GEOGRAPHIC PATTERNS IN PLANT–POLLINATOR MUTUALISTIC NETWORKS

Jens M. Olesen[1,3] and Pedro Jordano[2]

[1]*Department of Ecology and Genetics, University of Aarhus, Ny Munkegade Block 540, DK-8000 Aarhus, Denmark*
[2]*Estación Biológica de Doñana, CSIC, Pab. Perú, Avda. M. Luisa S/N, E-41013 Sevilla, Spain*

Abstract. Recent reviews of plant–pollinator mutualistic networks showed that generalization is a common pattern in this type of interaction. Here we examine the ecological correlates of generalization patterns in plant–pollinator networks, especially how interaction patterns covary with latitude, elevation, and insularity. We review the few published analyses of whole networks and include unpublished material, analyzing 29 complete plant–pollinator networks that encompass arctic, alpine, temperate, Mediterranean, and subtropical–tropical areas. The number of interactions observed (I) was a linear function of network size (M) the maximum number of interactions: $\ln I = 0.575 + 0.61 \ln M$; $R^2 = 0.946$. The connectance (C), the fraction of observed interactions relative to the total possible, decreased exponentially with species richness, the sum of animal and plant species in each community ($A + P$): $C = 13.83 \exp[-0.003(A + P)]$. After controlling for species richness, the residual connectance was significantly lower in highland ($>$1500 m elevation) than in lowland networks and differed marginally among biogeographic regions, with both alpine and tropical networks showing a trend for lower residual connectance. The two Mediterranean networks showed the highest residual connectance. After correcting for variation in network size, plant species were shown to be more generalized at higher latitude and lowland habitats, but showed increased specialization on islands. Oceanic island networks showed an impoverishment of potential animal pollinators (lower ratio of animal to plant species, $A : P$, compared to mainland networks) associated with this trend of increased specialization. Plants, but not their flower-visiting animals, supported the often-repeated statements about higher specificity in the tropics than at higher latitudes. The pattern of interaction build-up as diversity increases in pollination networks does not differ appreciably from other mutualisms, such as plant–seed disperser networks or more complex food webs.

Key words: food web; geographic variation; insects; interaction-web connectance; mutualism; networks; plant–animal interaction; pollination; specialization.

INTRODUCTION

Pollination interactions are among the most studied of all mutualisms. However, most of this research focuses on single plant species and their associated flower visitors or, at most, involves guilds of related plants or pollinators (Waser et al. 1996). Studies involving total communities of interacting plants and flower-visiting animals are much rarer. In 1987, Jordano analyzed the few community studies that were available at the time. He concluded that (1) facultative interactions of high generality are the rule; (2) the degree of connectedness of the mutualistic web covaries with species richness in ways similar to that of other food webs; and (3) most interactions are weak and, when considering the mutual effects of animals and plants, strongly asymmetric. He concluded that especially because of (1), research in interaction biology has to take place at the community level. However, this has rarely been done because, among other things, it requires labor-intensive sampling procedures, and several animal taxa pose taxo-

nomical difficulties. Several recent empirical studies, influential reviews, and pollination biology textbooks stress the generalized nature of pollination interactions (e.g., Feinsinger 1987, C. M. Herrera 1988, 1996, Ollerton 1996, 1998, Proctor et al. 1996, Waser et al. 1996, Elberling and Olesen 1999, Kanstrup and Olesen 2000, Olesen 2000, Ollerton and Watts 2000; but see Thompson 1994, Momose et al. 1998, Armbruster et al. 2000, Johnson and Steiner 2000, Rasmussen and Olesen 2000). Few of these studies, however, have attempted a quantification of generalization levels (Herrera 1996, Waser et al. 1996, Olesen 2000).

Discussions on generalization levels, of course, must be comparative. A flower-visiting species can only be termed a generalist in comparison to other pollinator species or to other kinds of mutualists or antagonists. A first discussion of the level of generalization in pollination soon requires a more formal macroecological analysis (Herrera 1996, Elberling and Olesen 1999, Magaard 1999, Kanstrup and Olesen 2000, Olesen 2000, Ollerton and Watts 2000, Rasmussen and Olesen 2000). Such an analysis requires some thought on how we should measure and express the level of generalization in pollination networks. At the moment, this

