Structure of a plant-pollinator network on a pahoehoe lava desert of the Galápagos Islands

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Plant-pollinator interactions are important for the evolution and survival of the species involved. Plant-pollinator networks on oceanic islands are often small in size and as a consequence the connectance is high suggesting a substantial generalisation level. Further, linkage level for insular plants is shown to be lower than on mainland. The present study investigates a plant-pollinator network on the Galápagos Islands that is unique because of its very small size. We recorded pollinator visits to plant species as well as pollen grains on insect bodies. The combination of these data increased the observed number of interactions. The values for connectance and linkage level for plants were found to be consistent with similar values found in other network studies. There were no relation between the abundance of plant species and the number of pollinating species. The dominating pollinator species was the Galápagos carpenter bee *Xylocopa darwini*. Specimens of the shorthorned grasshopper *Halmenus cuspidatus* turned out to carry pollen from five plant species out of twelve and are probably functioning as pollinator. Bagging experiments revealed dependency on insect visits for a high seed set for most of the plant species, but only one species *Plumbago scandens* seemed to possess a pollen limited seed set. The network showed an asymmetric pattern of number of interactions per species with a few species having several interactions and many species a few. This pattern is supposed to result in a rather robust community, but is also fairly sensitive if the dominant species are threatened. The high connectance value found could, however, counteract this vulnerability.

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Plant-pollinator interactions are of decisive significance for the long and short time survival of the species involved. These interactions have high impact on the evolution of the reproductive systems of the plant species in the mutualistic plant-pollinator network (Jordano 1987). Species on islands are often endemic (Adsersen 1995) and subjected to disturbances from introduced plants and animals that are likely to interfere with the mutualistic relationships. The effect on seed set for the plant species and on feeding of the pollinators is of paramount importance for survival of the indigenous organisms, therefore knowledge of the interactions is essential for conservation measures of the focal species and superior for the maintenance of biodiversity.

Communities on oceanic islands possess lower species diversity than on their mainland counterparts (Carlquist 1974). The resulting, frequently smaller, plant-pollinator networks often hold a simpler structure. Plant-pollinator networks including a low number of species are char-

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acterized by an on average higher percentage of realised interactions (connectance) compared to more species rich networks, thus a more generalized pattern of mutualistic interactions should be expected (Olesen and Jordano 2002). The few complete studies on plant-pollinator networks on oceanic islands including all species in a certain community (McMullen 1993, Olesen and Jordano 2002, Olesen et al. 2002, Dupont et al. 2003) show that the number of interactions per plant species is lower on islands compared to mainland systems (Olesen and Jordano 2002). Insularity as such has, however, no effect on size of connectance, number of interactions, and number of interactions per animal species.

The Galápagos Islands are situated 1000 km west of Ecuador. The flora consists of ca 500 species of flowering plants of which ca 300 are endemic. The reproductive systems of 66 of these species have been investigated (Rick 1966, McMullen 1990, Nielsen et al. 2000, 2002, Philipp et al. 2004). Most of the species were found to be self-compatible and some are able to self-pollinate without help from pollinators. The pollinator fauna has been recorded by Linsley et al. (1966) and McMullen (1993) who found that the Galápagos carpenter bee *Xylocopa darwini*, is responsible for the majority of insect pollinations. It is the only bee species found on the islands and has been recorded to visit 79 plant taxa (McMullen 1993). In addition, about fifty other insect species belonging mainly to Diptera, Hymenoptera and Lepidoptera were observed as flower visitors (McMullen 1993).

The present study aimed to investigate the structure of a plant-pollinator network in a sparsely vegetated lava desert of the Galápagos Islands. Data on observations of pollinator visitation were supplemented by recording the presence of pollen grains on pollinators and stigmas. In addition we investigated the importance of pollinators on seed set of the predominantly endemic plant species.

Material and methods

Locality

The locality studied was situated about two kilometres north-west of Puerto Villamil on the island Isabela, Galápagos Islands (GPS: 00°56′57.1″S, 090°58′038″W). The area is an extensive pahoehoe lava desert with sparse vegetation. We marked six 30 × 30 m plots where the vegetation was similar.

