Structure of a plant–flower-visitor network in the high-altitude sub-alpine desert of Tenerife, Canary Islands

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Confined within a volcanic caldera at 2000 m a.s.l., the sub-alpine desert of Tenerife, Canary Islands, harbors a distinct biota. At this altitude the climate is harsh and the growing season short. Hence, plant and animal communities, constituting the sub-alpine plant–flower-visitor network, are clearly delimited, both spatially and temporally. We investigated species composition and interaction structure of this system. A total of 11 plant species (91% endemics) and 37 flower-visiting animal species (62% endemics) formed 108 interactions. Numbers of interactions among species varied ten-fold within both plant and animal communities. Generalization level of a species was positively correlated with its local abundance. Two separate network analyses revealed a significantly nested structure. In relation to a plant–flower-visitor system, nestedness implies that specialized species (animals or plants) interact with a subset of the species pool visiting (animals) or being visited (plants) by more generalized species. Therefore, specialized, locally rare plants tend to be visited by generalized, locally abundant animals, and specialized, locally rare animals tend to utilize generalized, locally abundant food plants. Such patterns could have implications for conservation of the sub-alpine network, and stress the importance of preserving not only rare species, but also the more abundant ones, which may be key food resources or pollinators in the plant–flower-visitor network.

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In a pollination network flowering plants and their flower-visiting animals form a web of interactions. Co-existing plant species attract different numbers of animal species, some of which act as pollen vectors. Similarly, animal species of a network utilize varying numbers of available plant species as their food plants. Several studies have investigated total pollination networks, i.e. including all species of flowering plants and all species of flower-visiting animals within a defined area (Arroyo et al. 1982, Primack 1983, Jordano 1987 and references therein, Inouye and Pyke 1988, Ramirez 1989, Inoue et al. 1990, Kakutani et al. 1990, Kato et al. 1990, McMullen 1993, Kato and Miura 1996, Memmott 1999, Elberling and Olesen 1999, Kato 2000, Kanstrup and Olesen 2000, Olesen et al. 2002). These studies encompass networks of varying size, i.e. their numbers of plants or animals differ by more than an order of magnitude. Moreover, the different studies cover a variety of habitats, including arctic, temperate and tropical regions, and areas of different size. Previously, community studies have been concerned mostly with patterns of abundances and species richness or diversity rather than identities of species constituting the communities (i.e. species composition) (Worthen 1996). Thus, interaction structures within the systems have long been underemphasized. Recently, however, new approaches developed in other fields of biology, economics and social sciences have been used in the analysis of plant–animal interaction networks (Dicks et al. 2002, Bascompte et al. in press). Dicks et al. (2002)

found evidence of compartmentalization in two British grassland plant–flower-visitor networks. Species within compartments, i.e. subsections of the network, were more connected by interactions than species outside the compartment. On the other hand, Petanidou and Ellis (1996), who analyzed a Mediterranean shrub pollination network in Greece, found that interactions of specialized plants and animals were nested within more generalized interactions of their partner species. Furthermore, Bascompte et al. (in press) report significant nestedness for 48 pollination and fruit dispersal networks. Compartmentalization and nestedness describe two opposite extremes, although they are not necessarily mutually exclusive. For instance, interactions within compartments may be nested. Thus, both structures can be found at different scales in a network analysis.

Few studies have investigated total pollination networks on small oceanic islands (but see McMullen 1993, Olesen et al. 2002). This is surprising, as island floras and faunas are simple and often very distinct. Furthermore, due to their inherently small size and evolution in isolation from the mainland biota, island networks are often highly vulnerable to disturbance caused by human activity (Simberloff 2000, Cox and Elmqvist 2000). Because islands represent a relatively large fraction of the world biodiversity hotspots, i.e. areas of high endemism and high rates of habitat destruction, they are recommended as a focus of conservation efforts (Myers et al. 2000). Preservation of mutualistic interactions are of vital importance to long-term persistence of both plant and animal species in a natural network (e.g. Bond 1994, Buchmann and Nabhan 1996, Kearns and Inouye 1997, Kearns et al. 1998). Knowledge of composition and structure of island biotas is therefore of interest, especially in a conservation context.