conceptualization is in its very first phase (Johnson and Steiner 2000, Olesen 2000). Armbruster et al. (2000) distinguished between evolutionary and ecological specialization. The first category is defined as a process of evolving in the direction of more specialization, whereas the latter is a state and refers to having one to few interactions. Here, we are only speaking about ecological specialists and generalists. Janzen (1973) discussed generalization concepts briefly in the context of the tropical herbivore fauna. He stressed the importance of gathering data on the variation in relative fitness when a herbivore feed on different plant species. This applies to pollination interactions, too. Nutrient composition of nectar and pollen varies, as does the pollination effectiveness of individual flower-visiting animal species. Thus, studies of generalization level have to go beyond the mere counting of species interactions, or, as Janzen (1973:203) stated it, "... we cannot afford to forget that herbivores do not eat Latin binomials." Here, however, we only use the number of interactions between species of flowering plant and flower visitors as our measure of generalization level, because that is what is available in pollination biology at present. Thus, we are still forced to ignore that fact that plants are not pollinated by Latin binomials. Jordano's (1987) review had access to only one study that included the total flora and the flower-visiting fauna within a habitat (J. Herrera 1988). The rest of Jordano's database included various pollinator guilds and their mutualists (also see Waser et al. 1996). Since then, several studies of total networks have been published or are in press (Olesen 2000; J. M. Olesen and P. Jordano, *unpublished data*).

Here we describe how the generalization level varies among a set of 29 community-level networks of plant–pollinator interactions, and we analyze patterns of covariation with species richness, latitude, elevation, and insularity. Specifically, we address the following questions. Are interactions more specialized in the tropics than at higher latitudes? Do plant–pollinator interaction networks show higher specialization in island environments when compared to mainland? Are there predictable patterns of covariation between species richness and generalization level in plant–pollinator interactions?

METHODS

Properties of pollination mutualistic networks

A pollination network is here defined as a matrix **R** describing trophic and reproductive interactions between communities of P flowering plant species and A flower-visiting animal species within a well-defined habitat:

$$\mathbf{R} = [r_{ij}]_{AP}$$

where

$$r_{ij} = \begin{cases} 1 & P_i R A_j \\ 0 & \text{otherwise.} \end{cases}$$

Thus this matrix has nonzero r elements wherever animals harvest pollen, nectar, or receive other benefits from flower visitation, or wherever plants are pollinated or visited by flower-visiting animals. Here we only consider binary data, i.e., the presence or absence of an interaction in such a binary network, analogous to other types of networks, either biotic (Cohen 1978) or abiotic (Wasserman and Faust 1994, Watts and Strogatz 1998). Typically, mutualistic networks (Jordano 1987) are two-mode networks consisting of two sets of entities, i.e., plant and animal species. The units in this network (species) are connected in a bipartite graph whenever they interact (Wasserman and Faust 1994). In 18 out of the 29 networks included in the present analysis, authors quantified dependency in number of visiting encounters. The value can be used to estimate the relative strength of an interaction or the level of dependency between a pair of mutualists. We report detailed analyses of mutual dependency patterns in subsequent papers.

Network size (M) is given as

$$M = AP$$

where A and P are the total number of interacting animal and plant species in the habitat, respectively. M is thus a species richness, species density, or biodiversity measure indicating the maximum number of observable interactions. Generalization level in networks may be compared both at the species and the network level. Although sophisticated measures of interaction structure have been proposed (Ramirez 1989), most studies focus on a few descriptors. We use two measures at the network level, the total number of interactions in the network (I) and the connectance (C):

$$C = 100 \, I/M.$$

Connectance is the percentage of all possible interactions within a network that are actually established, i.e., it is a scale- or M-independent measure of the generalization level of a network (Jordano 1987). In addition, we use two measures at the species level: mean number of interactions across animal species (L_m, linkage level),

$$L_m = I/A$$

and mean number of interactions across plant species,

$$L_n = I/P.$$

We analyzed the dependency of these parameters on M, latitude, altitude, and insularity (i.e., whether the study took place on an oceanic island or in a mainland, or land-bridge island). Except for latitude, all variables were ln-transformed in order to achieve normality and a constant variance, and C was angular-transformed. To examine the relationships between network parameters and insularity, island and mainland networks were coded with dummy variables, values of 0.5 and 1.0, respectively. Pairwise relationships among variables

TABLE 1. Characteristics of complete plant–pollinator networks included in the present study.

