A year-long plant-pollinator network

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Abstract   In this work we analyse the pollination community in a South American forest known as 'talar'. This is a vegetal woody community that inhabits fossil coastal banks characterized by seasonal temperate weather and calcareous soil, at the coast of the Río de la Plata, in the province of Buenos Aires, Argentina. We obtained data of the interactions between anthophylous insects and entomophylous flowering plants over an extensive period of time. We showed that pollination system parameters, such as partners' identity, system size, and connectance, fluctuated among months, when sampled year-long. Maximal network size occurred in early spring and early autumn, when both the number of mutualistic species and the number of interactions peaked, and this was also when network asymmetry was higher than average. Monthly connectance of the plant-flower visitor matrix decreased to its lowest values at these peaks. Available data suggest that cumulative traditional connectance (i.e. the connectance calculated as the whole number of interactions registered in the community divided by the full size system) underestimates actual connectance values by a factor of *c*. 3 ×. Monthly values of connectance decreased exponentially as system size increased, and the distribution of interactions per species followed power-law regimes for animals, and truncated power-law regimes for plants, in accordance with patterns previously deduced from among-network cumulative communities studies. We think that either within or and among pollination networks, systems that are organized as power-law regimes may be a basic property of these webs, and provide examples of the fact. Both seasonal changes and interactions between mutualists like competition, and some degree of facilitation, may be very important to understand the performance of the system as a whole, and the role and importance of different species in the community. We suggest that communities of plant – pollinators that exhibit extended activity, such as temperate or tropical seasonal ones, should be studied through consecutive plant-pollinator webs rather than cumulative ones. The partition of the system into smaller serial parts allows us to obtain outstanding information of every short period. This information is flattened by the average effect when we considered the combined analysis of the whole data.

Key words: community interaction, mutualist, networks, phenology, pollinator, web, xeric forest.

INTRODUCTION

Network analyses of flowering plants and flower-visiting animals have recently been widely used to summarize plant-pollinator relationships and, for example, to detect changes in ecological gradients, to show the presence of generalist and specialist mutualists in the community, and to identify functional compartments (Elberling & Olesen 1999; Memmott 1999; Dicks *et al.* 2002; Malo & Baonza 2002; Medan *et al.* 2002; Vázquez & Simberloff 2002). These webs are descriptions of the observed set of interactions that occur between flowers and flower visitors at a given place and time (Olesen & Jordano 2002). Ideally, all partners in such a web coexist within a discrete, defined

area, and are simultaneously active in pollination activity. Thus, the non-occurrence of a particular interaction should indicate the failure of a potential visitor species to visit a particular plant species. However, when long periods of time are considered, the simple sum of all observed interactions may become increasingly inadequate because: (i) species shown as potential partners may have non-overlapping phenologies (Jordano 1987; Dicks *et al.* 2002; Olesen & Jordano 2002; Jordano *et al.* 2003); (ii) species with extended phenologies may appear to engage in more interactions than they typically engage in at any particular time (Waser *et al.* 1996); and (iii) possible seasonal changes that may occur in system size, symmetry, connectance and degree of generalization of the community's pollination cycle may be overlooked.

In our study we analysed overall plant–flower visitor interactions in a xeric temperate forest located at mid latitudes in Argentina (35°S), in which pollination

activity occurs throughout the year (Murriello *et al.* 1993). A similar study of a plant-pollinator web has been conducted in a phryganic ecosystem in Greece (Petanidou 1991), but other studies are rare.

In our study, we recorded the annual dynamics of plant-visitor assemblages and their interactions, using time-specific sequential webs, in order to analyse the variation of assemblage composition, connectance and degree of generalization. By comparing our results with those of other workers, we also provide some insight into which aspects of network structure would be resolved differently by sequential *versus* cumulative webs.

METHODS

Study area

The study area was located between 35°S, 57°30′-W and 35°20′S, 57°20′W, and is part of the MAB-UNESCO 'Parque Costero del Sur' Biosphere Preserve. The forest defined as 'talar' (Parodi 1940; Cagnoni & Faggi 1993) is considered extrazonal xeric vegetation of the Pampean Phytogeographical Province, with a wet temperate climate (Cabrera & Willink 1980).

