen and Jordano 2002, Ollerton and Cranmer 2002, and to which Moldenke 1975, 1979a,b, Primack 1978, Riveros 1991, Totland 1993, Medan et al. 2002 and Vázquez and Simberloff 2003, 2004 should be added) few have attempted to generate webs at more than one site (e.g. Arroyo et al. 1982, which studied 3 sites; Medan et al. 2002, 2 sites; Moldenke 1979a, 3 sites; Moldenke 1979b, 8 sites; Moldenke and Lincoln 1979, 5 sites; Primack 1978, 2 sites; Primack 1983, 5 sites; Totland 1993, 2 sites; Vázquez and Simberloff 2003, 8 sites) and in these studies sampling efforts at each site range (as estimated in Ollerton and Cranmer 2002) from eight days (Moldenke and Lincoln 1979) to 92 days (Primack 1983). Thus, our own sampling effort is well within the range of published studies.

A second concern is that our survey may undersample inter-annual variation, as it has been demonstrated that variation in pollinator communities can be very significant between years (Williams et al. 2001 for a recent review on bees). We hope to have partially circumvented this problem by sampling most sites (five out of eight) in at least two different seasons. Unfortunately, three sites were sampled for only one season (though two of them were visited twice within the same season) due to logistical reasons (our laboratory is ca 1500 km away from the study region!). Consequently, we have interpreted our own results with caution when this source of variation was likely to affect them. Furthermore, to evaluate to what degree successive samplings at each site contributed to detecting new species, we calculated the relative contribution of each sample to the total flower-visitor diversity recorded at each site (Results).

Finally, while in studies aimed at describing the overall diversity of a given group (as in this case would be the pollinators) multiple samplings over successive seasons and years are advisable to account for seasonal and inter-annual variation, when it comes to the functional aspects of the community to follow the same criteria

could be misleading. Most published studies, when describing the interaction structure of a p–p web, suppose all partners to coexist and to be simultaneously active in pollen presentation or pollen transport. However, a potential problem arises from the fact that in year-long active systems non-coincident phenologies may give rise to “forbidden links” (sensu Jordano et al. 2003), that is, impossible interactions between never-coincident partners. The existence of the problem has been already perceived (Jordano 1987, Martínez and Dunne 1998, Olesen and Jordano 2002, Olesen et al. 2002, Bascompte et al. 2003, Jordano et al. 2003) and its impact on the parameters used to describe network properties (several of which are used in the present study) has only recently been analyzed in some detail for p–p networks (Medan et al. 2005). Therefore, the use of shorter sampling periods can reveal more biologically relevant interaction patterns that a whole-system figure could obscure.

Overall, we have tried to be honest about the limitations of our own data set and we hope that the declared impact of sampling effort on our measures do not affect seriously our general conclusions and furthermore, make our own study more easily comparable to other data sets.

Statistical analysis

Except for Pre and Alt, all variables (I, A, P, S, M, A:P, L_A and L_P) were natural-log transformed and C was angular transformed in order to achieve normality and a constant variance (Sokal and Rohlf 1994). We performed all regressions using linear regression models. In partial regression analysis, R^2 , t and P values are accompanied with a sub-index corresponding to the independent variable referred. Deviations are standard errors unless otherwise noted.

Given the quantity of analyses performed, we used pathway analysis as a heuristic tool to summarize all the relationships we tested between variables (Fig. 1a; Vázquez and Simberloff 2004 for a similar approach).

Results

The pathway analysis in Fig. 1b summarizes the relationships between variables that resulted significant. Differences in sampling effort (SE) among sites had a significant effect on number of interactions (I), plants (P) and animals (A) recorded, as well as on connectance (C) estimations (F values of one-way ANOVAs were 8.76, 7.22, 8.40 and 11.43, respectively; all $df=1,6$ and $P<0.05$). Number of interactions was positively related to the maximum number of interactions, M ($R^2=0.91$, $F=67.54$, $df=1,6$; $P<0.001$, $L=41.29+0.05M$) and

to species richness, S ($R^2=0.90$, $F=57.34$, $df=1,6$; $P<0.001$, $L=-13.23+1.46S$). Incorporating SE as a second independent variable together with M or S did not significantly increase the percentage of variation in I explained by the regression models ($R^2=0.91$, $F=28.33$, $df=2,5$; $P<0.001$, $R^2=0.90$, $F=24.28$, $df=2,5$; $P<0.01$, respectively). Connectance, C, decreased very significantly with M ($R^2=0.99$, $F=2292.16$, $P<0.0001$) and with S ($R^2=0.96$, $F=178.19$, $P<0.0001$). When testing the dependency of C on Alt or Pre, SE was incorporated in the regression models together with M, but the percentage of variation it individually explained was not significant (Table 2). This is because M and S are directly correlated with SE (Pearson’s correlation coefficient: $r=0.81$ and 0.78 respectively, $df=6$ and $P<0.05$ for both) and M explained most of the observed variation (more than 99%, Table 2).