Source	Locality	Habitat
1) Arroyo et al. (1982)	Cordon del Copo, Chile	subandean scrub
2) Arroyo et al. (1982)	Cordon del Copo, Chile	cushion zone
3) Arroyo et al. (1982)	Cordon del Copo, Chile	subnival zone
4) Elberling and Olesen (1999)	Latnjajaure, Abisko, Sweden	rocky slope
5) Elberling and Olesen, *unpublished data*	Zackenberg, Greenland	tundra
6) Eskildsen et al., *unpublished data*	Ile aux Aigrettes, Mauritius	coralline island
7) J. Herrera (1988)	Doñana Nat. Park, Spain	scrub
8) Hocking (1968)	Hazen Camp, Canada	tundra
9) Inoue et al. (1990)	Kibune, Kyoto, Japan	mixed forest
10) Inouye and Pyke (1988)	Snowy Mountains, Australia	scrub/snow gum
11) Kakutani et al. (1990)	Kyoto City, Japan	urban area
12) Kato and Miura (1996)	Nakaikemi, Tsuruga, Japan	marsh
13) Kato et al. (1990)	Ashu, Kyoto, Japan	beech forest
14) Kato et al. (1993)	Mt. Kushigata, Japan	subalpine forest/meadow
15) Kevan (1970)	Hazen Camp, Canada	tundra
16) McMullen (1993)	Pinta, Galápagos Isles	volcanic southern slope
17) Mosquin and Martin (1967)	Melville Island, Canada	tundra valley
18) J. M. Olesen, *unpublished data*	Hestehaven, Denmark	wasteground
19) Olesen et al. (2002b)	Garajonay, Gomera, Spain	laurel forest
20) J. M. Olesen, *unpublished data*	Hestehaven, Denmark	beech–oak forest
21) J. M. Olesen, *unpublished data*	Hestehaven, Denmark	salt bog
22) Olesen et al. (2002a)	Flores, Acores, Portugal	coastal cliff
23) Percival (1974)	Southeastern Jamaica	coastal scrub
24) Petanidou (1991)	Daphni, Greece	phrygana
25) Primack (1983)	Arthur's Pass, New Zealand	grassland
26) Primack (1983)	Cass, New Zealand	grassland
27) Primack (1983)	Craigieburn, New Zealand	grassland
28) Ramirez (1989)	Canaima National Park, Venezuela	open forest
29) Schemske et al. (1978)	Brownfield, Illinois, USA	deciduous forest

Note: Abbreviations are: A, number of animal species; P, number of plant species; M, network size (= AP); I, number of interactions recorded; C, connectance ($C = 100\ I/M$).

were analyzed by least squares regression with permutation tests, and significance levels were estimated with $N = 5000$ resamplings (Manly 1991, Legendre et al. 1994).

Potential methodological biases

A set of complete pollination networks extracted from literature and our own research were collated and analyzed (Table 1). They originated from highly disparate sites all over the world. A serious shortcoming of the data set was the lack of information about pollination networks in tropical lowland rain forests (but see Kress and Beach 1994, Kato 1996, Momose et al. 1998, Kanstrup and Olesen 2000). In these habitats, 98–99% of the flowering species may have biotic pollination (Bawa 1990).

In each publication, the data set was reanalyzed; some of the estimates presented here may differ from original values given by authors. Blackburn and Gaston (1998) considered a set of methodological issues that have to be addressed in such a macroecological analysis (sensu Brown 1995:6), and some of these issues will be discussed. The networks were biogeographically biased and, for that reason, could not be regarded as completely independent data points. Arctic–alpine networks dominated and the tropical lowland was completely missing. The flower-visiting animal communities in the tropical lowland studies of Kress and Beach

(1994), Kato (1996), and Momose et al. (1998) were not sufficiently resolved taxonomically to be included. However, we assume that relationships found in this paper can be extrapolated to networks at all latitudes, and that similar patterns are present in both the Northern and Southern Hemisphere. These assumptions are, however, debatable (Blackburn and Gaston 1996).

In network studies, information on species and interactions is often pooled across the entire study season, study period, or a major part of it (cumulative studies sensu Schoenly and Cohen [1991], or aggregated studies). As a consequence, phenological overlap between some of the animal and plant species may be low or even nonexistent, e.g., as in Reader (1975). The importance of this fact is often ignored. In the present review, it becomes a serious pitfall. Petanidou (1991) is a remarkable exception, because she considered the continuous turnover of interactions throughout four successive years.

Most studies in field ecology only last for one season or one year. This was true also for most of the present pollination studies. However, it is well known that the flower-visitor fauna in a habitat may vary tremendously in composition between seasons (e.g., C. M. Herrera 1988). In addition, we would expect a tendency to census a smaller proportion of all interactions within a network with increasing M, because a diminishing observation time becomes available to each species. On

TABLE 1. Extended.