Collection of basic data of the system

We visited the site on average 1.2 times per month between August 1998 and May 2001 to collect the data for this study. At each visit, we recorded all interactions that we observed between enthomophylous flowering plants and anthophylous flower visiting insects. We defined an interaction as a visit made by an insect to a flower, in which the visitor contacts either anthers or stigmas, or both. However, observations were not made in sufficient detail to confirm that all interactions were mutualistic and led to effective pollination.

Plants

We recorded the flowering status for all flowering plants by visual observation performed by one or two observers walking along five 500 m transects. Three transects were parallel to the Rio de la Plata riverside, and two transects were perpendicular to the banks. We spent about 90 min walking each transect and trapping insects. We began transect surveys in the morning and finished at dusk. We worked mainly on sunny days, but the weather sometimes changed while we were working. We called *interactive plants* those observed to have at least one interaction during the study period.

Forty-one interactive plant species were observed. However, since species in three of the genera observed (*Eryngium* spp., *Geranium* spp. and *Oxalis* spp.) were difficult to differentiate in the field they were combined and the phenological information of only 37 plants was used. The information was obtained by collating our data into 12 *c.* 30-day periods (hereafter: months), each starting on the 21st of a given calendar month and ending on the 20th of the following calendar month, and annotated by season (spring, summer, autumn, and winter, each of which was considered to last three months), i.e. Sp1 corresponding to the period between 21 September and 20 October (the 1st month of southern hemisphere Spring) and Su1 for the period between 21 December and 20 January, etc. The 21st was chosen as a cut-off date because it was considered to be more closely matched to the year's seasons than standard calendar months. One-month samples were considered sufficient to summarize the interactions, since the plant and animal species were, on average, pollination-active for 4–5 months (see Results) and thus no substantial species turnover was expected to occur within one-month periods.

Flower visitors and record of flower–visitor interactions

Adults of visitor species were sampled through:
1. Observation and/or capture of insects on flowering plants.
2. Use of pan traps filled with diluted sucrose solution with a drop of detergent.
3. Direct observation of flying individuals while walking along transects.

It is well-known that pan traps may not sample all potential anthophilous species and that they may trap some nonanthophilous groups. For this reason, pan traps were used as a means of confirming visual contemporary records of flower visitors, and as evidence of the presence of known flower visitors on dates in which these were not directly recorded on flowers.

There were three hummingbird species in the study area, but none was abundant. We could not make reliable observations of their activity. So, as to enhance sample methodology, we excluded them from the study and concentrated on insects.

All insects collected were first morphotyped; then, a subsample was pinned, and individuals were identified into their species whenever possible, in many cases with the assistance of specialists (see Acknowledgements).

The phenological information of the confirmed 104 taxa of flower visitors was arranged using the same method used for plants. The species in three genera (*Tatochila autodice* – *T. vanvolxemii*, *Vanessa carye* – *V. braziliensis*, and two *Anthrenoides* spp.) could not be

differentiated in the field. So they were combined and only 101 insect species were analysed.

Dynamics of assemblage composition and analysis of interactions

In order to obtain a measurement of the degree of similarity among assemblages of mutualists in different months, we calculated a *similarity index* I = [2D/(A + B)], where D is the number of plant and animal species shared between two consecutive months, and A and B represent the number of species in each of these months. We arbitrarily assigned the calculated value to the second month of the pair. Thus, the index expresses the similarity between the assemblage of a given month and that of the previous month. A further measurement of relatedness among assemblages was obtained by computing similarity indexes for all possible month pairs and by using them in a multidimensional scaling analysis (Borg & Lingoes 1987). Analyses were conducted both for plants and animals as well as for joint assemblages. We also averaged similarity indexes of month pairs separated by increasing time (until a maximum of a sixth-month). This provided us with an estimate of the degree of assemblage heterogeneity that would be associated with increasingly cumulative web samples.

We defined *participance* as the percentage of potential mutualists that were actually involved in interactions in a given month. This was calculated as: $P = [(av + ah)/(pv + ph)] \times 100$.