As expected, A:P had a significant effect on I_A ($F=13.99$, $df=1,6$, $P<0.01$), though not on I_P ($F=5.18$, $df=1,6$, $P=0.063$; Table 2). Thus, to account for differences in symmetry we incorporated A:P as a second independent variable when analyzing the dependency of I_A and I_P on Alt or Pre.

In sites that were visited twice, the first survey contributed on average ca 73.0% (range: 68.4–77.4, Fig. 2) of the total diversity of each site. In sites that received three visits the first and second surveys accounted for 76.7 and 13.4%, respectively (ranges: 69.1–84.4 and 4.3–20.9, respectively, Fig. 2). The recorded diversity of all main groups of flower visitors (Hymenoptera, Diptera, Coleoptera and Lepidoptera) increased in a similar manner following successive visits (analysis not shown).

The eight sites encompassed interactions by a total of 413 different animal species and 111 plant species. A and P had a mean (range) of 92 (38–122) and 24 (17–34) species, respectively (Table 1). I ranged between 64 and 231 (mean 154; Table 1). Connectance varied between 4.8% and 9.9% (mean 7.3%; Table 1).

The diversity of the pollinator assemblage did neither respond to changes in Pre ($R_{PreSE}^2=0.68$, $t_{Pre}=1.67$, $P_{Pre}=0.25$; Table 2) nor Alt ($R_{AltSE}^2=0.59$, $t_{Alt}=-0.37$, $P_{Alt}=0.72$; Table 2). In both cases, SE explains most variation, resulting in a low partial R-square for Pre and Alt.

When accounting for variation in M and SE, C did not significantly respond to changes in altitude ($t_{Alt}=0.90$, $P_{Alt}=0.41$) or precipitation ($t_{Pre}=-0.84$, $P_{Pre}=0.44$). After accounting for differences in symmetry, Pre had no effect on I_P ($R^2=0.54$, $t_{Pre}=-0.91$, $P_{Pre}=0.40$) or I_A ($R^2=0.77$, $t_{Pre}=1.28$, $P_{Pre}=0.25$) and neither did Alt on I_P ($R^2=0.53$, $t_{Alt}=-0.87$, $P_{Alt}=0.42$) or I_A ($R^2=0.71$, $t_{Alt}=0.56$, $P_{Alt}=0.59$).

The composition of the visitor assemblage varied along the gradient (Fig. 3) with no significant influence of differences in sampling effort among sites.