Latitude	Altitude (m)	A	P	M	I	C
33° S	2200–2600	101	84	8484	361	4.3
33° S	2700–3100	64	43	2752	196	7.1
33° S	3200–3600	25	36	900	81	9.0
68° N	985	118	24	2832	242	8.5
75° N	25	76	31	2356	456	19.4
20° S	5	13	14	182	52	28.6
37° N	25	179	26	4654	412	8.9
82° N	500	81	29	2349	179	7.6
35° N	300–740	840	112	94 080	1876	2.0
36° S	1860–2040	81	36	2916	253	8.7
35° N	60	315	113	35 595	774	2.2
36° N	45	187	64	11 968	430	3.6
35° N	620–959	679	91	61 789	1193	1.9
36° N	1850	356	90	32 040	865	2.7
82° N	100	91	20	1820	190	10.4
1° S	15–580	22	10	220	27	12.3
75° N	100	18	11	198	38	19.2
56° N	5	82	26	2132	249	11.7
28° N	1200	55	29	1595	145	9.1
56° N	5	42	8	336	79	23.5
56° N	5	40	10	400	72	18.0
38° N	10	12	10	120	30	25.0
19° N	5	36	61	2196	178	8.1
38° N	135–215	666	131	87 246	2933	3.4
43° S	900	60	18	1080	120	11.1
43° S	600–800	139	41	5699	374	6.6
43° S	1600–1800	118	49	5782	346	6.0
6° N	1350	46	47	2162	151	7.0
40° N	300	33	7	231	65	28.1

a real web, Goldwasser and Roughgarden (1997) simulated variation in sampling effort and found that its impact on web properties was profound. They stressed that detection of interactions lags far behind detection of species, biasing most properties of a web. This might be a minor problem in pollination networks because animal and plant species are not included before they make a visit to a plant species or receive a visit from an animal species, respectively.

Pollination networks are difficult to delimit spatially, e.g., in Feinsinger and Colwell (1978), where hummingbirds visit flowers over several altitudinal zones, or in Snow and Snow (1972), where an entire valley with probably many different habitats is treated as an entity. The reviewed studies spanned study areas of 0.01–30 ha, but several studies did not give precise plot size. This variation in methods among studies constrained the comparative analysis.

In classic food web literature, taxonomic resolution varies. Taxonomic species, operational taxonomic units, or researcher-identified species are being lumped together into ''trophic species'' or ''kinds of organisms'' (e.g., Cohen 1978). Species sharing predator or prey may be grouped together and counted as a single matrix entry, or species simply may be grouped on their resemblance in behavior and morphology. In some of the pollination studies, a few of the most taxonomically difficult pollinator groups (e.g., *Lasioglossum* bees in Inouye and Pyke [1988]) or groups suspected to be of minor ecological importance were not always resolved to species level. Such an incomplete breakup of certain taxa is a major problem to an analysis such as the present one because it must, to some extent, affect generalization level. However, Hall and Raffaelli (1991) and Sugihara et al. (1997), among others, have shown that aggregation of taxonomic and trophic entities does not markedly change the behavior of web properties. In particular, a high number of trophically equivalent taxa, such as in this study, with only two major roles (pollinated plants and pollinators), seems to reduce the scaling sensitivity of web properties (Jordano 1987). Food chain length, on the other hand, is sensitive to aggregation.

Most food web catalogues have been criticized for being incomplete and tending to produce artificial patterns (Martinez 1991, Polis 1991). However, the networks analyzed here have only two trophic levels and represent a taxonomically and ecologically more homogeneous set of studies than food webs in general. Therefore, in spite of all the caveats, we believe that the approach is valid and of interest to a discussion of species assembly processes, biogeographic variation in generalization, coevolution, and biodiversity (Waser et al. 1996).