Here, pv stands for the number of *potential visitors* (i.e. those animal species that had at least one recorded interaction in any month at the study, but not necessarily in the month under consideration), av for the number of *active visitors* (i.e. those species with

at least one interaction in the month under consideration), ph for the number of *potential hosts* and ah for the number of *active hosts*.

Considering s as the number of interactions, we also computed a *potential connectance* as

$C_p = (s/pv \times ph) \times 100$, and an *actual connectance* as $C_a = (s/av \times ah) \times 100$, for every month. In addition, we calculated a *cumulative connectance* for the complete study period (i.e. assuming that all active mutualists were present all year round) as $C = (s/av \times ah) \times 100$.

RESULTS

Basic parameters of the assemblage and their interactions

The overall size of our observed system was 37 plant species, 101 insect species, and 367 interactions. Cumulative connectance, calculated in the traditional way, was $C = 7.4\%$. Overall characteristics of the year-long plant-flower visitor system are shown in Table 1.

Plants were visited by a mean of 4.1 ± 2.0 (mean + SD) insect species. Interactions were unevenly distributed among hosts. During most of the year, either one or a few plant species interacted with a high number of available partners, while a large proportion of the plant hosts interacted with a reduced number of insect mutualists. The distributions of interactions did not significantly depart from normality (Kolmogorov-Smirnov D-tests, $P > 0.05$).

On average, each insect mutualist visited a mean of 1.3 ± 0.2 (mean + SD) plant species. The frequency distributions of visitor interactions were less uniform than those of the plants (Fig. 1). As a consequence, the distributions of animal interactions significantly

Table 1. Dynamics of system properties of the talar plant-flower visitor network

| System property	Winter			Spring			Summer			Autumn		
	W1	W2	W3	Sp1	Sp2	Sp3	Su1	Su2	Su3	F1	F2	F3
Potential visitors (pv)	27	29	40	64	43	49	32	23	11	40	26	21
Potential hosts (ph)	6	9	11	22	21	18	17	21	23	19	13	9
Active visitors (av)	14	13	28	51	29	47	12	11	5	26	11	13
Active hosts (ah)	6	4	4	15	12	9	9	7	6	12	3	3
Interactions (s)	20	16	33	81	48	56	19	13	6	47	12	16
Potential system size (pv*ph)	162	261	440	1408	903	882	544	483	253	760	338	189
Active system size (av*ah)	84	52	112	765	348	423	108	77	30	312	33	39
Active system asymmetry (av/ah)	2.3	3.2	7	3.4	2.4	5.2	1.3	1.9	0.8	2.1	4.4	4.3
Assemblage similarity with previous month	0.23	0.35	0.41	0.41	0.54	0.41	0.29	0.31	0.48	0.37	0.31	0.69
Potential connectance (s/pv*ph)*100	12	6	8	6	5	6	3	3	2	6	4	8
Actual connectance (s/av*ah)*100	24	31	29	11	14	13	18	17	20	15	36	41
Participance (av + ah)/(pv + ph)*100	60.6	44.7	62.7	76.7	64.1	83.6	42.9	40.9	32.4	64.4	35.9	53.3