In this study we investigated a network of plants and their flower-visiting animals in a sub-alpine desert on the island of Tenerife, Canary Islands. This system was found to be especially suitable for a network study as it is clearly delmited in both space and time: spatially, the sub-alpine desert zone of Tenerife is confined to the high mountain region (above 2000 m a.s.l.), which is delimited by the rim of a volcanic caldera. In this high-altitudinal zone the climate is harsh, with high irradiation, periodic drought, strong winds and extreme temperature ranges. Temporally, the growing season is confined to the short sub-alpine summer. Peak flowering period during which nearly all plant species bloom is only around one month (Fig. 1). Hence, the network of interactions linking plants and their flower-visiting animals is delimited within a short period of time. Few but distinct species of plants and animals inhabit the sub-alpine desert zone (Bacallado 2000). The whole area (18 900 ha) is now preserved in the Teide National Park. Olesen et al. (2002) emphasize the vulnerability of small island ecosystems, stating that island pollination
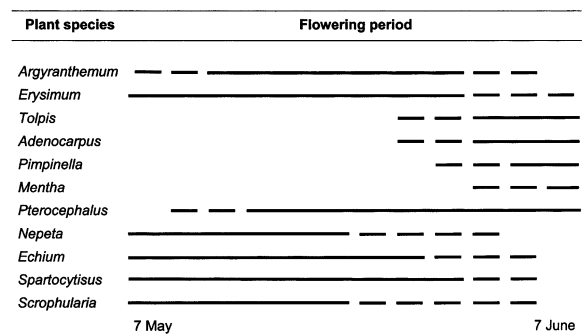

Fig. 1. Flowering phenology of the 11 study species at Cementerio de los Tajinastes from 7 May to 7 June 2001. Unbroken lines indicate peak flowering period, broken lines indicate the beginning or end of flowering.

systems may be especially susceptible to invasive species. However, the plant and animal communities in the high altitude zone of Tenerife may be relatively resistant to invasion. A study by Dickson et al. (1987) indicated that introduced plant species are present but generally fail to become invasive, possibly due to the extreme climatic conditions.

In this study we address the following questions: 1) What characterizes the species compositions of the plant and animal communities constituting the sub-alpine pollination network of Tenerife? 2) Are any patterns found in specialization and generalization of plant and animal species? 3) Are nested or anti-nested structures found in the pollination network? If structured, what are the possible structuring forces? 4) Are some species or groups of species network keystones, i.e. having a disproportionately large role in maintaining community structure? 5) What are the implications of network structure for invasion success and possible impacts of the introduced honey bee *Apis mellifera* L. in the sub-alpine zone? *Apis mellifera* is the most abundant flower-visitor, and is known to be an effective floral resource collector (e.g. Collins et al. 1984, Seeley 1987, Sugden et al. 1996). Thus, its presence in the system may be quite influential.

Materials and methods

Study site

The study was carried out at Cementerio de los Tajinastes (28°13′N, 16°38′W, 2050 m a.s.l.), within the Teide National Park. The study site was a 300 × 400 m plot of sparse, low shrub vegetation typical of the sub-alpine desert. Twelve flowering plant species were found in the plot (Table 1). No animals were observed visiting the flowers of *Carex calderae* (Cyperaceae). Presumably it is wind-pollinated and is thus omitted from our analysis of the plant–flower-visitor network.

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Table 1. Plant species of Cementerio de los Tajinastes.

Family	Species	Distribution[1]	Abundance[2]
Brassicaceae	*Erysimum scoparium*	e	3
Fabaceae	*Spartocytisus supranubius*	e	4
	Adenocarpus viscosus	e	1
Apiaceae	*Pimpinella cumbrae*	e	3
Boraginaceae	*Echium wildpretii*	e*	4
Lamiaceae	*Nepeta teydea*	e	2
	Mentha longifolia	n	2
Scrophulariaceae	*Scrophularia glabrata*	e	3
Dipsacaceae	*Pterocephalus lasiospermus*	e*	2
Asteraceae	*Argyranthemum teneriffae*	e*	2
	Tolpis webbii	e*	3
Cyperaceae	*Carex calderae*	e*	–

[1] Distribution of the plant species: n = native, e = endemic, e* = national park endemic, according to Bramwell and Bramwell 1990.
[2] Abundance classes: rare (1) to dominant (4), as described in the text.