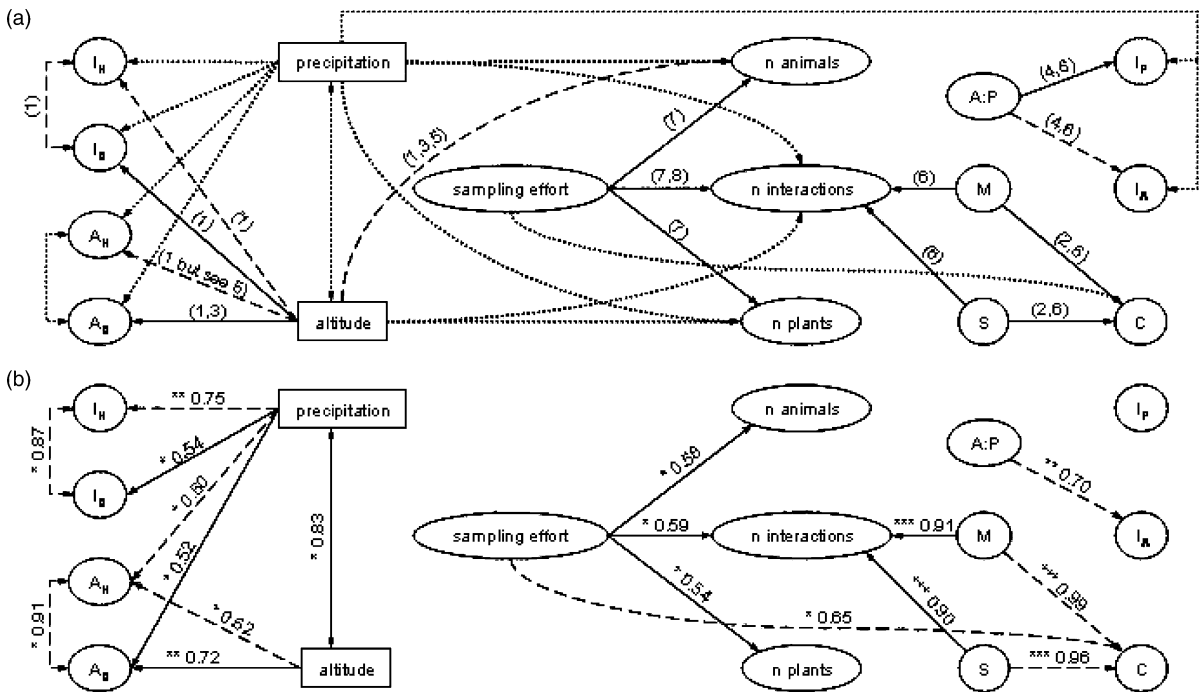


Fig. 1. (a) Path analysis of relationships between environmental and system properties of eight p-p communities along a rainfall gradient in NW Patagonia (Argentina) that were tested in the present study. Effects for which there is observational evidence in previous studies are indicated with numbers above the corresponding arrow: (1) Arroyo et al. 1982, (2) Jordano 1987, (3) Kearns 1992, (4) Elberling and Olesen 1999, (5) Medan et al. 2002, (6) Olesen and Jordano 2002, (7) Ollerton and Cranmer 2002, (8) Vázquez and Aizen 2003. (b) Path analysis of significant relationships between variables of the same dataset. Significance of effects and R-square of simple linear regressions or correlation coefficients between variables is indicated above each arrow (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). In both figures, one-headed arrows represent direct causal relationships; two-headed arrows represent correlations; continuous lines indicate positive effects; dashed lines indicate negative effects. In (a), dotted lines indicate relationships of unknown effect. Abbreviated variables are: proportion of network interactions accumulated by Hymenoptera (I_H) and Diptera (I_D); relative frequency in the flower visiting fauna for the same orders (A_H and A_D , respectively); system symmetry (A:P); maximum possible number of interactions (M); system size (S); connectance (C); mean number of interactions across plants (I_P) and animals (I_A). For further details on variables see Table 1. Obvious mathematical relationships between variables are not shown (e.g. between n animals and A:P).

Abundances of Coleoptera, Lepidoptera and other minor taxa of flower visitors showed no consistent pattern along the Pre gradient. However, there was a significant shift in the proportions of Hymenoptera (Hym) and Diptera (Dip) along the gradient (Fig. 3, 4). While bees dominated the easternmost (dryer) end of the gradient (ca 43% of bees vs 28% of flies at CT; Fig. 3, 4), towards the wetter environments there was a gradual replacement of bees by flies, which became the major component of the visitor assemblage (at LQ, 43% flies vs 25% bees; Fig. 3, 4). The participation of bees and flies in the interaction web along the rainfall gradient followed a similar trend (Fig. 5a). As a result, there was a strong negative correlation between Hym and Dip throughout the gradient both in terms of the percentage participation in the visitor fauna (Pearson $r = -0.91$, $P < 0.01$) and in the proportion of interactions accumulated (Pearson $r = -0.87$, $P < 0.01$). The models including Alt performed better than the Pre models at explaining differences in relative frequency of Hym and Dip in the visitor fauna (A_H and A_D , respectively;

Table 3). Conversely, Pre models had higher R-square than Alt models at explaining the proportion of interactions accumulated by Hym and Dip (I_H and I_D , respectively; Table 3).

For the latitude at which our eight sites are located (39–40° S) Elberling and Olesen's (1999) model predicts relative frequencies of Diptera between 39.6 and 40.6%, which is very close to our eight sites average (40.7%, weighed average: 38.5%). However, note that for the individual sites in our gradient Diptera vary in frequencies from 27.9% (at LL) to 63.2% (at PP).

In the canonical correspondence analysis, the overall correlation between both sets of variables (Pre, Alt and SE vs. $A_D:A_H$, $I_D:I_H$ and S) was not significant (most probably due to the small sample size, Stevens 1986) and, besides, the observed trends are in accordance with the general results thus far shown (analysis not shown).

We additionally compared our results with those of previous studies in the same area of our study. Aizen et al. (2002) provided the average percentage of Hymenoptera and Diptera for Nahuel Huapi (1850 mm;

Table 2. Summary of results of stepwise multiple regression between plant–pollinator network properties (A, P, I, C, I_P, I_A), and the independent variables sampling effort (SE) and mean annual precipitation (Pre) of eight sites in NW Patagonia, Argentina. Non-significant variables were included in the models as a way to show the percent variability they explained on their own. M and A:P although not being true independent variables were included in the models to account for variation owed to direct mathematical relationships between variables (e.g. as in C=L/M). Abbreviations as in Table 1.

| Effect on | Variable | Partial r ² | Model r ² | Partial F value | Partial P | Total P |
|----------------|----------|------------------------|----------------------|-----------------|-----------|------------|
| A | SE | 0.58 | 0.58 | 8.40 | P < 0.05 | P < 0.05 |
| | Pre | 0.10 | 0.68 | 1.67 | P = 0.25 | P = 0.054 |
| P | SE | 0.54 | 0.54 | 7.22 | P < 0.05 | P < 0.05 |
| | Pre | 0.19 | 0.74 | 3.73 | P = 0.11 | P < 0.05 |
| I | M | 0.91 | 0.918 | 67.54 | P < 0.001 | P < 0.001 |
| | Pre | 0.002 | 0.921 | 0.17 | P = 0.69 | P < 0.01 |
| C | SE | 0.004 | 0.925 | 0.23 | P = 0.65 | P < 0.05 |
| | M | 0.99 | 0.9974 | 2292.16 | P < 0.001 | P < 0.0001 |
| | SE | 0.0001 | 0.9975 | 0.27 | P = 0.62 | P < 0.0001 |
| I _P | Pre | 0.0004 | 0.9979 | 0.70 | P = 0.44 | P < 0.0001 |
| | SE | 0.54 | 0.54 | 7.31 | P < 0.05 | P < 0.05 |
| | A:P | 0.15 | 0.70 | 2.71 | P = 0.16 | P < 0.05 |
| I _A | Pre | 0.07 | 0.77 | 1.28 | P = 0.32 | P = 0.084 |
| | A:P | 0.69 | 0.69 | 13.99 | P < 0.01 | P < 0.01 |
| | SE | 0.17 | 0.87 | 7.31 | P < 0.05 | P < 0.01 |
| | Pre | 0.06 | 0.94 | 5.25 | P = 0.08 | P < 0.01 |