F, fall; Sp, spring; Su, summer; W, winter.
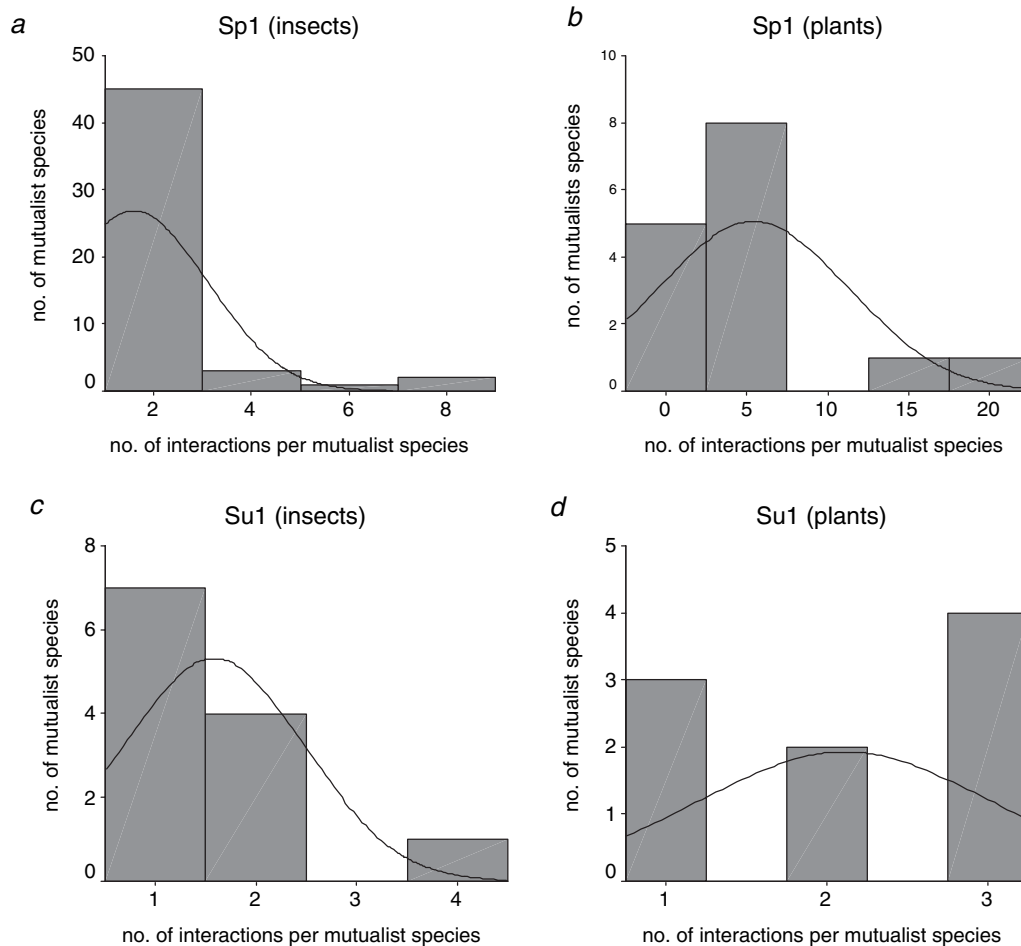
Fig. 1. Seasonal variation in the frequency distribution of generalization level of insect visitors and plant hosts and in the talar. Shown are two contrasting months (*a* and *b* corresponding to Sp1 and; *c* and *d*, corresponding to Su1, insects and plants distribution of interactions per mutualist species, respectively). A normal fit corresponding to sample values is shown in each histogram plot.

Table 2. Between-month similarity of flowering plant and animal assemblages in the Talar. Values corresponded to the averages of the similarity indexes for the 12 possible combinations of consecutive month's pairs separated by increasing distances

Between month distance	1	2	3	4	5	6
Average similarity						
Plants	0.49 ± 0.21	0.33 ± 0.14	0.28 ± 0.16	0.17 ± 0.12	0.14 ± 0.14	0.01 ± 0.12
Animals	0.37 ± 0.14	$0.31 +/- 0.09$	0.29 ± 0.11	0.29 ± 0.08	0.28 ± 0.05	0.28 ± 0.09

departed from normality (Kolmogorov-Smirnov *D*-tests, $P < 0.05$). Throughout the study, the most species-rich families among active insects were Muscidae and Syrphidae (13 spp. each), followed by Halictidae (8), Apidae (7), Vespidae and Nymphalidae (5).

Plants

Different species of plants flowered at different periods over the year, but simultaneously active hosts peaked both in early spring and in early autumn. Plants presented flowers over 5.1 ± 2.6 months (mean + SD). Average similarity between plant assemblages was low (<0.5) when we compared months that were consecutive, and decreased monotonically, with increased temporal separation. Flowering plant assemblages separated by six months did not share any species (Table 2).

The distributions of interactions in plant species did not significantly depart from normality (see above), but some pairs of distributions were signifi-

cantly different; (Brandt-Snedecor tests, $P < 0.05$) (Fig. 1).