Sampling procedure

Flower-visiting animals were observed on the plant species from 7 May to 7 June 2001. This period comprised the peak flowering period of all species (Fig. 1). Observations were made from sunrise (7:00 h) to sunset (21:00 h), although mainly during the peak period of insect activity (10:00–17:00 h). All observation days were sunny, and temperatures at noon exceeded 20°C with a maximum of 25–27°C. Plant species were selected at random and observed for 5–20 min at a time. This was repeated at different times of the day and at different plant individuals until additional observation effort did not increase number of visitor species. Using this observation procedure, each plant species was observed for a minimum of 1 h. During the entire study period, a total of 145 observation hours were spent during 15 observation days. Interactions were recorded as present only when flower-visiting animals were observed probing for nectar or eating/collecting pollen. Only these animals could be regarded as potential pollinators. To avoid reducing local pollinator populations by sampling, animals were identified in the field whenever possible. Unknown insect species were caught and identified by taxonomists (see acknowledgements). Animals were identified to species or subspecies and plants were identified to species. Collected insect specimens are deposited in the Dept of Ecology and Genetics, Univ. of Aarhus, Denmark.

A rough measure was used to estimate abundances of both plant and animal species in the study system. Species were assigned to abundance classes ranging from rare to very common. Abundance classes of flowering plants were defined as: 1) Rare, few individuals in the plot. 2) Occasional, found in some places within the plot and/or low conspicuousness to potential flower-visitors. 3) Common, many individuals, clumped or dispersed within the plot. 4) Very common species, numerically dominant and/or high conspicuousness to potential flower-visitors. Similarly, abundance classes of flow-

animals were categorized according to their importance as flower-visitors: 1) Rare, only one or a few individuals observed during the study. 2) Occasional, several individuals observed during the study. 3) Common, almost always observed during an observation day. 4) Very common, mostly observed in even short observation periods. 5) Dominant throughout most of the study.

Descriptive statistics

The number of animal species is denoted A, number of plant species P and number of interactions in the network I. System size is defined as $M = A \times P$. These network characteristics were calculated for the Tenerife sub-alpine network in addition to other sub-alpine, alpine and arctic total network studies.

Linkage level denotes the number of interactions per species, i.e. linkage level L_m of an animal species m is the number of plant species visited by m, and linkage L_n of a plant species n is the number of animal species visiting n. To compare linkage level distributions for animals and plants, linkage level was standardized as relative linkage of animal species $l_m = L_m/P$ and relative linkage of plant species $l_n = L_n/A$. Species with high linkage levels utilize many partner species, and thus are more generalized than species with low linkage levels. A possible relation between generalization (linkage level) and abundance was tested statistically by using the non-parametric Spearman's correlation coefficient ρ.

Network statistics

Based on presence-absence data in the plants × animals matrix, the structure of the plant–flower-visitor network was investigated using nestedness analysis (Bascompte et al. in press). In nested systems, smaller species assemblages are perfect subsets of larger species assemblages. Quantitative measures of nestedness were

originally developed to analyse patterns of species occurrences and absences on a set of islands or in habitat fragments (Patterson and Atmar 1986, Atmar and Patterson 1993, Cook 1995, Lomolino 1996, Worthen 1996, Wright et al. 1998, Patterson and Atmar 2000). This concept can also be applied to a pollination network, envisioning plants as "islands" and flower-visiting animals as "species". However, in contrast to the system of species assemblages on a group of islands, the pollination matrix consists of species in both rows and columns. Thus, reciprocally, food plant species of each flower-visiting animal species can be regarded as a group or an assemblage of "species" depending on an "island" (the animal). Pollination networks are perfectly nested if the most specialized plants are visited by perfect subsets of animal species assemblages visiting more generalized plant species. Similarly, the most specialized animals will be using food plants, which are perfect subsets of those used by more generalized animals. On the contrary, networks are antinested if different plants attract different parts of the total flower-visitor pool, and vice versa if different animals utilize different food plants. Anti-nestedness can occur if the system is structured by e.g. competitive exclusion (checkerboard distribution).