Movia et al. 1982), Chiloé (2178 mm; C. Smith-Ramírez, pers. comm.), and Riveros et al. (1991, 1996) for Puyehue National Park (3500 mm; C. H. Lusk, pers. comm.). The actual percentage of Hym and Dip of this data fell within the 95% confidence intervals of our own respective regression models, except for the percentage of Hymenoptera at Puyehue National Park (Fig. 4). With regard to total diversity figures, Riveros et al. (1991, 1996) at Chile's Puyehue National Park (79 km west of our PP site, 40°44'S; 72°49'W) recorded 31 plant and 50 flower-visiting insect species after 175 hours of observations. Riveros et al.'s low animal diversity is similar to that we found at PP (38 spp.), which suggests that our 48 hours SE was in fact relatively efficient, though it may seem low when compared to other sites. Another survey (Vázquez and Simberloff 2003, 2004) at Nahuel Huapi, a site with a Pre similar to our LT site, reported 97 species of putative pollinators to the flowers of 15 plant species. This value is slightly lower than the 113 animal species we here report for LT site. Note that the Nahuel Huapi

figures result from a considerably higher sampling effort: 452 hours distributed from early October to late February during two consecutive flowering seasons.

Discussion

This study described the variation in properties of eight p–p (plant–pollinator) webs along a rainfall gradient. To our knowledge, this is the first published study of this type.

Pollination specialization and the humidity gradient

Returning to our original questions, do mutualistic interactions become more ecologically specialized (generalized) towards the dry (wet) end of the gradient? None of the specialization measures we calculated (C at

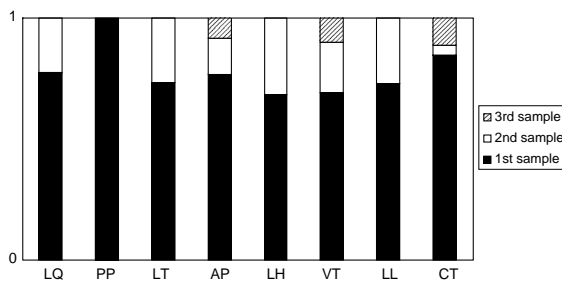


Fig. 2. Relative contribution to the flower–visitor diversity of successive surveys to eight sites along a humidity gradient in NW Patagonia, Argentina. From left to right, sites are ordered by decreasing mean annual precipitation (Pre) to reflect actual geographic position (Pre decreases to the east). For details on study sites see Table 1.

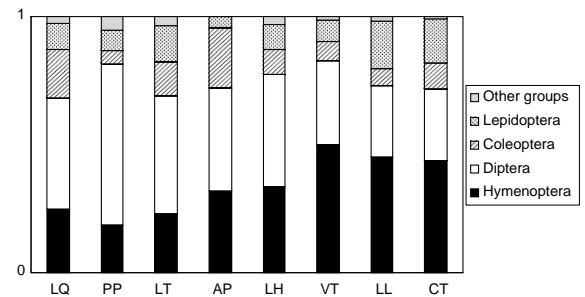


Fig. 3. Relative composition of the flower-visiting fauna of eight plant–pollinator networks along a humidity gradient in NW Patagonia, Argentina. From left to right, sites are ordered by decreasing mean annual precipitation (Pre) to reflect actual geographic position (Pre decreases to the east). For details on study sites see Table 1.

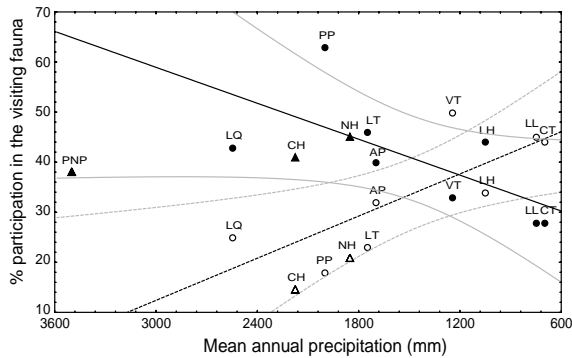


Fig. 4. Relationship between precipitation and relative frequency (%) of Diptera (closed circles) and Hymenoptera (open circles) in the flower-visiting fauna of eight plant–pollinator mutualistic networks in NW Patagonia, Argentina. Six additional data points (not included in the model calculations) are plotted overlapped to our own as a means of evaluating the “goodness” of our own models. They correspond to Nahuel Huapi (NH), Chiloé (CH) and Puyehue National Park (PNP): Hymenoptera (open triangle) and Diptera (closed triangle). Best-fitting linear regressions (Table 3) and 95% confidence intervals are included for Hymenoptera (dashed line) and Diptera (solid line). PNP datapoints are overlapped. As compared to Fig. 5a, values on X axis are extended in order to include the Pre value of PNP site.