The size and structure of a pollination network may have both historical and recent ecological determinants (Ricklefs and Schluter 1993). However, the first has rarely been addressed. Some lineages might have spe-
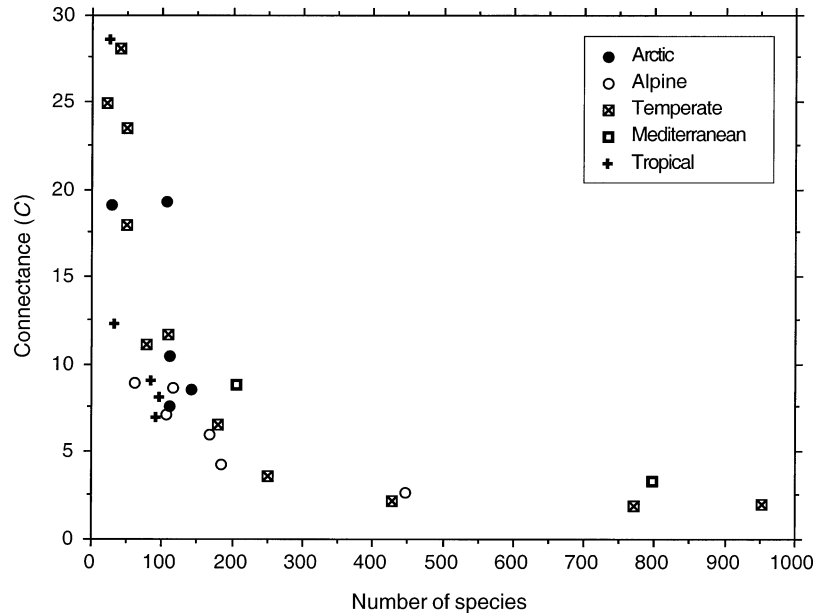
FIG. 1. Relationship between connectance (*C*) and species richness, the total number of animal and plant species (*A* + *P*), in plant–pollinator mutualistic networks from different biogeographic regions (see Table 1).

ciated considerably in certain regions and thus contributed disproportionately to the communities. Phylogenetic relatedness might generate spurious patterns between generalization level and network size, latitude, and altitude. However, incomplete knowledge, especially of insect phylogeny, precludes phylogenetic correction of the results in the present study. Despite these shortcomings, we believe that the results are robust as a preliminary approximation to the pattern of connectedness in the few complete plant–pollinator networks presently available.

RESULTS

Twenty-three papers included data on 29 pollination networks between all flowering plant and flower-visitor species within a habitat (Table 1). They encompassed a total of 4575 animal species and 1271 plant species. The networks (Table 1) belonged to five broadly defined biogeographical categories (numbers refer to entries in Table 1): arctic (4, 5, 8, 15, 17), alpine (1–3, 10, 14, 27), temperate (9, 11–13, 18, 20–22, 25–26, 29), Mediterranean (7, 24), and subtropical–tropical (6, 16, 19, 23, 28). They included five oceanic island networks and 24 mainland networks (including the New Zealand [25–27] ones as mainland).

Flower-visiting animals (*A*) and flowering plants (*P*), respectively, had a mean, median, and (range) of 158, 81, (12–840) and 44, 35, (7–131) species (Table 1). The number of network interactions (*I*) varied between 27 and 2933 (mean 426, median 626; Table 1), and its positive relationship with network size (*M*) could be approximated, after transformation, by a log-log linear function ($\ln I = 0.575 + 0.61 \ln M$; $R^2 = 0.946$). Con-

nectance (*C*) varied between 2% and 29% (mean 11%, median 9%; Table 1), and decreased exponentially with total number of species (*A* + *P*), $C = 13.83 \exp[-0.003(A + P)]$; $R^2 = 0.616$ (Fig. 1). There was a marginal trend for *C* to differ among biogeographic regions when accounting for differences in species richness (*A* + *P*) ($F = 2.73$, df = 3, 21, $P = 0.053$; Fig. 1). Connectance, *C*, decreased with *M* ($R^2 = 0.811$; Fig. 2), with no difference among biogeographic zones ($F = 0.79$, df = 3, 21, $P > 0.20$). In addition, L_n (mean interactions across plant species) increased with *M* ($R^2 = 0.341$), whereas L_m (mean interactions across animal species) did not ($R^2 = 0.032$; Table 2).