Observations of interactions

We observed each plant species for 30 min at a time, recording each visit and counting how many flowers or capitula each insect visited. Each plant species was observed between 1 and 3.5 h. Totally, we observed the flowers for 34 h during five consecutive days. The observations were mainly carried out between 8 am and 5 pm. The weather was most of the time sunny with a little wind and a temperature mostly between 30 and 35°C. At the beginning of the observation periods each of us, four people, chose one of the six plots randomly in the morning. Within each plot the plant species were observed in a random order. During observations the insect visitors were identified in the field. Only insects probing the flowers were recorded. Specimens for pollen collection and final identification were caught in adjacent similar areas.

Pollen on insects and stigmas

The distribution of pollen grains on insect bodies was analysed by catching insects with net and removing pollen from their bodies. This was done by taking the insect from the net into a vial with a plastic grid across one opening. The insect was pushed gently towards the plastic net with a stamp. We removed pollen from all-over the surface of the insect with a lump of glycerol-gelatine hold with a pair of forceps. The gel lumps were in the field placed on a microscope slide, heated and covered by a cover glass. In order to observe the dispersal of pollen grains at the site we collected well exposed stigmas which were also mounted in the field in glycerol-gelatine on microscope slides.

Seed set without pollinators

To document the dependence of insect visits on seed production we bagged four flowers in bud stage and marked four open pollinated flowers as controls on each plant species.

Phenology of flowers/capitula

To relate the amount of insect visits to the length of anthesis we recorded the phenology of ten flowers from nine of the species. These were the species visited during day time, and with sufficient amount of flowers in bud.

Abundance of plant species

The frequency of each plant species at our locality was estimated by randomly placing circles of two meters in diameter, 20 times within each of our six plots, noting the species within the circle and counting the number of open flowers in these circles.

Results

System parameters

The locality included 15 plant species flowering of which 10 were observed visited by six insect taxa during daytime (Table 1). Half of these plant species were endemic to the Galápagos Islands (Appendix, Table S1). This is also the case for the main pollinator, *Xylocopa darwini*. Twenty-seven percent of the potential number of interactions was realized when using the data from flower observations only. The limited time available for flower observations was probably not sufficient to reveal the total network. To counteract this we combined observations with sampling of pollen from insect bodies by which the total amount of interactions increased to 33% out of the total number possible (Table 1 and 2). To test the level of saturation of interactions detected, a rarefaction analysis without replacement (Colwell 2005) was carried out using every 0.5 h observation period as separate samples and type of interaction (e.g. *Scalesia affinis – Xylocopa darwini*, *Pectis tenuifolia – Lepidanthrax tinctus*, etc.) as "species" (Fig. 1). The number of expected interactions increases quickly as the number of observation periods increase but with more observation periods the curve increases more slowly. We then added the "pollen on insect" samples. Every insect (Tables 3 and 4) was treated as a sample and the interactions obtained by the pollen species found were, likewise to the procedure above, used as "species". The resulting graph (Fig. 1) has a similar appearance as the graph built on observations alone.

The average linkage level was lower for plants than for insects (Table 1 and Fig. 2). The degree of nestedness (Bascompte et al. 2003) expressed by "temperature" was not calculated for the presence-absence data in the present plant-pollinator network since this analysis was not suitable for very small networks (W. Atmar pers. comm.).

Plant-pollinator interactions

During the 34 h of observations 159 visits from insects on 10 species of plants were recorded. In general, the Galápagos carpenter bee *Xylocopa darwini* was by far the dominating pollinator at the locality studied (Table 2 and Fig. 3A). There is, however, a considerable difference between the data from the direct observations and the data from the indirect evidence of flower visits, the pollen sampled from the insect bodies (Table 2). In both cases the Galápagos carpenter bee was the dominant visitor. We caught 13 female and three male Galápagos carpenter bees and they carried on average pollen from 2.8 ($\pm$1.6) (range 0–6) different species and on average 112.1 ($\pm$245.6) (range 0–1028) pollen grains (Table 3). A rarefaction analysis without replacement (Colwell 2005) of number of interactions obtained by sampling pollen from *Xylocopa darwini* showed by the decreasing curve (Fig. 4) that we caught a sufficient number of carpenter bee specimens to get the amount of information available by this method. We caught two grasshoppers (*Halmenus cuspidatus*, Acrididae, Fig. 5) on which pollen grains from four plant species was found, and two individuals of the fly species *Lepidanthrax tinctus* (Bombyliidae) with pollen grains from five plant species (Table 4). Together with direct observations of visits in flowers these two species turned out to visit five and six plant species, respectively (Table 2).