the community level, and I_A and I_P at the species level) showed a clear pattern of variation throughout the Pre gradient. After accounting for differences in symmetry (A:P) between systems, the mean number of interactions across plants or animals showed no consistent change in response to Pre variation. After accounting for differences in M, generalization level of the entire community (measured as C) did not seem to indicate p–p interactions become more specialist or generalist towards either end of our gradient. As noted above, almost all the variation in C found in our dataset (0.99) could be explained using a logistic linear expression of M (Results), leaving virtually no unexplained variation, and no satisfactory reason to include other variables in the model. The adjustment found between C and M is considerably higher than the 0.81 reported for a set of 29 p–p networks reviewed by Olesen and Jordano (2002). This difference can probably be explained by the fact that the eight p–p networks in our study (contrasting with studies listed in Olesen and Jordano’s review) were surveyed following the same methodology and by roughly the same team of observers across sites, thus reducing “observational errors” and the associated unexplained variation.

Is flower visiting fauna more diverse towards the humid end of the gradient? Our results indicate that the wetter environments do not show a higher diversity of flower-visiting taxa. This is consistent with the idea that, despite their tropical Gondwanian origin, the southern temperate forests have undergone repeated cycles of faunal extinction because of the major geological and

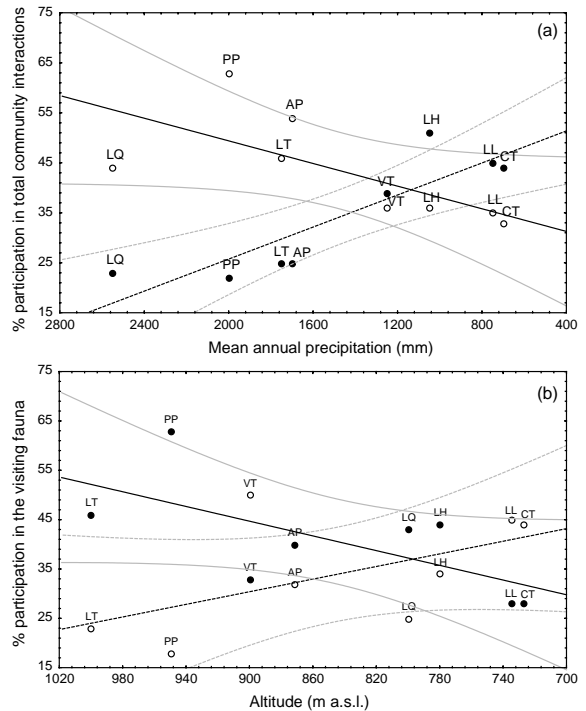


Fig. 5. (a) Relationship between precipitation and proportion of network interactions accumulated (%) by Diptera (closed circles) and Hymenoptera (open circles) in the flower-visiting fauna of eight plant–pollinator mutualistic networks in NW Patagonia, Argentina and (b) Relationship between altitude and relative frequency (%) of Diptera (closed circles) and Hymenoptera (open circles) for the same networks. Pre and Alt axis are reversed to better reflect the actual geographic position of sites. In both figures best-fitting linear regressions (Table 3) and 95% confidence intervals are included for Hymenoptera (dashed line) and Diptera (solid line).

paleoclimatic events that took place in the past in this region (Hinojosa and Villagrán 1997, Aizen and Ezcurra 1998). Even when this depauperation has been found not to be as dramatic as first suggested (compare Aizen and Ezcurra 1998 and Aizen et al. 2002) it may still account for the lack of differences described.

Does any particular visitor taxon dominate the visitor assemblages towards either extreme of the gradient? Since flies were more abundant at higher latitudes and altitudes, i.e. at lower temperatures (Arroyo et al. 1982, Elberling and Olesen 1999, but see Medan et al. 2002), the fact that in our study dipterans were more common at wetter sites in our study raises the question of whether the most humid end is also the coldest one due to the associated higher elevations. In fact, extrapolating from temperature charts (Movia et al. 1982), there is a decrease in mean annual temperature (MAT) from CT (ca 10°C) to LQ (ca 8°C) that is roughly associated to differences in altitude (Table 1). While this small variation may explain some of the observed differences in assemblage composition, we believe that the pattern

Table 3. Summary of models describing the response to Pre and Alt of the percent participation of Hymenoptera and Diptera in the composition of the visitor assemblage (A_H and A_D , respectively) and in the interactions of the plant–pollinator networks (I_H and I_D , respectively). All regressions $df = 1, 6$.