Five plant species had 10 or more simultaneous interactions at least during one month. *Colletia spinosissima* was involved in 39% of all interactions in the system during this plant's most active flowering period (late winter and early spring), while *Schinus longifolia* and *Scutia buxifolia* were involved in 11% and 24%, respectively, of the mid- and late-spring interactions. *Tagetes minuta* (10%) and *Jodina rhombifolia* (21%) dominated the autumn–winter period. *Colletia spinosissima* had the highest number of mutualists (43 visitor species). This may have been related to the paucity of alternative blooming species, and to *C. spinosissima* presenting a large number of flowers at a time. No correlation was found between a plant species' number of mutualists and the length of its flowering period.

Insects

Adult insects were active for 4.0 ± 3.2 months (mean ± SD). Average similarity was low (<0.4) when we compared assemblages from consecutive months, and became stable at around 0.3 at greater month spans (Table 2).

The overall abundance of flower visitors, as estimated by species richness, was strongly bimodal, with a main peak at late winter and during spring, and a second peak in autumn, both coinciding with peaks of captured individuals. Between-month changes in the proportions of the diverse insect orders were significant (χ^2 test, $P < 0.0001$). During summer, flies declined while butterfly and bee species increased.

On average, each insect mutualist visited 1.3 ± 0.2 (mean + SD) plant species. Thus, the generalization level was lower than that for plants. The distribution frequency of animal interactions significantly departed from normality (Kolmogorov-Smirnov D-tests, $P < 0.05$) except in early and late summer (Kolmogorov-Smirnov D-tests, $P > 0.05$). Only the month pairs F1-W3 and F1-Sp3 differed significantly (Brandt-Snedecor tests, $P < 0.05$) and were less uniform than the plant patterns (Fig. 1).

Only three insect species visited more than three mutualist flower species in at least one month. The three most interaction-rich flower visitors had long activity periods and their cumulative plant assemblages were comparatively large (*Apis mellifera:* 20 mutualists, active all year round; *Toxomerus* sp.1: 17 mutualists, active over 10 months; *Astylus quadrilineatus:* 16 mutualists, active over six months).

Opposite to the plants there was a statistically significant relationship between visitor permanence in the system (i.e. the number of months in which a given visitor showed interactions). The total number of plant mutualists recorded for the visitor had a functional relation: $y = 0.5375 + 1.6733x - 0.0647x^2$; where y stands for the phenophase duration in months and x for the number of interactions; $R^2 = 0.5276$; $P < 0.0001$). Thus, permanence was predictably associated with the number of established interactions.

Variations in active system size, participance and connectance

The active system size varied over the year (Table 1). It was smallest in early- and mid-winter and in late summer when participance was also the lowest.

The plant participance was lower than that of flower visitors and varied more over the year. All plants had interactions at the start of winter (participance = 100%) but participance decreased to 23% in mid-autumn (Table 1).

The visitor participance decreased from 96% (late spring) to 37.5% (early summer). Connectance ranged from 11% to 41% (average = 22%) and was negatively associated with the system size [$C_a = 0.973$ (system size) $- 0.327$; $R^2 = 0.69$].

The connectance values were lowest for the spring and autumn peaks and the values for individual months were higher than cumulative connectance (7.4%).

Cumulative distributions [P (k)] of number of interactions per flower visitor (k) showed good fits to power-law curves [P (k) = k-γ] (Table 3), while distributions of interactions per plant gave a better fit to truncated power-law curves [P (k) = k-γ exp (–k/kx)] than to power-law curves (in both expressions γ is the fitted constant and kx is the truncation value). Monthly interaction patterns followed the tendency, known only for entire webs (Jordano *et al.* 2003) for the preferential associations of interactions with already interaction-rich partners (Barabási & Albert 1999).

The variation in the number of interactions followed the changes in the number of animal mutualists more closely than those in plant mutualists ($r = 0.9$ *vs* 0.82, respectively; $P < 0.05$). Within most months, the patterns of interactions of plants and animals differed significantly with plants being usually more generalized than visitors (Brandt Snedecor test, $P < 0.05$) (Fig. 1).