Pollen grains found on stigmas

We inspected stigmas of the species flowering in our plots (Appendix, Table S2, Fig. 3B). All stigmas had much pollen from conspecific individuals. At some stigmas we found, however, also pollen grains from other species (Appendix, Table S2). The number and amount of alien pollen on stigmas varied across species. *Chiococca alba* received pollen from *Scalesia affinis* only, but exported pollen to five different species. *Scalesia affinis* exported pollen to five different species but also received pollen from five species. Similarly, *Waltheria ovata* got pollen from four different species and delivered grains to three different species. The rest of the species exchanged pollen with a lower number of species.

Table 1. Characterizing figures for the pollination network at Isabela, The Galápagos Islands. The visitation matrix combines the interactions obtained by observations and collecting pollen from insects.

	Observation matrix	Pollen load on insects matrix	Visitation matrix
No. of animal species, A	6	3	6
No. of plant species, P	10	9	12
System size, M = A×P	60	27	72
Total number of interactions, I	16	17	24
Connectance, C = I × 100/M	26.7	63.0	33.3
Average number of interactions across pollinator species (average linkage level)	2.7$\pm$3.2	6.0$\pm$2.6	4.2$\pm$4.0
Average number of interactions across plant species (average linkage level)	1.3$\pm$1.2	1.5$\pm$1.3	2.1$\pm$1.2

Table 2. Interactions among insect and plant species recorded by observations of visits during daytime (■) and by pollen load on insects (○).

Plant species	Carpenter bee (*Xylocopa darwini*)	Fly (*Lepidanthrax tinctus*)	Grasshopper (*Halmenus cuspidatus*)	Butterfly (*Phoebis sennae*)	Fly (Muscidae)	Small fly
Chiococca alba	■ ○	○	○			
Cordia lutea	■					
Cordia revoluta	○					
Darwiniothamnus tenuifolius	■ ○	■ ○	■			
Jasminoserius thouarsii	■					
Lippia rosmarinifolia	○					
Opuntia echios	■ ○	○	○			
Passiflora foetida	■ ○					
Pectis tenuifolia	■ ○	■			■	■
Plumbago scandens				■		
Scalesia affinis	■ ○	■ ○	○			
Waltheria ovata	■ ○	○	○			

Frequency of insect visits during daytime

During our observation periods we noted the number of flowers or capitula visited by each visitor. This enables us to calculate the number of visits per flower or capitula per hour (Table 5). *Jasminoserius thouarsii*, *Passiflora foetida* and *Scalesia affinis* got the highest number of visits per hour. Species such as *Pectis tenuifolia* and *Chiococca alba* got very few visits per hour. These figures should, however, be seen in connection with the length of anthesis (Table 5). The species studied had flowers or capitula in anthesis from 4 h (*Passiflora foetida*) to 5 d (*Chiococca alba* and *Scalesia affinis*) (Table 5). The results show that only *Plumbago scandens* seems to suffer from a low average amount of visitations. The other species got a rather high, but very different number of visits during anthesis of each flower or capitulum, with *S. affinis* and *J. thouarsii* getting the highest scores.
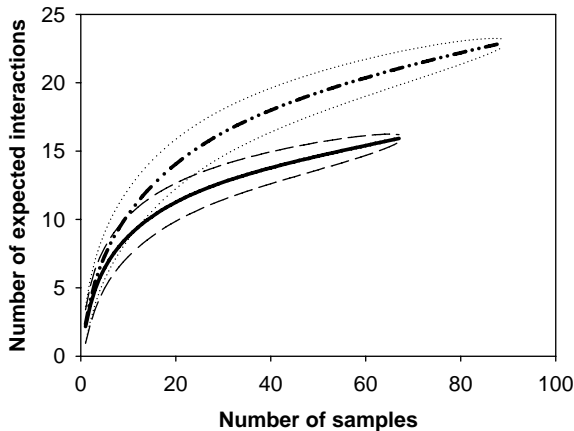

Fig. 1. Sample based rarefaction curves obtained after 50 randomizations without replacement. The solid line shows expected number of interactions when each sample is 0.5 h of observation period, totally 68 samples. The dashed line shows the combination of interactions found by observations with those obtained from sampling pollen on insect bodies. The thin lines are ±1 SD.