Several metrics for measuring nestedness have been proposed. However, to date there is no consensus among ecologists regarding the metric or null models used in statistical tests of nested structure (see review in Wright et al. 1998). We used the metric "system temperature", T, an index of matrix nestedness. System temperature ranges from 0°, indicating perfect nestedness, to 100° when the system is completely anti-nested. Contrary to other metrics, T measures deviations from perfect nestedness across both row and column data simultaneously, rather than solely across rows. Thus, T appears especially suitable for analyzing pollination systems, in which rows and columns can be interchanged. Moreover, T is independent of system size and number of interactions, and thus allows quantitative comparison of different systems (Atmar and Patterson 1993, Wright et al. 1998, Patterson and Atmar 2000). To assess level of nestedness, rows and columns of the matrix are first reorganized as a maximally packed matrix: plant and animal species are arranged in order of linkage level, from the most generalized species (highest number of interactions) to the most specialized species (lowest number of interactions). In a perfectly nested matrix all present interactions will be concentrated in the upper left corner and along the upper and left edges of the matrix, while absent interactions will be found in the lower right part of the matrix (Fig. 2a). The line separating the presences and absences in a perfectly nested matrix is called the boundary threshold. In a non-perfectly nested matrix, some absences are
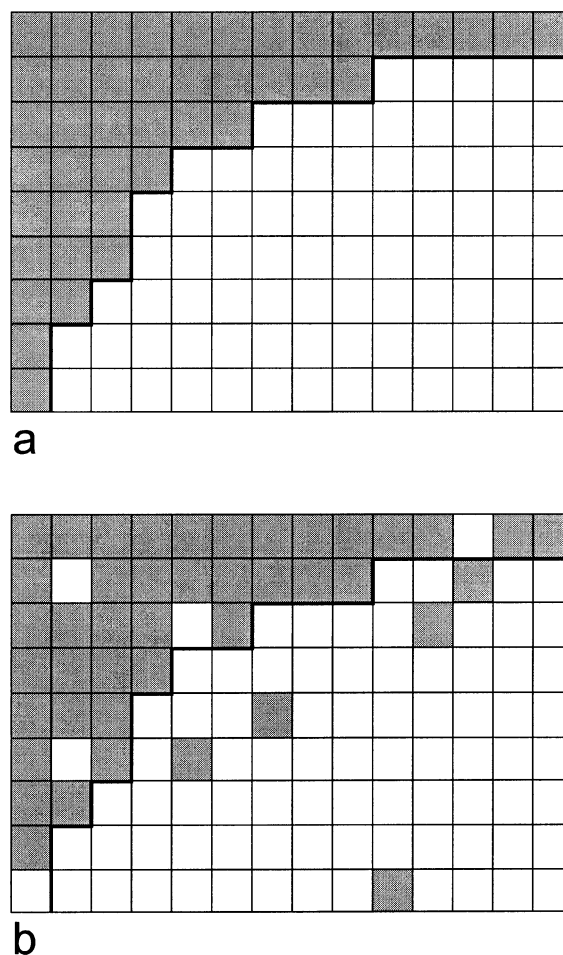

a

b

Fig. 2. Maximally packed matrices of (a) a perfectly nested system and (b) a system deviating from perfect nestedness. In a pollination matrix, rows represent plant species, which are ranked in order of generalization, the upper species having the highest linkage level. Columns represent animal species, arranged in order of generalization, the species to the left having the highest linkage level. Realized interactions are shaded, absent interactions white. The border separating presences from absences in a perfectly nested matrix is called the boundary threshold.

found in the upper left part of the matrix, and some presences are found in the lower right corner (Fig. 2b). System temperature T is a measure of the deviation of such unexpected presences and absences from the boundary threshold. The statistical significance of an observed T-value is evaluated using Monte Carlo simulations, which generates randomly assembled matrices of a similar size (A × P) and fill (I) as the observed matrix (Atmar and Patterson 1993). The ability of simulation models to detect non-random nested patterns has been shown to depend strongly on choice of null model (Cook and Quinn 1998, Wright et al. 1998, Brualdi and Sanderson 1999, Jons-

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son 2001). We use the simple null model of Patterson and Atmar (1986, 2000), which generates random networks constraining only the total number of interactions in the system. T was calculated and tested statistically using the program "Nestedness Calculator" (Atmar and Patterson 1995), based on 1000 randomizations. Temperature was calculated for our network, in addition to sub-alpine, alpine and arctic total pollination networks of other studies.

To investigate if patterns of species abundances accounted for network structure, we used a method developed by Lomolino (1996) for testing causality of nestedness. Firstly, species assemblages represented by the rows in the network matrix are sorted by the suspected causal factor, in our case local abundance. The sorted matrix is then compared to perfectly nested matrices of equal size and fill to calculate a measure of nestedness D. Statistical significance of a nested pattern is tested by comparing the observed D-value to those obtained from null matrices. The latter are constructed by reordering rows of the original data matrix at random, species distributions within rows being unaltered. Contrary to system temperature analysis, simultaneous departures of row and column data cannot be measured. Thus, two separate analyses were done: 1) Rows (plant species) in an animals × plants matrix were ranked in order of plant abundances. 2) Rows (animal species) of a plants × animals matrix were ranked according to animal abundances. The analyses were done using a program written in BASIC (Lomolino 1996). Statistical significance of causality was assessed after 999 randomizations of the data matrices.