Sequential *versus* cumulative webs

We found that all system variables fluctuated over the year. System size and number of interactions showed differences of one order of magnitude between maximal and minimal values. Maximal system activity occurred in early spring and early autumn, when the

Table 3. Fitted models to the distributions of interactions per species for the plant-flower visitor network of the talar

Month	Power law (insects) γ	Power law (plants) γ	Truncated power law (plants)	
			γ	k_x
W1	−2.07798	−0.714719	−0.361950	9.231571
W2	−2.40692	−0.651795	−0.305075	10.32360
W3	−2.84610	−1.010350	−0.975142	93.47674
Sp1	−2.03697	−0.623114	−0.174074	7.960225
Sp2	−1.81838	−0.680173	−0.084845	5.818533
Sp3	−2.76303	−0.870643	−0.761012	29.73674
Su1	−1.65566	−0.972511	−0.955679	169.3503
Su2	−2.69463	−1.316410	−1.312240	694.3731
Su3	−2.57973	†	†	†
F1	−1.40257	−0.826368	−0.588649	14.79229
F2	−3.57841	−0.688467	−0.440970	13.04081
F3	−2.40692	−0.663502	−0.214954	8.077748

†Values are provided for each month except where data were insufficient for calculation.

numbers of mutualistic species and of interactions peaked, system asymmetry was higher than average, visitor richness was highest (Table 1), and when some of the talar-characteristic zoophilous woody species were in bloom.

Actual connectance of the plant-visitor matrix decreased to its lowest values at the time of activity peaks of the system, but even these figures were higher than cumulative connectance.

We suggest that cumulative webs have the potential disadvantage of including heterogeneous subsets in the analysis, a risk that could increase as the web covers longer periods. Also, consecutive monthly assemblages shared on average less than 50% of their plant species and 40% of their animal species. Similarity further decreased with increasing between-month spans, indicating that it would have been inappropriate to sample this system at lower resolution, because periods of two months or longer would have included a substantial amount of non-overlapping species (Table 2). Moreover, inspection of similarity indexes and multidimensional scaling analysis suggested that there are three assemblage subsystems (winter + spring, summer, and autumn) are included in the talar network, a pattern that would probably not have emerged had sampling been done at lower resolution (Fig. 2).

Our results fit well to an exponential function (actual connectance = 0.3474·exp[−0.0179·S]; $R^2 = 0.51$ where S = mutualist species richness), but the curve differs significantly (Student-*t*-test, $P < 0.008$) from the one obtained by Olesen and Jordano (2002). Our connectance values for the individual months were distributed in the lower system size region of the curve of Olesen & Jordano (Fig. 3).

The comparison reveals that a network property emerging from the analysis of several independent studies can underlie the dynamics of a single system.
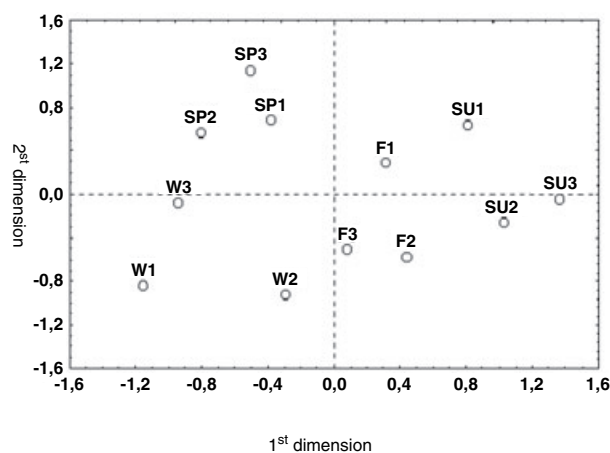

Fig. 2. Multidimensional scaling analysis of assemblage similarity in the Talar. F, fall; SP, spring; SU, summer; W, winter.

As shown above, the uniqueness of the talar 'system' may be only apparent, as three subsets of mutualists followed each other over the annual cycle.