Insect observations during night

The occurrence of species with plenty of flowers which were not visited at all during daytime (Appendix, Table S1), but produced fruits, suggested night visitations. During two nights we observed visitors to some of the rarely visited species in our plots. *Sarcostemma angustissima* was visited by moths from the families Tortricidae and Noctuidae (e.g. *Epidromia zephyritis*, Fig. 6). *Lippia rosmarinifolia* and *Cordia revoluta* were mainly visited by small species of moths, e.g. *Shafferiessa galapagoensis* (Pyralidae: Phicitinae). Generally many taxa of insects were active during night and may have importance as pollinators, e.g. longhorn grasshoppers (Tettigoniidae), cockroaches (Blattidae), ant lions (Myrmeleontidae), ants (Formicidae), and several species of beetles (Coleoptera), especially longhorn beetles (Cerambycidae). Most of these were never seen during day. We did not observe systematically during nights since we did not bring the appropriate equipment and consequently these observations are not included in the plant-pollinator network as described in Table 1.

Frequency of plant species at the site studied

By noting the presence of plant species within circles with an area of 3.14 m^2 we got the frequency of each species (Appendix, Table S1). The two most frequent species were not flowering or not insect pollinated, respectively. We also noted the number of open flowers within our circles (Appendix, Table S1). There was no correlation between plant abundance or flowering frequency and the size of linkage level (Spearman correlation, r = 0.24 and r = 0.33, p > 0.05, respectively).

Seed set

Seed set recorded in open pollinated and bagged flowers showed that the majority of the species in our plots were

Table 3. Number of pollen grains collected on the surface of 16 *Xylocopa darwini* specimens (ordered after date of sampling). The grey background indicates the plant species on which *Xylocopa* was caught. X*ylocopa* no. 8, 9 and 13 were caught flying.

Xylocopa ID and sex	*Chiococca alba*	*Cordia lutea*	*Darwiniothamnus tenuifolius*	*Lippia rosmarinifolia*	*Opuntia echios*	*Passiflora* sp.	*Pectis tenuifolia*	*Scalesia affinis*	*Waltheria ovata*
1 ♀									3
2 ♀	1							50	1
3 ♀	1				1		5	75	4
4 ♂	12			4		1			1
5 ♀	5			5					5
6 ♀	13							196	3
7 ♀	1		2			1		3	1
8 ♀	13	1		5				26	4
9 ♀	12		1		25			1012	21
10 ♀					1	1			
11 ♀								11	10
12 ♀	2							24	
13 ♂	23			2	1			80	23
14 ♀	3		1					56	6
15 ♀	7			10				23	46
16 ♂	3							92	

dependent on insect visits to get a maximal seed set (Appendix, Table S3). Some species do not seem to be able to produce seeds at all without insect pollination. We found one seed in bagged flowers of *Plumbago* and *Waltheria* out of 35 and 180 flowers, respectively. These seeds could well be the result of flowers being too close to the bag and pollinated through it.

Discussion

Effects of the small network size

Generally, the relative number of realized interactions (the connectance) increases as the size of the network

Table 4. Number of pollen grains collected on two grasshoppers and two flies. One grasshopper and one fly were caught in flowers – the grey background indicates the plant species. One grasshopper was caught resting on a leaf and one fly was caught flying.

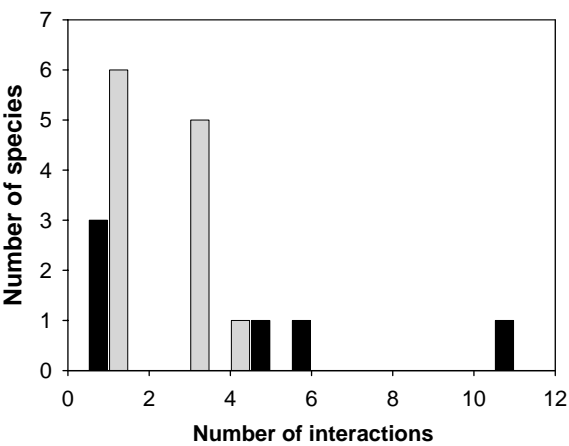|	Grasshopper (*Halmenus cuspidatus*)		Fly (*Lepidanthax tinctus*)	
Chiococca alba	6		1	–
Darwiniothamnus tenuifolius	–		4	52
Opuntia echios	1		–	1
Scalesia affinis	33	1	13	38
Walteria ovata	6	2	–	18
Unknown	5	–	–	–