Network properties may depend upon network size, *M*, and its effect may be controlled for by doing regression analysis on residuals (Bengtsson 1994) or by partialling out the effects of *M* in multiple regression analyses. We accounted for differences in *M* by incorporating this variable into a multiple regression when including latitude, altitude, and insularity as independent variables (Table 2). The studies spanned a wide latitudinal range from 1° to 82° and included both the northern and southern hemispheres. However, 16 of the networks fell within the range from 33° to 43° (N or S latitude). When accounting for variation in network size (*M*), *C* increased marginally with latitude ($R^2_{M\text{Lat}} = 0.829$, $t = 1.67$, $P_{\text{Lat}} = 0.05$ for the partial effect of latitude), and decreased with altitude ($R^2_{M\text{Alt}} = 0.851$, $t = -2.64$, $P_{\text{Alt}} < 0.005$), whereas insularity had no effect ($R^2_{M\text{Isl}} = 0.818$, $t = 0.65$, $P_{\text{Isl}} = 0.15$; Table 2, Fig. 2). The number of interactions (*I*) also increased with latitude ($R^2_{M\text{Lat}} = 0.957$, $t = 2.55$, $P_{\text{Lat}} < 0.01$) and decreased with altitude ($R^2_{M\text{Alt}} = 0.953$, $t = -1.91$, P_{Alt}
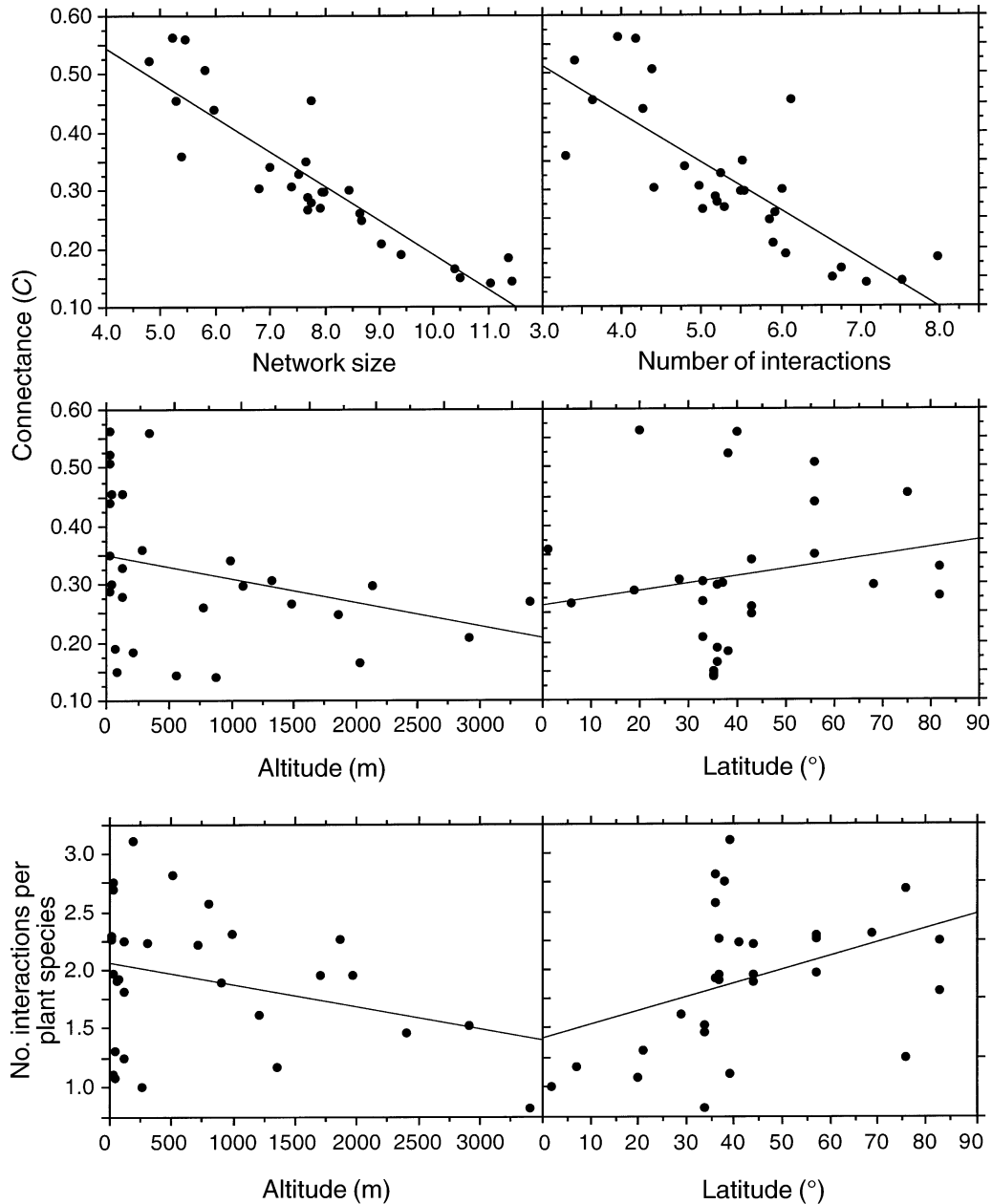
FIG. 2. Relationships between connectance (C) and different parameters of plant–pollinator mutualistic networks: network size (M), $C = 0.783 - 0.059M$ ($R^2 = 0.811$); number of interactions (I), $C = 0.762 - 0.083I$ ($R^2 = 0.625$); number of interactions per animal species (L_m), $C = 0.327 - 0.011L_m$ ($R^2 = 0.001$); altitude (E), $C = 0.350 - 4.409 \times 10^{-5}E$ ($R^2 = 0.118$); and latitude (L), $C = 0.265 + 0.001L$ ($R^2 = 0.040$). Also shown are the relationships between number of interactions per plant species (L_m) and altitude (E), $L_n = 2.056 - 1.897 \times 10^{-4}E$ ($R^2 = 0.092$); and latitude (L), $L_n = 1.418 + 0.012L$ ($R^2 = 0.156$). For all regressions, variables M, I, L_m, and L_n were ln-transformed, and C was angular-transformed as arcsine $(C/100)^{1/2}$. These equations do not account for differences in network size, M (see Table 2).