DISCUSSION

A plant-flower visitor network describes the interactions that occur at a given place and time (Olesen & Jordano 2002). All partners in such a web are supposed to coexist and to be simultaneously active in pollen presentation or pollen transport. However at the community blooming peak (when flowering of several species overlaps), periods longer than one month inevitably include non-overlapping species. Many available data about pollination communities proceed from longer periods of data (Arroyo *et al.* 1982; Herrera 1986; 1988; Motten 1986; Inouye & Pyke 1988; Schoenly & Cohen 1991; Elberling & Olesen
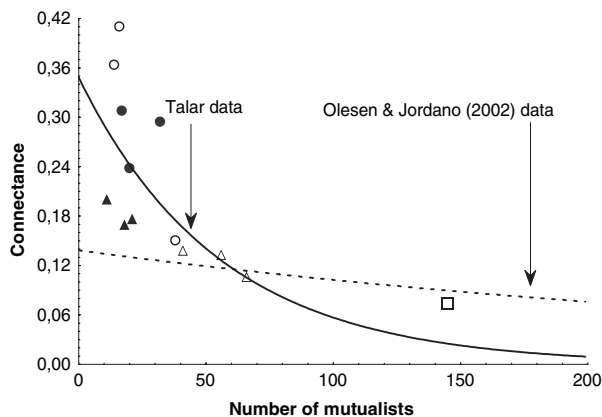
Fig. 3. Relationship between actual connectance and system size (number of species) in the Talar. Solid circles, winter months; open circles, spring months; solid triangles, summer months; open triangles, fall months; open square, overall connectance value (calculated assuming that all system mutualists were simultaneously active). An exponential fit (continuous line) is added to the plot ($y = 0.3474 \cdot \exp$ $(-0.01792 \cdot x)$. For comparison purposes, an exponential fit corresponding to connectance/system size values of 29 plant-pollinator networks analysed by Olesen and Jordano's (2002) is also added [dashed line, $y = 0.13842 \cdot \exp$ $(-0.003 \cdot x)$].

1999), producing 'cumulative' webs. Such webs have the advantage of including most or all species present in a community in only one diagram or table. The disadvantage of these studies becomes more serious as longer periods are considered: (i) species shown as potential partners may in fact have non-overlapping phenologies (Jordano 1987; Dicks *et al.* 2002; Olesen & Jordano 2002; Jordano *et al.* 2003), so a-non-interaction between a given pair of species may be due to authentic lack of visitation but also to the fact that these species are not simultaneously active; (ii) species with extended phenologies may account for more interactions than they have at any particular time, which may lead to exaggerated generalization scores; and (iii) possible changes in system size (the number of interaction partners), connectance (number of observed plant–visitor interactions/number of all possible interactions) and degree of generalization (the number of species a particular mutualist interacts with) of the community's pollination cycle may be overlooked.

In seasonal systems, the temperate forest of our study, plants and flower visitors are active during periods varying from several days to several weeks. Consecutive webs, each reflecting the pattern of interactions during a discrete time span, would describe interactions only among partners with coincident phenologies, and reveal oscillations in the number of partners and their degree of generalization, and changes in the connectance of the system.

This work analysed the pollination community on the basis of a comparatively large data set and, and it

provides a description of the dynamics of a plant-visitor web over its entire annual cycle. By sampling the web at monthly intervals we detected fluctuations in parameters such as assemblage composition, system size and connectance that cannot be resolved by cumulative studies.

We also recorded the presence of mutualists independently of their interactions. This led us to introduce the participance variable, which showed that the perceived web very probably did not include all potential interactions occurring in the system.

Methodological problems

The disadvantage of pooling data within years in a cumulative study may be compensated for by an increased chance of detecting rare interactions. We worked on the assumption that for every monthly period, the pooling procedure detects a 'hard core' of permanent mutualists and interactions, to which a minor 'periphery' of less stable participants is attached. While much additional study would be needed clearly to separate signal and noise in our system, the quality of our data seems adequate for our present purposes.

As webs become larger, observation time devoted to individual species diminishes, and the risk of detecting a smaller proportion of the existing interactions increases (Goldwasser & Roughgarden 1997). It has been argued that this might be only a minor problem in pollination networks because animal and plant species are not included until the interaction is observed (Olesen & Jordano 2002). However, there is a growing awareness of the problems associated with insufficient sampling in the study of plant-pollinator webs (Ollerton & Cranmer 2002; Vázquez & Aizen 2003).