Fig. 2. Number of interactions per plant (grey) and pollinator (black) species. Data combine interactions revealed by observations with those obtained by sampling pollen on insects.

system decreases (Jordano 1987). The plant-pollinator network studied at Isabela, one of the islands in the Galápagos archipelago, is small. Actually, it is the smallest yet studied (Olesen and Jordano 2002, Dupont et al. 2003). A small size was expected since the flora and fauna on islands generally are poor. The percentage of 27 of realized interactions based on observation data only is of the same order of magnitude that was found on two other oceanic islands: Tenerife (26, Dupont et al. 2003) and Ile aux Aigrettes, Mauritius (29, Olesen et al. 2002). The rarefaction analysis showed (Fig. 1) that if we have used more observation time more interactions were probably revealed. The curve shows, however, sign of saturation why the number of new interactions would most likely be low. To supplement the direct observations of visits to flowers we sampled pollen from insect bodies. These data increase the percentage of realized interactions to 33. Once more, a rarefaction analysis shows that this value could probably increase moderately especially if more flies and grasshoppers had been collected. The present connectance value is the highest found in plant-pollinator networks studied until now (Olesen and Jordano 2002, Dupont et al. 2003) and thus in agreement with the general principle that the smaller the network the higher the connectance. The combination of collection of pollen from bodies of pollinators with observations of pollinations revealed some interactions, which are not caught by observations alone. The increase in number of interactions by looking at pollen loads on insects is at the same level (ca 20%) as found in a study in a tropical rain forest (Kanstrup and Olesen 1999).

In a survey on plant-pollination networks no effect of insularity on connectance and number of interactions per pollinator species was found (Olesen and Jordano 2002). Number of interactions per plant species, however, decreased significantly on islands. In our investigation the average number of interactions is 2.1 per plant

A

Cordia revoluta Lippia rosmarinifolia
Waltheria ovata Opuntia echios
Chiococca alba Passiflora foetida
Scalesia affinis Jasminoserius thouarsii
Darwiniothamnus tenuifolius Cordia lutea
Pectis tenuifolia Plumbago scandens
Small fly
Muscidae Phoebis sennae
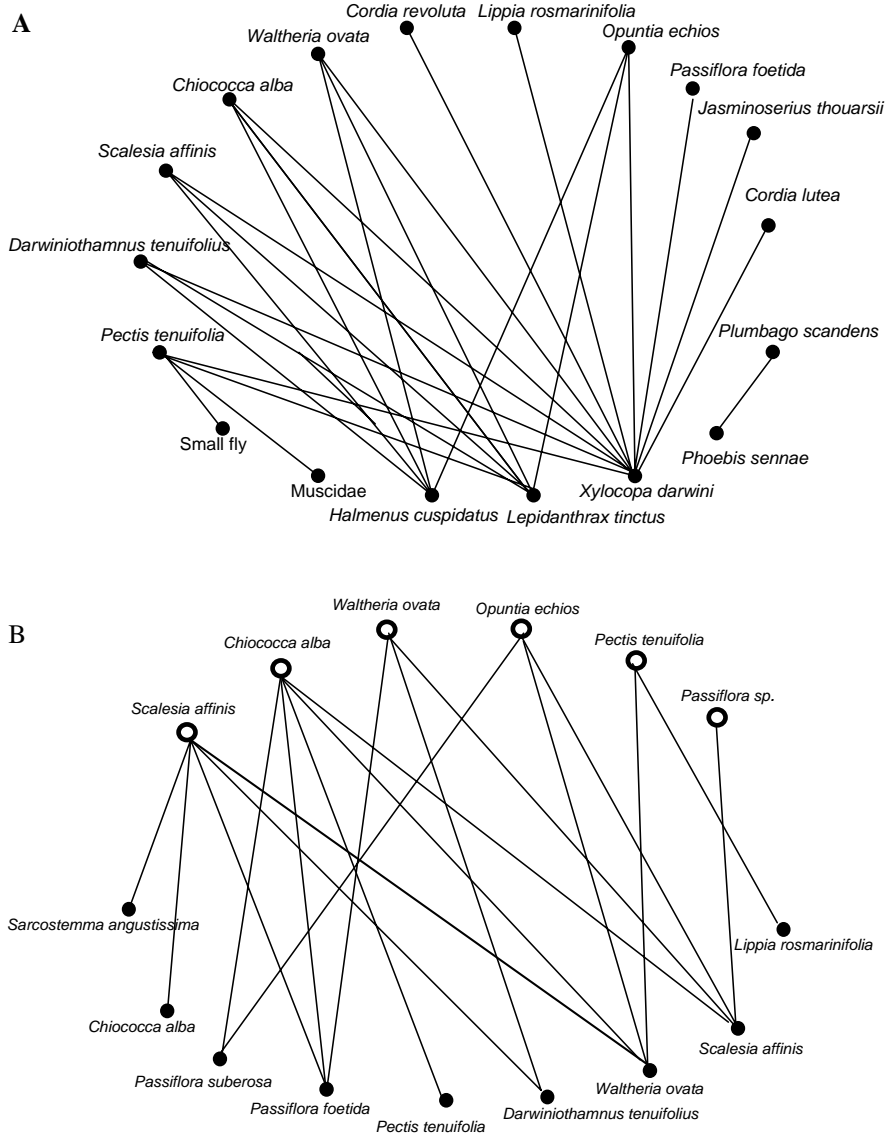Halmenus cuspidatus Lepidanthrax tinctus Xylocopa darwini