$= 0.03$), and insularity had no effect ($R^2_{M\mathrm{Isl}} = 0.043$, $t = 1.25$, $P_{\mathrm{Isl}} = 0.30$; Table 2). The number of interactions per animal species (L_m) did not change with latitude, altitude, or insularity ($R^2 < 0.054$, $t < 0.80$, $P > 0.20$ in all cases; Table 2). In contrast, the number of interactions per plant species (L_n) increased significantly with latitude ($R^2_{M\mathrm{Lat}} = 0.533$, $t = 3.27$, $P_{\mathrm{Lat}} =$

0.002; Table 2), decreased with altitude ($R^2_{M\mathrm{Alt}} = 0.504$, $t = -2.92$, $P_{\mathrm{Alt}} = 0.004$; Table 2), and also decreased in island environments ($R^2_{M\mathrm{Isl}} = 0.169$, $t = 2.14$, $P_{\mathrm{Isl}} = 0.02$; Table 2).

After controlling for variation in species richness ($A + P$), the residual connectance was significantly lower in highland (>1500 m elevation, the category "al-

TABLE 2. Summary of results for least-squares regressions between network variables; significance was tested by permutation with $N = 5000$ iterations.

Network parameter	M	Latitude	Altitude	Insularity
Connectance (C)	-0.9007***	0.1353***	-0.2027**	0.0904[NS]
No. interactions (I)	0.9727***	0.1039**	-0.0826*	0.0458[NS]
No. interactions per plant sp. (L_n)	0.5840***	0.3572**	-0.3141**	0.3768*
No. interactions per animal sp. (L_m)	0.1796[NS]	-0.0567[NS]	0.1517[NS]	-0.1100[NS]

Notes: Values in column 2 are standardized regression coefficients. Network size, M, was included in the regressions for latitude, altitude, and insularity to correct for differences in network size. Values in columns 3–5 are thus standardized partial regression coefficients. C was angular transformed prior to analyses; other variables were ln-transformed.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, nonsignificant; all with Bonferroni correction.

pine'') than in lowland networks ($F = 4.49$, df $= 2$, 27, $P = 0.04$; Fig. 3) and differed marginally among biogeographic regions ($F = 2.71$, df $= 4, 24$, $P = 0.05$; Fig. 3). Both alpine and tropical networks showed a trend for lower residual connectance, after controlling for variation in species richness. The two Mediterranean networks showed the highest residual connectance.

DISCUSSION

The level of connectedness in complete communities of plant–pollinator mutualists decreased with increasing species richness in a way similar to that previously reported for sections of mutualistic networks (Jordano 1987) or other biotic networks (e.g., Cohen 1978, Sugihara et al. 1989). Our comparative analysis showed that, after correcting for variation in network size, connectance only decreased marginally toward the tropics, but decreased highly significantly with altitude. Corrected connectance did not vary between island and mainland networks. After correcting for variation in network size, plant species were shown to be more generalized at higher latitude and lowland habitats, and showed increasing specialization on islands. The number of interactions of an animal species was not affected significantly by these three biogeographical variables.

Thus plants, but not their flower-visiting animals, support the often-repeated statements about higher specificity in the tropics than at higher latitudes. These results, however, hide a lot of variation. Different plant and animal groups may behave very differently and constitute very different proportions of the total communities at the different sites (Herrera 1996, Olesen 2000). For example, Elberling and Olesen (1999) showed that the relative frequencies of the four major pollinator orders changed latitudinally: bees were more common at low latitudes, whereas dipterans dominated at high latitudes. Michener (1954), however, showed that bees did not vary in their generalization level with latitude. Thus a next step would be a macroecological analysis of the major flower-visitor orders, families, or genera, and the major plant families, separately.