The fact that many confirmed mutualists often failed to interact (*participance* was on average 55.2%, although it occasionally reached 100%) despite being present in the system, could be due to an inadequate sampling schedule, to very low interaction frequencies, or to both of them. Had our sampling effort been grossly insufficient, the values of *participance* may have been expected to decrease as the system size increased, as a result of our failure to identify active mutualists when the web became increasingly complex. In fact, participance *increased* with both potential system size ($y = 0.027 \cdot x + 41.8$; $R^2 = 0.44$) and actual system size ($y = 0.052 \cdot x + 46.1$; $R^2 = 0.61$). Thus, we are confident that non-recorded interactions were either uncommon or nonexistent. Several factors might have produced one or the other result. The probability of observing interactions was lower at the beginning and the end of a species' phenology. The interactions of low-abundance mutualists were probably very sparse and thus prone to be overlooked during sampling.

Plant species displaying few flowers per individual (either intrinsically or because of grazing, as probably occurred with some herbs) could also have had rare, undetected interactions.

Variation of system parameters and seasonality

In the talar, plant–flower–visitor interactions occurred throughout the year, but spring and autumn appeared to be the most favourable seasons. In this area, temperatures are lowest and can get below zero during June and July (Burgos 1968). Thus the low activity observed during the winter was possibly related to low temperatures. The coincidence of a small amount of rainfall and high temperatures generates a soil water deficit from January to March and this may be strongly related to the summer activity decline.

Besides showing a reduced system size and the consequent increase in connectance, the summer season had two additional distinct features: specialized visitor groups (bees and butterflies) were more species-rich, and more herbs were flowering during this period.

The spring activity peak covered much or all of the bloom of the three most interaction-rich plants in the system (*Colletia spinosissima, Schinus longifolia* and *Scutia buxifolia*); these may represent the main nectar and pollen source in the system, thus playing a crucial role in the community. This kind of very profitable species has been named differently by different authors: cornucopia species by Moldenke and Lincoln (1979), keystone species by Memmott (1999) and core species by Ne'eman *et al.* (2000). During the unfavourable part of the year, i.e. mid-autumn to mid-winter, the bloom of *Jodina rhombifolia* might be important in sustaining a visitor assemblage that later visited late-winter and early spring plants. The more abundant visitors of *J. rhombifolia* (n of captured individuals >10) (*Apis mellifera*, Augochlora *semiramis, Brachygastra lecheguana, Condylostylus erectus,* Muscidae sp. 7, *Palpada distinguenda, Toxomerus* sp.1) and of C. *spinosissima* (*Astylus quadrilineatus, Bombus bellicosus, Dialictus* sp. 2*,* Muscidae sp. 2, and *Vanessa* spp.) later took part in the assemblages of spring plants, thus suggesting some sort of facilitation mechanism.

The simultaneous occurrence of a few taxa with many interactions and many species with few interactions has already been observed in other systems (Moldenke & Lincoln 1979; Elberling & Olesen 1999; Memmott 1999; Dicks *et al.* 2002; Medan *et al.* 2002; Jordano *et al.* 2003). Our results support the notion that a non-normal distribution of the number of mutualistic interactions is of common occurrence, at least for flower visitors. Jordano *et al.* (2003) showed that in plant-pollinator networks, the distribution of specialization-generalization levels faintly tends to show a power-law regime for animal taxa and, more clearly, a truncated power-law regime for plants. Our results (which reflect the dynamics of a single network through its annual cycle) are coincident with those obtained by Jordano *et al.* (2003), suggesting that the organization of plant-pollinator networks according to power-law regimes may be a basic property of these systems. The interaction frequencies of plants were rather uniform, particularly because in most assemblages the frequencies of low-interacting plants were low. A possible explanation resides in the lack of specialized interactions in this system, i.e. most insect species could visit most plants and therefore there were few plants receiving only one species of visitor.

The variability both in the abundance of species that interact year-long as well as in phenological changes in flowering and insect appearances showed that simple cumulative webs were a limited tool for the deep analysis of a pollination system.

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