Fig. 3. (A) Plant-pollinator network (interactions combine data from observations with data from sampling of pollen from insects), (B) plant-plant network (open circles denote the "pollen donors" and closed circles the receptors). Both networks analysed with Pajek (Nooy et al. 2005)

B

Waltheria ovata Opuntia echios
Chiococca alba Pectis tenuifolia
Scalesia affinis Passiflora sp.
Sarcostemma angustissima Lippia rosmarinifolia
Chiococca alba Scalesia affinis
Passiflora suberosa Waltheria ovata
Passiflora foetida Darwiniothamnus tenuifolius
Pectis tenuifolia

species (Table 1), a figure lower than any of the figures in other plant-pollinator networks (Fig. 7). Also the average number of interactions per pollinator species is low in the present study. The high value of connectance suggest a high level of generalization but the average number of interactions per plant (2) and pollinator (4) species do not seem to support this statement. Two system traits can elucidate this apparent contradiction. Firstly, the low number of interactions per pollinator species is a result of a highly skewed distribution with the Galápagos carpenter bee as a pronounced generalist and the other pollinators less so, ensuring a low average number of interactions per pollinator species on one hand but a high total number of interactions on the other hand. Secondly, the low number of pollinator

species at our locality makes it impossible for the plant species to get a high linkage level.

Pollinator activity

Xylocopa darwini was by far the dominant pollinator as has been documented in many cases (Linsley et al. 1966, McMullen 1989, 1990, 1993), whereas most of the other pollinators were seen infrequently. The most surprising result was the diversity of pollen grains on the two specimens of shorthorned grasshopper *Halmenus cuspidatus* caught (Fig. 5). We saw the grasshopper in capitula of *Scalesia affinis*, although it did not visit the species during our periods of observation. The
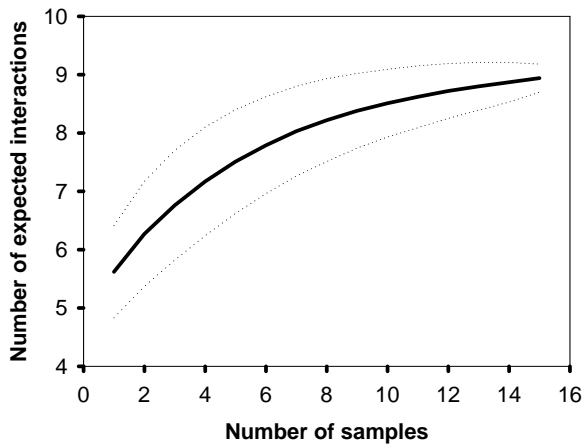
Fig. 4. Rarefaction curves for the 16 *Xylocopa darwini* sampled for collection of pollen on their bodies. The thin lines are ±1 SD.

occurrence in flowers might be accidental, but it could also suggest that this species in fact eats pollen. It is mentioned by McMullen (1993) that shorthorned grasshoppers were found on *Justicia galapagana* Lindau and could be pollinators. Further, it has been found in other cases that plants on islands get unexpected pollinators, such as lizards (Nyhagen et al. 2001, Olesen and Valido 2003, 2004). The significance of the activity of the grasshoppers for pollination still remains to be shown but there seems to be the necessary basis (pollen on bodies and high activity level) for grasshopper mediated pollination to occur.