| | Pre | Alt |
|-------|--|--|
| A_H | $\ln A_H = -0.50 - 0.0004 \text{ Pre}$ $R^2 = 0.60, F = 9.36, P < 0.05$ | $\ln A_H = 1.22 - 0.0028 \text{ Alt}$ $R^2 = 0.62, F = 9.92, P < 0.05$ |
| I_H | $\ln I_H = -0.44 - 0.0004 \text{ Pre}$ $R^2 = 0.75, F = 18.10,$ $P < 0.01$ | $\ln I_H = 0.80 - 0.0022 \text{ Alt}$ $R^2 = 0.44, F = 4.83,$ $P = 0.07$ |
| A_D | $\ln A_D = -1.38 + 0.0003 \text{ Pre}$ $R^2 = 0.52, F = 6.61,$ $P < 0.05$ | $\ln A_D = -2.89 + 0.0023 \text{ Alt}$ $R^2 = 0.72, F = 15.67,$ $P < 0.01$ |
| I_D | $\ln I_D = -1.25 + 0.0002 \text{ Pre}$ $R^2 = 0.54, F = 7.28, P < 0.05$ | $\ln I_D = -2.16 + 0.0015 \text{ Alt}$ $R^2 = 0.45, F = 5.06, P = 0.06$ |

found is mainly due to the much stronger changes in Pre described. The existing evidence of the influence of rainfall patterns on the distribution and abundance of bees worldwide, further supports this view. For many groups of organisms, including Diptera, the tropics are the areas of maximum numbers of genera and of species, and of maximum morphological diversity (Gaston and Williams 1996, Ollerton and Cranmer 2002). However, bees appear to attain their greatest abundance and greatest number of species, not in the tropics, but in various warm temperate, xeric regions of the world (Michener 1979, 2000). Interestingly, this world-wide pattern, for which there are various proposed explanations, such as larval habitat requirements (Michener 1979, 2000, Kearns 1992), seems to be repeated, though in a much smaller scale, in our gradient. The gradient studied here reveals itself as a proper scenario for further research on the causes of this pattern.

In addition, even when a large scale model such as Elberling and Olesen's (1999) is a good predictor of the average composition of flies for an entire region, a gradient approach such as ours can reveal major patterns of variation in response to differences in local environmental conditions. This additional local dimension may help to 'fine tune' the more general models.

The diverse performance showed by our Pre and Alt regression models in explaining different attributes of the community along the gradient leaves open an interesting issue. In our p–p communities, the system structure (i.e. composition of the visitor fauna) was better explained by altitude (Fig. 5b), whereas its function (i.e. percentage of interactions established) was more strongly associated to another factor (precipitation; Fig. 5a). This is an example of the complexity of the factors that influence the structure and behavior of plant–pollinator systems, of which much remains to be understood. We hope that this first insight into the effect of rainfall gradients on the structure and function of entire p–p systems will encourage future research in this area.

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References

- Aizen, M. A. and Ezcurra, C. 1998. High incidence of plant–animal mutualisms in the woody flora of the temperate forest of southern South America: biogeographical origin and present ecological significance. – *Ecol. Austral.* 8: 217–236.
- Aizen, M. A., Vázquez, D. P. and Smith-Ramírez, C. 2002. Natural history of plant–animal mutualisms in the temperate forest of southern South America. – *Rev. Chil. Hist. Nat.* 75: 79–97.
- Arroyo, M. T. K., Primack, R. and Armesto, J. 1982. Community studies in pollination ecology in the high temperate Andes of central Chile. I. Pollination mechanisms and altitudinal variation. – *Am. J. Bot.* 69: 82–97.
- Arroyo, M. T. K., Cavieres, L., Peñaloza, A. et al. 1996. Phytogeographic relationships and species richness patterns in the temperate rain forest flora of South America. – In: Armesto, J., Villagrán, C. and Arroyo, M. T. K. (eds), *Ecología de los bosques nativos de Chile*. Editorial Universitaria, pp. 71–100.
- Austin, A. T. and Sala, O. E. 2002. Carbon and nitrogen dynamics across a natural gradient of precipitation in Patagonia, Argentina. – *J. Veg. Sci.* 13: 351–360.
- Bascompte, J., Jordano, P., Melián, C. J. et al. 2003. The nested assembly of plant–animal mutualistic networks. – *Proc. Natl Acad. Sci. USA* 100: 9383–9387.
- Bernardi, N. 1973. The genera of the family Nemestrinidae (Diptera: Brachycera). – *Arq. Zool.* 24: 211–318.
- Darwin, C. 1859. On the origin of species by means of natural selection. – John Murray, London. [reprint 1964. – Harvard Univ. Press]
- Elberling, H. and Olesen, J. M. 1999. The structure of a high latitude plant–flower visitor system: the dominance of flies. – *Ecography* 22: 314–323.
- Gaston, K. J. and Williams, P. H. 1996. Spatial patterns in taxonomic diversity. – In: Gaston, K. J. (ed.), *Biodiversity: a biology of numbers and differences*. Blackwell Science, pp. 202–229.
- Hawkins, B. A., Field, R., Cornell, H. V. et al. 2003. Energy, water, and broad-scale geographic patterns of species richness. – *Ecology* 84: 3105–3117.
- Hinojosa, F. and Villagrán, C. 1997. Historia de los bosques del sur de Sudamérica, I: antecedentes paleobotánicos, geológicos y climáticos del Terciario del cono sur de Sudamérica. – *Rev. Chilena Hist. Nat.* 70: 225–239.
- Jobbágy, E. G., Paruelo, J. M. and León, R. J. C. 1995. Estimación de la precipitación y de su variabilidad interanual a partir de información geográfica en el NW de la Patagonia, Argentina. – *Ecol. Austral.* 5: 47–53.
- Jordano, P. 1987. Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. – *Am. Nat.* 129: 659–677.