Results

A total of 38 species and subspecies of animals were observed visiting the 11 species of flowering plants in the sub-alpine zone, forming a total of 108 interactions (Fig. 3). Of the animals, 23 (61%) taxa were endemic, 12 (32%) were native, one (3%), *Apis mellifera*, was introduced and two (5%) were of unknown status. Endemicity was especially high among the Hymenoptera, which encompassed 15 (83%) endemic taxa, one (6%) native, one (6%) introduced, and one (6%) taxon of unknown status. Among the plant species, 10 (91%) were endemic and one (9%) was native. No introduced animal-visited plants were found at the study site. Thus, the sub-alpine desert supports a distinct biota, composed predominantly of endemic plants and animals. The animals belonged to four different orders (Aves, Hymenoptera, Lepidoptera and Diptera), of which hymenopteran and dipteran species were numerically dominant (Table 2). In terms of numbers of individuals, hymenopterans were most abundant, and hence appeared to be the most important group of flower-visitors in the sub-alpine network. Plant species belonged to eight different families. Ten of the 11 plant species are Canarian endemics, and the distributions of four species are restricted exclusively to the sub-alpine zone of Tenerife. Although geographically restricted, many of these species were locally abundant (Table 1).

A relatively high number of possible interactions was established in the Tenerife pollination network compared to other sub-alpine, alpine and arctic networks (Table 3). Linkage level for animal species (L_m) ranged
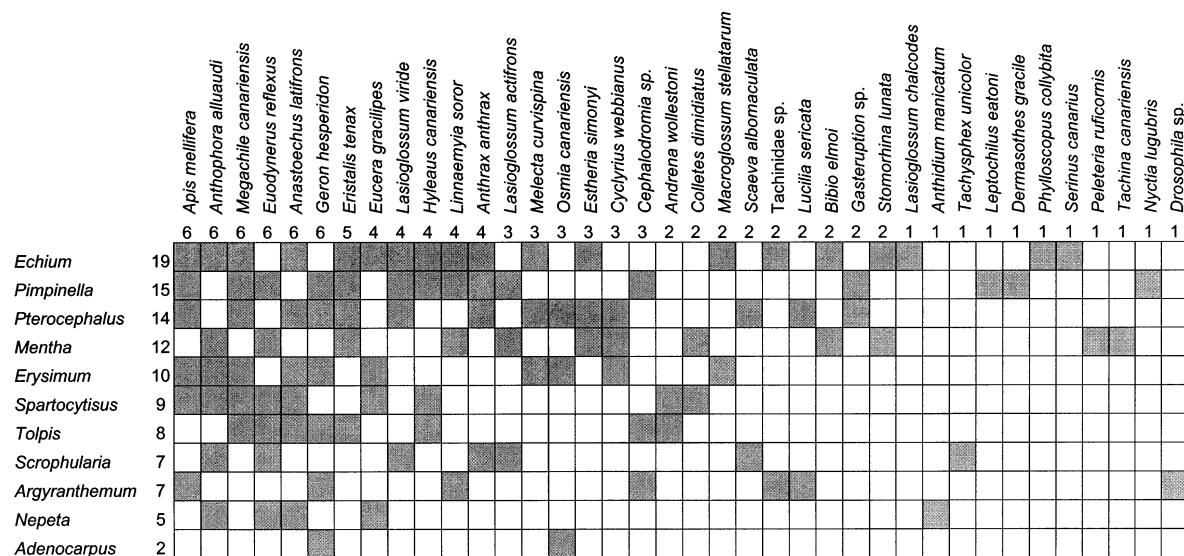

Fig. 3. The maximally packed plant–flower-visitor matrix of the Tenerife sub-alpine system. Numbers along the borders of the matrix indicate linkage levels of the species. Actual interactions are shown shaded.

Table 2. Flower-visiting animal community of Cementerio de los Tajinastes.

