



# Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists

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**Abstract.** The structure of pollination networks is described for two oceanic islands, the Azorean Flores and the Mauritian Ile aux Aigrettes. At each island site, all interactions between endemic, non-endemic native and introduced plants and pollinators were mapped. Linkage level, i.e. number of species interactions per species, was significantly higher for endemic species than for non-endemic native and introduced species. Linkage levels of the two latter categories were similar. Nine types of interaction may be recognized among endemic, non-endemic native and introduced plants and pollinators. Similar types had similar frequencies in the two networks. Specifically, we looked for the presence of ‘invader complexes’ of mutualists, defined as groups of introduced species interacting more with each other than expected by chance and thus facilitating each other’s establishment. On both islands, observed frequencies of interactions between native (endemic and non-endemic) and introduced pollinators and

plants differed from random. Introduced pollinators and plants interacted less than expected by chance. Thus, the data did not support the existence of invader complexes. Instead, our study suggested that endemic super-generalist species, i.e. pollinators or plant species with a very wide pollination niche, include new invaders in their set of food plants or pollinators and thereby improve establishment success of the invaders. Reviewing other studies, super generalists seem to be a widespread island phenomenon, i.e. island pollination networks include one or a few species with a very high generalization level compared to co-occurring species. Low density of island species may lead to low interspecific competition, high abundance and ultimately wide niches and super generalization.

**Key words.** Azores, biological invasions, endemism, Mauritius, mutualisms, pollination, super generalist.

## INTRODUCTION

According to the equilibrium model of island biogeography (MacArthur & Wilson, 1967), the number of species on an island is a dynamic balance between immigration and extinction. Biotic resistance describes the level at which biotic factors (i.e. already established species) in an environment resist invasion of new species through competition, predation and parasitism

(Simberloff & von Holle, 1999). However, upon arrival on an island, alien species establish not only antagonistic interactions but also mutualistic ones with species already present, e.g. pollination interactions. These factors in a community are termed biotic facilitation (*sensu* Simberloff & von Holle, 1999). In contrast to biotic resistance, most studies of invasions ignore facilitative interactions (Richardson *et al.*, 2000). These authors go so far as to say that a paradigmatic shift in invasion biology is needed to move the focus of research away from competitive to mutualistic

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interactions. Simberloff & von Holle (1999) concluded from a review of the literature that facilitation seems to be just as important as resistance; they suggest that there is no obvious support for the biotic resistance paradigm.

A prominent feature of studies of island biotas is information on the proportions of endemic, non-endemic native and introduced species. The island of Mauritius, for example, has 1416 flowering plant species (Strahm, 1993) of which 22% are endemic, 26% non-endemic native and 52% introduced. Endemic, non-endemic native and introduced species vary in their history. For example, it is of great importance to the species-receiving island biota whether an introduced plant or pollinating animal forms interactions with an introduced or a native species. Interactions may be categorized into various types: endemic interactions (i.e. interactions between endemic plants and endemic pollinators), non-endemic native interactions (i.e. interactions between native plants and native pollinators), introduced interactions (i.e. between introduced plants and introduced pollinators) and mixed interactions (for example, between introduced plants and endemic pollinators). Studies on pollination interaction types on islands may supply important information about species and interaction assembly dynamics and biotic resistance and facilitation.

D'Antonio & Dudley (1993) introduced the concept 'invader complex' to label invader–invader facilitation. For example, the introduced water buffalo in Australia leads to a large-scale invasion of alien plants. Simberloff & von Holle (1999) suggested the term invasional meltdown for the process by which invasive species facilitate one another, leading to an acceleration in both invasion and impact. Thus, if invaders are more likely to interact with each other, large groups of introduced species may build up with increasingly detrimental consequences for the native island biota. We would like to examine whether invader complexes exist in pollination systems. Introduced species interacting more frequently than expected by chance alone constitute our definition of an invader complex. If introduced species are more generalized than native ones, i.e. if they establish or have the capability to establish many interactions with other species, they will more easily interact with newly introduced species and thus

facilitate the establishment of these. Invasive plants, for example, with a generalized pollination biology are expected to achieve more initial reproductive success and thus a higher establishment probability than specialized pollinated plants (Johnson & Steiner, 2000; Richardson *et al.*, 2000). Thus, in the initial establishment phase, alien species involved in highly co-evolved and specialized mutualisms are expected to be at a disadvantage. However, if both plant and pollinator become established, this disadvantage may become advantageous (Richardson *et al.*, 2000). In Florida, introduced fig species (*Ficus*) started invading when their obligate pollinator wasps were also introduced (Simberloff & von Holle, 1999).

We address the following questions using data from plant–pollinator networks from oceanic islands. (a) Does generalization level (here termed linkage level) differ between endemic, non-endemic native and introduced species? and (b), do frequencies of interactions between native and introduced species differ from random expectations? In particular, do introduced species preferentially interact, i.e. do invader complexes exist? In order to reach some generality in our conclusions, we answer these questions using data from two widely separated islands: the Mauritian offshore islet Ile aux Aigrettes in the Indian Ocean and the Azorean Flores in the Atlantic Ocean.