- Jordano, P., Bascompte, J. and Olesen, J. M. 2003. Invariant properties in coevolutionary networks of plant-animal interactions. – *Ecol. Lett.* 6: 69–81.
- Kearns, C. A. 1992. Anthophilous fly distribution across an elevation gradient. – *Am. Midl. Nat.* 127: 172–182.
- Kearns, C. A. and Inouye, D. W. 1997. Pollinators, flowering plants, and conservation biology. – *Bioscience* 47: 297–307.
- Kearns, C. A., Inouye, D. W. and Waser, N. M. 1998. Endangered mutualisms: the conservation of plant-pollinator interactions. – *Annu. Rev. Ecol. Syst.* 28: 83–112.
- Malo, J. E. and Baonza, J. 2002. Are there predictable clines in plant-pollinator interactions along altitudinal gradients? The example of *Cytisus scoparius* (L.) Link in the Sierra de Guadarrama (Central Spain). – *Div. Distr.* 8: 365–371.
- Martínez, N. D. and Dunne, J. A. 1998. Time, space, and beyond: scale issues in food web research. – In: Peterson, D. L. and Parker, V. T. (eds), *Ecological scale: theory and application*. Columbia Univ. Press, pp. 207–226.
- Medan, D., Montaldo, N. H., Devoto, M. et al. 2002. Plant-pollinator relationships at two altitudes in the Andes of Mendoza, Argentina. – *Arct. Antarct. Alpine Res.* 34: 233–241.
- Medan, D., Basilio, A. M., Devoto, M. et al. 2005. Measuring generalization and connectance in temperate, long-lasting systems. – In: Waser, N. and Ollerton J. (eds), *Specialization and generalization in plant-pollinator interactions*. Univ. of Chicago Press (in press).
- Michener, C. D. 1979. Biogeography of the bees. – *Ann. Mo. Bot. Gard.* 66: 277–347.
- Michener, C. D. 2000. *The bees of the World*. – John Hopkins Univ. Press.
- Moldenke, A. R. 1975. Niche specialization and species diversity along a California transect. – *Oecologia* 21: 219–242.
- Moldenke, A. R. 1979a. Pollination ecology within the Sierra Nevada. – *Phytologia* 42: 223–282.
- Moldenke, A. R. 1979b. Pollination ecology as an assay of ecosystemic structure: convergent evolution in California and Chile. – *Phytologia* 42: 415–454.
- Moldenke, A. R. and Lincoln, P. G. 1979. Pollination ecology in Montane Colorado: a community analysis. – *Phytologia* 42: 349–379.
- Movia, C. P., Ower, G. H. and Pérez, C. E. 1982. Estudio de la vegetación natural de la Provincia del Neuquén. – Ministerio de Economía y Hacienda. Subsecretaría de Estado de Recursos Naturales.
- Olesen, J. and Jordano, P. 2002. Geographic patterns in plant-pollinator mutualistic networks. – *Ecology* 83: 2416–2424.
- Ollerton, J. and Cranmer, L. 2002. Latitudinal trends in plant-pollinator interactions: are tropical plants more specialised? – *Oikos* 98: 340–350.
- Paruelo, J. M., Beltrán, A. M., Jobbágy, E. et al. 1998a. The climate of Patagonia: general patterns and controls on biotic processes. – *Ecol. Austral* 8: 85–101.
- Paruelo, J. M., Jobbágy, E. G. and Sala, O. E. 1998b. Biozones of Patagonia (Argentina). – *Ecol.* 8: 145–153.
- Petanidou, T. 1991. Pollination ecology in a phryganic ecosystem. PhD thesis. – Aristotle Univ., Thessaloniki, Greece.
- Petanidou, T. and Ellis, W. N. 1993. Pollinating fauna of a phryganic ecosystem: composition and diversity. – *Biodiv. Lett.* 1: 9–22.
- Petanidou, T., Ellis, W. N., Margaris, N. S. et al. 1995. Constraints on flowering phenology in a phryganic (east Mediterranean) ecosystem. – *Am. J. Bot.* 82: 607–620.
- Potts, S. G. and Willmer, P. G. 1997. Abiotic and biotic factors influencing nest-site selection by *Halictus rubicundus*, a ground-nesting halictine bee. – *Ecol. Entomol.* 22: 319–328.
- Potts, S. G., Dafni, A. and Ne'eman, G. 2001. Pollination of a core flowering shrub species in Mediterranean phrygana: variation in pollinator diversity, abundance and effectiveness in response to fire. – *Oikos* 92: 71–80.
- Potts, S. G., Vulliamy, B., Dafni, A. et al. 2003. Response of plant-pollinator communities to fire: changes in diversity, abundance and floral reward structure. – *Oikos* 101: 103–112.
- Primack, R. B. 1978. Variability in New Zealand montane and alpine pollinator assemblages. – *N. Z. J. Ecol.* 1: 66–73.
- Primack, R. B. 1983. Insect pollination of New Zealand montane flora. – *N. Z. J. Bot.* 21: 317–333.