Order	Family	Species	Distribution[1]	Abundance[2]
Aves	Sylviidae	*Phylloscopus collybita canariensis*	e	3
	Fringillidae	*Serinus canarius*	e	3
Hymenoptera	Eumenidae	*Euodynerus reflexus*	e	2
		Leptochilus eatoni eatoni	e	1
	Sphecidae	*Tachysphex unicolor simonyi*	e	1
	Tiphiidae	*Dermasothes gracile gracile*	e	1
	Colletidae	*Colletes dimidiatus dimidiatus*	e	2
		Hylaeus canariensis	e	3
	Andrenidae	*Andrena wollestoni*	e	1
	Halictidae	*Lasioglossum arctifrons arctifrons*	e	2
		L. chalcodes chalcodes	e	1
		L. viride viride	e	3
	Megachilidae	*Anthidium manicatum*	n	1
		Megachile canariensis	e	2
		Osmia canariensis	e	1
	Anthophoridae	*Anthophora alluaudi alluaudi*	e	3
		Eucera gracilipes	e	4
	Apidae	*Melecta curvispina*	e	2
		Apis mellifera	i	5
	Gasteruptiidae	*Gasteruption* sp.	?	1
Lepidoptera	Lycaenidae	*Cyclyrius webbianus*	e	1
	Sphingidae	*Macroglossum stellatarum*	n	1
Diptera	Bibionidae	*Bibio elmoi*	e	1
	Bombyliidae	*Anastoechus latifrons*	n	2
		Anthrax anthrax	n	1
		Cephalodromia sp.	n	2
	Calliphoridae	*Geron hesperidum*	e	3
		Lucilia sericata	n	2
	Drosophilidae	*Drosophila* sp.	n	1
	Sarcophagidae	*Stomorhina lunata*	n	1
	Syrphidae	*Nyctia lugubris*	n	1
		Eristalis tenax	n	2
		Scaeva albomaculata	n	2
	Tachinidae	*Estheria simonyi*	e	1
		Linnaemyia soror	e	1
		Peleteria ruficornis	n	1
		Tachina canariensis	e	1
		unidentified	?	2

[1] Distribution: i = introduced, n = native, e = endemic, according to Moreno 1988 (Aves), Hohmann et al. 1993 (Hymenoptera), Baez 1998 (Lepidoptera) and M. Baez pers. comm. (Diptera).
[2] Abundance classes: rare (1) to dominant (5), as described in the text.

from 1 to 6 plant species (mean $\pm$ SD = 2.84 $\pm$ 1.76), equivalent to relative linkage levels (l_m) of 0.09 to 0.55. Linkage level of plant species (L_n) ranged from 2 to 19 animal species (mean $\pm$ SD = 9.82 $\pm$ 4.87), corresponding to relative linkage levels (l_n) of 0.05 to 0.50. Thus, ranges of generalization levels, when measured as percentage of realized interactions out of all possible interactions, were similar for plants and animals. Distributions of linkage levels were right-skewed for both plant and animal species, skewness being slightly higher for animals ($s_a = 0.69$) than for plants ($s_p = 0.38$) (Fig. 4). A positive correlation was found between abundance and generalization level (linkage) of a species for both plants (N = 11, ρ = 0.51, p = 0.11) and animals (N = 38, ρ = 0.49, p = 0.002), although the correlation was not statistically significant for the plant species. Hence, species interacting with many other species also tend to be the most abundant in the community.

System temperature T, i.e. departure from perfect nestedness, was 33.24°, which is significantly lower than expected by chance (T in 1000 Monte Carlo simulations, mean $\pm$ SD = 49.28° $\pm$ 6.33°, P(T < 33.24) = 0.006). Thus, the network is characterized by a nested structure, which is significantly more orderly than if plant species were visited randomly by animals, or animal species were feeding randomly on plants. The analysis of causality furthermore showed that the network is significantly nested when rows of the plants $\times$ animals matrix are ordered according to animal abundances (p = 0.009). However, the animals $\times$ plants matrix ordered according to plant abundances was not significantly nested (p = 0.79). Analyses of other subalpine and arctic networks revealed that system temperatures were low, and in all cases, except Arthur's Pass National Park, New Zealand, the nested structure was highly significant (Table 3).

Table 3. System characteristics and temperature of published sub-alpine, alpine and arctic pollination networks.