Another subject which should be pursued is the insect activity during nights. Several night-flying Lepidoptera were seen, and their impact on pollination is probably high inferred from the seed set of the species, which got

Fig. 5. The grasshopper (*Halmenus cuspidatus*) on which pollen from five different plant species was found (photo by H. R. Siegismund).

no visits during daytime. Two of the species with most flowers in the area were not visited during daytime, namely *Sarcostemma angustissima* and *Lippia rosmarinifolia*. These species are members of another night-occurring network with an unknown number of moths as indicated by our night observations.

The activity patterns of pollinators are also reflected in the deposition of non-specific pollen grains on stigmas. Since *Xylocopa darwini* visits nearly all of the flowering species at our study site, all plant species are connected, and it could potentially be possible to find pollen from all species on the stigmas of any species. This is, however, not the case. Some species receive alien pollen from a higher number of species than others (Fig. 3B). This pattern could be due to some degree of constancy for each *Xylocopa darwini* individual, as also pointed out by Linsley et al. (1966).

Importance of visits by insects

Often plants immigrating to islands loose their self-incompatibility system in the process of establishing. If they were not self-compatible already they become so. Later in the evolution established species may develop some kind of outcrossing promoting feature (Barrett 1998). Bagged flowers of our study species had no seed set or a lower seed set than openly pollinated control flowers (Appendix, Table S3). The result of studies of hermaphroditic flowering plants at the Galápagos Islands was that most of these were reported to be self-compatible and automatically self-pollinated (Rick 1966, McMullen 1990). The present results showed that a major part of our study species was dependent on pollinators for seed set, and got a very low or no seed set when pollinations were excluded. This means that pollinator visitation is vital for the long term survival of most of the species. We found that only one of our species, *Plumbago scandens*, received less than one visit per flower during its anthesis. Pollen limitation of seed set in *P. scandens* is supported by the fact, that we did not find any pollen on its stigmas (Appendix, Table S2), and that only 67% of the openly pollinated flowers set seeds (data not shown).

Some of the species got many visits. One of the two most visited species is *Jasminoserius thouarsii*. This species did not set any seeds in our bags or after open pollination. We can not explain this. The other of the two is *Scalesia affinis*, which we in an earlier study have shown to be mostly self-incompatible and thus requires visits to get functional seeds (Nielsen et al. 2003). When considering the high number of visits, the phenology of the capitulum should be taken into account. During the five days of anthesis of each capitulum in *S. affinis* ca 10–15 new florets open each of the first four days. The capitulum needs visits every day to get pollen dispersed

Table 5. Survey of the number of insect visits to each of the studied plant species per time unit. The rightmost column is based on a daily activity period for insects of 12 h. The "small flies" are omitted from this table because they were too small to quantify.

Plant species	Hours of observation	Number of flowers or capitula observed 0.5 h each	Length of anthesis per flower or capitulum	Number of visits h^{-1}					Total number of visits h^{-1}	Estimated number of visits during anthesis
				Carpenter bee (*Xylocopa darwini*)	Fly (*Lepidanthrax tinctus*)	Grasshopper (*Halmenus cuspidatus*)	Butterfly (*Phoebis sennae*)	Fly (Muscidae)		
Chiococca alba	2.5	326	4-5 d	0.20					0.20	9.6
Cordia lutea	1.0	4		0.50					0.50	
Cordia revoluta	2.0	22								
Darwiniothamnus tenuifolius	2.0	53	2 d	0.19	0.11	0.04			0.34	8.2
Jasminoserius thouarsii	1.0	2	2 d	6.00					6.00	144.0
Lippia rosmarinifolia	3.5	90								
Opuntia echios	1.5	3		2.00					2.00	
Passiflora foetida	2.5	24	4 h	3.83					3.83	15.3
Passiflora suberosa	1.0	2								
Pectis tenuifolia	3.5	55	4 d	0.04	0.22			0.04	0.26	12.5
Plumbago scandens	1.0	62	1 d	0.03			0.03		0.06	0.7
Portulacca oleracea	1.5	20	4 h							
Sarcostemma angustissima	3.5	219								
Scalesia affinis	4.0	19	5 d	2.21	0.74				2.95	177
Waltheria ovata	3.5	75	1−2 d	0.83					0.83	10.0