Our study revealed a marked trend for decreasing plant generalization level in island environments, independent of any parallel trend in network size. An im-

poverishment of potential animal pollinators on oceanic island environments is associated with this trend: island networks showed a markedly lower ratio of animal to plant species ($A : P$) than mainland networks. Decreased island generalization for plants involves visitation by a narrow range of distinct taxonomic groups, often including taxa such as reptiles or passerine birds that are not considered pollinators on mainland environments (J. M. Olesen and A. Valido, *unpublished manuscript*). Our finding is the general trend. However, specialized main-
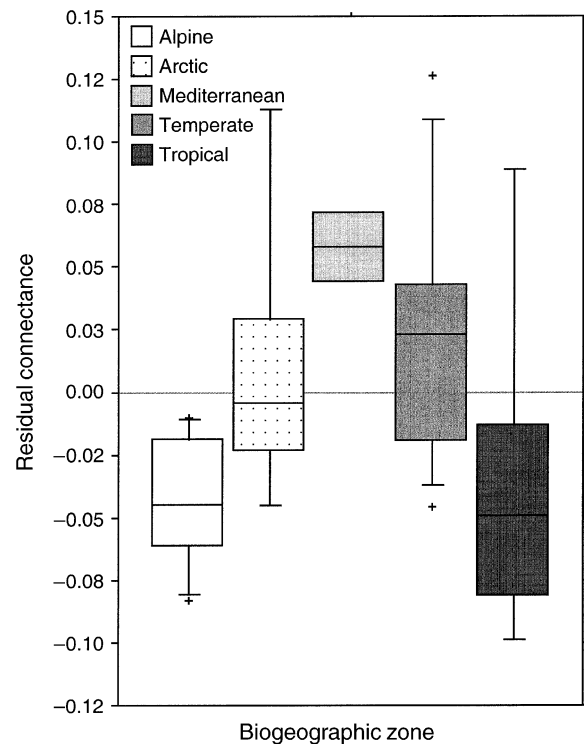

FIG. 3. Differences in connectance, after correcting for differences in network size (M) among plant–pollinator networks from different biogeographic regions and located at different elevations (see Table 1). Highland is equal to ''alpine.'' The median is marked by the center horizontal line splitting the data in halves, and the upper and lower hinges (the edges of the box) split the remaining halves in half again; outliers, designated +, lie between the upper hinge and 1.5 (upper hinge − lower hinge).

land clades of plants are reported to evolve generalist clades on islands (Armbruster and Baldwin 1998).

In plant–pollinator mutualistic networks, species are each other's niches. If more plant species accumulate in an area, the spectrum of resources to flower-visiting animals is increased, too. Whittaker (1977) even called organic diversity self-augmenting. As shown in this study, the local level of species richness affects individual species and their biotic interactions. However, it is unclear how this occurs. If tropical habitats are saturated with species, their higher density of species should cause more interspecific competition, reduce niche overlap, and cause species to become more specialized. Janzen (1973) regarded tropical communities as "full." He thus assumed that the size of the community is determined by energy availability and competition. This was supported in our present study by the plants, but not by their flower-visiting animals. However, if the "tropics are not full, competition is irrelevant" (MacArthur 1972:219). Thus, in spite of the high diversity of flower-visiting animals in the tropics, the animals' food plant niche dimension may not be "full." A higher diversity of flower-visiting animals may not necessarily result in more specialization if the spectrum of exploited resources is increased concordantly (MacArthur 1972:222). A different picture emerged when we compared island and mainland networks. Plants responded to insularity by becoming less generalized, whereas the animal generalization level was unrelated to insularity. Thus, decreased latitude and insularity had the same effects.

Our approach illustrates the fact that extensive generalization in plant–pollinator interactions is the rule rather than the exception (Waser et al. 1996), and demonstrates that very few plant or pollinator taxa are indeed specialized. Moreover, the pattern of increasing interactions as diversity in pollination networks increases does not seem to differ appreciably from other mutualisms such as plant–disperser networks (Jordano 1987), or from more complex food webs. Endorsing the plea of Waser et al. (1996), we certainly need more community-wide studies to address the intricacies of plant–pollinator networks. However, a more thorough analysis of existing networks using new methodologies and concepts would probably be even more productive in our efforts to understand the ecology and evolution of networks and biological complexity.

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