Location	Altitude (m)	Latitude	A^1	P^2	I^3	Fill[4]	T_{obs}[5]	T_{random} (mean $\pm$ SD)[6]	Source
Andes, Chile	2200–2600	33°S	64	43	196	7.1	3.96	14.02° $\pm$ 0.93° ***	Arroyo et al. 1982
Andes, Chile	2700–3100	33°S	25	36	81	9.0	9.02	21.40° $\pm$ 2.00° ***	Arroyo et al. 1982
Andes, Chile	3200–3600	33°S	101	83	361	4.3	7.50	21.24° $\pm$ 3.42° ***	Arroyo et al. 1982
Abisko, Sweden	985	68°N	118	23	242	8.9	13.92	26.18° $\pm$ 2.07° ***	Elberling and Olesen 1999
Snowy Mts., Australia	1860–2040	36°S	81	36	252	8.6	9.57	27.48° $\pm$ 2.14° ***	Inouye and Pyke 1988
Arthur's Pass, New Zealand	900	43°S	60	18	120	11.1	26.46	28.95° $\pm$ 3.64° n.s.	Primack 1983
Cass, New Zealand	600–800	43°S	138	41	376	6.6	7.47	22.31° $\pm$ 1.41° ***	Primack 1983
Craigieburn Mts., New Zealand	1600–1800	43°S	118	49	346	6.0	5.98	20.11° $\pm$ 1.32° ***	Primack 1983
Tenerife, Spain	2050	28°N	38	11	108	25.8	33.24	49.28° $\pm$ 6.33° *	this study

[1] Number of animal species.
[2] Number of plant species.
[3] Number of interactions.
[4] % of realized interactions (I) of the total possible number of interactions (A × P).
[5] Actual system temperature.
[6] Mean and standard deviation of 1000 randomizations of the plant–flower-visitor matrix. Levels of significance of T: $p < 0.0005$ = ***; $p < 0.05$ = *; $p > 0.05$ = n.s.

Discussion

Composition of plant and animal communities

High levels of endemicity characterized the plant and animal communities forming the sub-alpine plant–flower-visitor network of Tenerife. Endemism was especially high in Hymenoptera. When considering
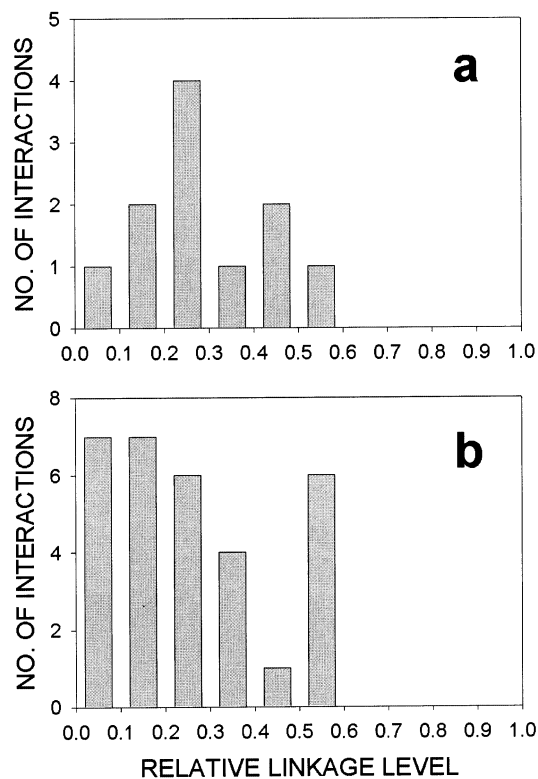

Fig. 4. Patterns of generalization. Frequency distribution of relative linkage levels of (a) plants (l_n), and (b) animals (l_m).

abundance and presumably pollination efficiency, this is probably the most important group of pollinators in the network. A dominance of Hymenoptera as pollinators is contrary to the pollination environment of many oceanic islands, where especially large bees are absent or rare, e.g. the Galapagos (McMullen 1993), Hawaii (Kato et al. 1999), Samoa (Bryan 1931), Aldabra (Woodell 1979) and the Izu Islands, Japan (Inoue 1993). The Canary Islands, although close to Africa, are located > 1000 km from the Mediterranean region, which is thought to have been the main source of origin of the Canarian fauna and flora (Sunding 1970, 1979, Juan et al. 2000). However, a chain of submerged seamounts in the eastern North Atlantic (Geldmacher et al. 2000) may have formed stepping-stones for dispersing species during periods of lowered sea level in geological time (F. Taravera pers. comm.). Mediterranean climate regions are especially rich in bee species (Michener 1979). Hence the Mediterranean affinity of the Canarian biota could explain the relative predominance of bees. A similar explanation for a high richness of bees was proposed for the Andean zone in central Chile. These mountaintops are habitat islands of alpine zone within a Mediterranean climate region (Arroyo et al. 1982). However, in sub-alpine and alpine zones of temperate regions, bee diversity is lower and Diptera are abundant (Primack 1983, Lloyd 1985, Inouye and Pyke 1988). In the arctic, Diptera are the most dominant flower-visitors (Elberling and Olesen 1999, Larson et al. 2001).