Fig. 6. *Sarcostemma angustissima* visited by *Epidromia zephyritis* (Noctuidae) during night (photo by H. R. Siegismund).

and ovules fertilized (Nielsen et al. 2002, 2003). Calculating the number of visits per floret gives accordingly a much lower visitation rate. The same is true for the two other species belonging to the Asteraceae even though *Pectis tenuifolia* has only ca 15 florets per capitulum.

Patterns of interactions

Patterns of interaction networks are shown to have great influence on community dynamics (Montoya et al. 2003). Networks are often found to be asymmetric with a few nodes having many connections and most nodes a few links (small world) (Jordano 1987, Dunne et al. 2002, Berlow et al. 2004). Regarding such networks, it has for food webs been shown that removal of

highly connected species has a large impact on the network, for instance in terms of extinctions of other species. Removal of random species has fewer consequences (Dunne et al. 2002). Further, the effect of removing most connected species is less if there is a generally high connectance in the network (Dunne et al. 2002). The present system is small but conforms partly to this general small world pattern by having *Xylocopa darwini* as a dominant pollinator (Fig. 3A). Among the different plant species, however, none of the species were especially highly connected. The number of links could reflect the abundance of the species (Stang et al. 2006). We have no data for the abundance of the pollinator species. For the plant species no correlation was found between the abundance of flowers of the species and the number of different insect species visiting the plant species in the present study (Appendix, Table S1 and S2). The asymmetric structure of the present small network suggests that it is robust towards random changes in the network composition but on the other hand vulnerable towards precise attacks on the dominant species having most links (Olesen 2003, Dunne et al. 2002). The present network is also characterized by having a high connectance. This was expected as the size of the network is small but also the fact that most of the plant species visited during daytime in the present study possess easily accessible flowers with short (<0.5 cm) nectar holder tubes. This trait has been shown to promote the generalization of the system (Stang et al. 2006) resulting in a high connectance value. A positive correlation between connectance values and robustness has been shown for food webs (Dunne et al. 2002). If this is also the case for plant-pollinator networks the high connectance in the present network could to some degree counteract the vulnerability of the small world interaction pattern.

Conclusions

The present plant-pollinator network represents the smallest size yet investigated. A consequence of this is the highest value of connectance and lowest value of number of interactions per plant species ever reported. The network shows an asymmetric pattern of number of interactions per species. The significance of these results is that the investigated community appears rather robust. If, however, the dominant pollinator (*Xylocopa darwini*) is negatively affected by e.g. disturbances, the long term survival of the community is threatened.
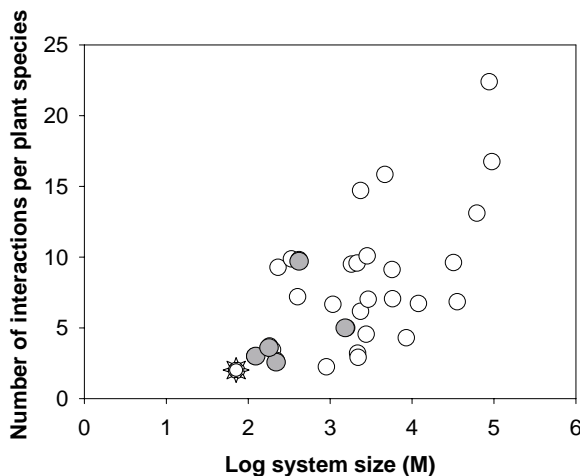

Fig. 7. Number of interactions per plant species in 31 network studies. The star-like dot is from the present study. The rest of the dots are from Olesen and Jordano (2002) and Dupont et al. (2003) and of these the grey circles represent studies on oceanic islands.

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