- Proctor, M., Yeo, P. and Lack, A. 1996. Pollination, community and environment. – In: *The natural history of pollination*. Timber Press, pp. 384–411.
- Raven, P. and Axelrod, D. 1974. Angiosperm biogeography and past continental movements. – *Ann. Mo. Bot. Gard.* 61: 539–673.
- Raven, P. and Axelrod, D. 1975. History of the flora and fauna of Latin America. – *Am. Sci.* 63: 420–429.
- Riveros, M. G. and Smith-Ramírez, C. 1996. Patrones de floración y fructificación en bosques del sur de Chile. – In: Armesto, J., Villagrán, C. and Arroyo, M. T. K. (eds), *Ecología de los bosques nativos de Chile*. Editorial Universitaria, pp. 71–100.
- Riveros, M. G., Humaña, A. M. and Lanfranco, D. 1991. Actividad de los polinizadores en el Parque Nacional Puyehue, X Región, Chile. – *Medio Ambiente* 11: 5–12.
- Riveros, M. G., Humaña, A. M. and Arroyo, M. K. 1996. Sistemas de reproducción en especies del bosque valdiviano (40° Latitud Sur). – *Phyton* 58: 167–176.
- Smith-Ramírez, C. and Armesto, J. J. 1994. Flowering and fruiting patterns in the temperate rainforest of Chiloé, Chile: ecologies and climatic constraints. – *J. Ecol.* 82: 353–365.
- Sokal, R. R. and Rohlf, F. J. 1994. *Biometry: the principles and practice of statistics in biological research*. – Freeman.
- Soriano, A., Alippe, H. A., Sala, O. E. et al. 1976. Ecología del pastizal de coirón amargo (*Stipa speciosa*) del Sudoeste de Chubut. – *Acad. Nacional de Ciencias Agrícolas y Veterinarias* 30: 1–13.
- Steffan-Dewenter, I. and Tschamtkke, T. 1999. Effects of habitat isolation on pollinator communities and seed set. – *Oecologia* 121: 432–440.
- Steffan-Dewenter, I., Münzenberg, U. and Tschamtkke, T. 2001. Pollination, seed set and seed predation on a landscape scale. – *Proc. R. Soc. Lond. Ser. B* 268: 1685–1690.
- Steffan-Dewenter, I., Münzenberg, U., Buerger, C. et al. 2002. Scale-dependent effects of landscape context on three pollinator guilds. – *Ecology* 83: 1421–1432.
- Steffen, W. L., Scholes, R. J., Valentin, C. et al. 1999. The IGBP terrestrial transects. – In: Walker, B. H., Steffen, W. L., Canadell, J. et al. (eds), *The terrestrial biosphere and global change. Implications for natural and managed ecosystems*. Cambridge Univ. Press, pp. 66–87.
- Stevens, J. 1986. *Applied multivariate statistics for the social sciences*. – Lawrence Erlbaum Assoc., Hillsdale NJ.
- Thompson, J. N. 1998. The population biology of coevolution. – *Res. Popul. Ecol.* 40: 159–166.
- Totland, O. 1993. Pollination in alpine Norway: flowering phenology, insect visitors, and visitation rates in two plant communities. – *Can. J. Bot.* 71: 1072–1079.
- Traveset, A. V. 1999. Ecology of plant reproduction: mating systems and pollination. – In: Pugnaire, F. I. and Valladares, F. (eds), *Handbook of functional plant ecology*. Marcel Dekker, Inc, pp. 545–588.
- Tschamtkke, T. and Brandl, R. 2004. Plant-insect interactions in fragmented landscapes. – *Annu. Rev. Entomol.* 49: 405–430.
- Vázquez, D. P. and Aizen, M. A. 2003. Null model analyses of specialization in plant-pollinator interactions. – *Ecology* 84: 2493–2501.
- Vázquez, D. P. and Simberloff, D. 2003. Changes in interaction biodiversity induced by an introduced ungulate. – *Ecol. Lett.* 6: 1077–1083.
- Vázquez, D. P. and Simberloff, D. 2004. Indirect effects of introduced ungulates on pollination and plant reproduction. – *Ecol. Monogr.* 74: 281–308.

- Vitousek, P. M. and Matson, P. A. 1991. Gradient analysis of ecosystems. – In: Cole, J., Lovett, G. and Findlay, S. (eds), Comparative analyses of ecosystems: patterns, mechanisms and theories. Springer, pp. 287–298.
- Waser, N. M., Chittka, L., Price, M. V. et al. 1996. Generalization in pollination systems, and why it matters. – *Ecology* 77: 1043–1060.
- Williams, N. M., Minckley, R. L. and Silvera, F. A. 2001. Variation in native bee faunas and its implications for detecting community change. – *Conserv. Ecol.* 5: 57–89.
- Zegers, C. D. 1993. Bosques templados de Chile y Argentina. Variación, Estructura y Dinámica. – Editorial Universitaria, Santiago, Chile.