Network structure

The plant–flower-visitor network of the sub-alpine zone of Tenerife was significantly nested when species were ordered after linkage level. Nestedness implies that specialized plants attracted a smaller subset of animals

visiting more generalized plant species, and that specialized animals fed on a subset of the food plant species of more generalized animals. Therefore, specialized plants were most likely to receive visits from generalized animals, and specialized animals were most likely to utilize generalized food plants. Because generalization level was found to be related to species abundance, the observed pattern of nestedness may imply that the network is "abundance structured". In other words, the most common plant species are visited by many flower-visitors, and the most common animal species visit a wide range of food plants. This pattern was confirmed by the causality analysis. Species abundance has been shown to be correlated with e.g. geographical range, life history traits, genetic structure, and patterns of species interactions, and could thus be an important structuring force in plant–flower-visitor networks (Gaston 1994, Kunin and Gaston 1997). J. M. Olesen (unpubl.) compared species diversity, abundance and generalization level of plant–flower-visitor interactions from published sources, and found a significant positive correlation between species abundance and generalization in 15 of 16 networks. Theoretical models have shown that passive sampling based on species frequencies can produce a nested structure (Andrén 1994, Cutler 1994, Worthen 1996). Abundance could in this context be thought of as a measure of the relative importance of a species in the network. Distribution of flower-visitors among plant species could, for instance, be determined by the plants' relative contribution of resources to flower-visiting animals. An analysis of quantitative food webs, which include species abundances and frequencies of interactions could be rewarding (Memmott 1999). Different plant species are, however, difficult to compare quantitatively, as they differ in amount and quality of rewards offered to flower-visitors in addition to number of flowers, individuals and spatial coverage at a site (Kearns and Inouye 1993). In our study it is probably not possible to detect causal patterns of plant abundances, due to the relatively small system size and coarse abundance measures. Analysis of larger networks using more detailed and biologically relevant abundance measures could reveal patterns, which may not be evident in simple systems. Furthermore, as our plant–flower-visitor network was not perfectly nested, other factors may also influence interaction structure of the network, e.g. floral morphology or flower-visitor behavior, which could exclude certain plant-animal combinations (Fægri and van der Pijl 1979, Proctor et al. 1996). In fact, system temperature of the sub-alpine plant–flower-visitor network of Tenerife was much higher, and thus the system less nested, than most other sub-alpine, alpine and arctic systems (Table 3). It is difficult to detect any large-scale trends in patterns of nestedness, given only nine total pollination networks from five locations. Further investigation is needed to reveal if system temperature is related to geographical factors such as latitude, isolation or climate.

Many studies, which have been cited as examples of total pollination systems, are only subsections of networks. Some include only the most abundant plant species (Bosch et al. 1997) or certain growth forms, e.g. perennials (Herrera 1988). Others lump plants or flower-visiting animals in large taxonomical or morphological groups (McCall and Primack 1992, Bosch et al. 1997, Hingston and McQuillan 2000). Network structures detected in such partial systems may not necessarily reflect structures of the total network. It also remains to be investigated why some total networks are compartmentalized, while in others interactions are significantly nested, and to what degree nested structures and compartments may be found in the same network. Compartmentalization analysis of our network revealed only one compartment for the whole system (unpubl.).

Implications for conservation

The unique Canarian sub-alpine network is characterized by many generalized interactions and a nested structure. This implies that the abundant and generalized species are also the keystones on which the existence of the more rare species is based, both with respect to flower-visitors and food plants. Hence, conservation efforts should focus not only on the rare species, but also on the dominant ones.

A final note concerns the influence of the introduced honey bee *Apis mellifera* which is extremely abundant in the sub-alpine zone during the flowering season. It is difficult to assess if, and how, network composition and structure is altered by the presence of honey bees. However, if the native system is structured mainly by species abundances, it is likely that the massive introduction of honey bees has affected the plant-animal network. Our observations showed that honey bees visited more than half of the plant species. Because honey bees are effective resource collectors, especially when present in high numbers, they could potentially deplete flowers of nectar, and hence be a strong competitor of native pollinators in the Tenerife sub-alpine system (Kraemer and Schmitt 1997, Dupont et al. unpubl.). Several studies of island ecosystems report a decline in native bee species observed on flowers in the presence of *A. mellifera* (Roubik 1978, Kato 1992, Wenner and Thorp 1994, Kato et al. 1999). Further studies are, however, required to assess the impact of introduced honey bees on plants and animals native to the sub-alpine zone of Tenerife.

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