## MATERIALS AND METHODS

### Concepts and approach

Jordano (1987) analysed a set of pollination and seed dispersal community studies and concluded that facultative interactions of high generality are the rule. That is, most species establish several interactions and the strength, or importance, of any one interaction is weak. An obvious consequence of this is that research on interaction biology has to take place at the 'network' level. A pollination network is here defined as a two-dimensional matrix describing trophic and reproductive interactions between a community of flowering plant species ( $P$ ) and a community of pollinating animal species ( $A$ ) within a defined habitat. Network size is given as  $M = A \times P$  and it may be regarded as a species richness, species density or biodiversity measure. If all species of pollinators and flowering plants within a habitat

are included in the matrix, the network is said to be 'total'. For example, see Jordano (1987), Elberling & Olesen (1999), Memmott (1999), Kanstrup & Olesen (2000), Olesen (2000), and Olesen & Jordano (2002).

Here, level of generalization refers to number of species interactions and was compared both at species and network level. We used two measures at network level: total number of interactions in the network,  $I$ , and network connectance,  $C = 100 \times (I/M)$ , which is the percentage of all possible interactions within a network that are actually established, i.e. it is a scale- or  $M$ -independent measure of generalization level (DeAngelis, 1975; Jordano, 1987). In addition, we used two measures at species level: number of interactions of animal species  $m$  (linkage level,  $L_m$ ) and number of interactions of plant species  $n$  ( $L_n$ ).

In order to answer if invader complexes exist in island pollination networks, we compared observed proportion of introduced interactions with proportions obtained if species interacted randomly. If the proportions of observed introduced interactions was larger than expected by chance, we conclude that invader complexes exist.

### Potential methodological biases

Here, we termed all flower-visiting animals pollinators. Even for a few species, it is a very laborious task to ascertain to what extent this is actually true and no community study has never determined this (Memmott, 1999). We tacitly assumed that variation in visitation explained a substantial part of the variation in pollination. Even network studies based on flower-visitation data are few in number because, in addition to other factors, they require labour-intensive sampling and several animal groups pose taxonomic difficulties.

In network studies, information on species and interactions is often pooled across the entire study season. Consequently, phenological overlap between some of the animal and plant species may be low or even non-existent. This was ignored here because most plants and animals on Ile aux Aigrettes were flowering or active for several months of the year (S. Venkatasamy, unpublished data) and the flowering season on Flores was short and flowering of most plants took place simultaneously (J.M. Olesen, unpublished

data). In Mauritius, data were sampled at two widely separated periods and in Flores we sampled all our data during the peak flowering season.

Most studies in field ecology only last for one season. This was also true here. However, it is well known that the pollinator fauna at a site may vary tremendously in composition within and between seasons (e.g. Herrera, 1988; Olesen & Warncke, 1989). In addition, we expect to census a smaller proportion of all interactions within a network with increasing  $M$ , because of diminishing observation time for each species. This may be a minor problem in our pollination networks because animal and plant species were not included before they make or receive a visit, respectively, and because we chose to compare two networks of approximately a similar size ( $M$ ).

Pollination networks are difficult to delimit spatially and in published studies the size range of study sites varies tremendously (J.M. Olesen, unpublished data). The two networks in this study, however, were easy to delimit (see below).

### Study sites and periods

Pollination networks from two oceanic islands were compared. (a) Flores: the western-most island of the Azores. It is a steep-sided, verdant volcanic island reaching an elevation of 913 m. The study site was a 25-ha rocky cliff and a human-disturbed area just north of the main city Santa Cruz, consisting of an open herb community. It was delimited by the sea and the airport, and by fields and roads. The study on Flores took place in July 2000. (b) Ile aux Aigrettes: a 26-ha inshore islet 600 m off the south-east coast of Mauritius. Ile aux Aigrettes has the largest remaining fragment of coastal forest which once was widespread in Mauritius (Dulloo *et al.*, 1997). The study here took place in November 1998 and June 1999. All plant species on the islet were included in the study if they were flowering during the study periods. Thus, we regarded the islet as one coherent pollination network where all animals had the possibility to visit all plants.

The study sites on Flores and Ile aux Aigrettes were divided into 33 and 37 quadrates, respectively, each measuring  $100 \times 100$  m. Marginal ones included some sea areas. Each day we randomly selected 1–5 quadrates depending on weather conditions, and one or several flowering

individuals of each plant species within each quadrat were chosen for pollination observations. If a flowering individual was large we chose c. 1 m<sup>2</sup> of its flowering 'canopy' surface for flower visitation observations and if plants were small, all individuals of the species within an area of 1 m<sup>2</sup> were selected for observations. Observations on Ile aux Aigrettes were carried out from 07:00 to 11:00 and from 14:00 to 17:00 and only in sunny weather, encompassing a total of 341 intervals of 30 min each. Most often, only one species was kept under observation at a time. Observations on Flores were carried out from 09:00 to 16:00 and only in sunny weather, for a total of 226 intervals of 30 min. Some of the pollinators not identified to species in the field were preserved for subsequent identification at the Entomological Division of the Faculty of Agriculture, University of Mauritius (for the Ile aux Aigrettes material), and at the Entomological Divisions of the Natural History Museum, Aarhus, and the Zoological Museum, Copenhagen (for the Flores material) where vouchers are deposited. Frey (1938) and Davis & Barnes (1991) were the main sources. Plants are deposited at the Herbarium of the Mauritian Sugar Research Institute, Réduit, Mauritius, and at the Herbarium of the University of the Azores, Angra do Heroísmo, Terceira, the Azores.

### Data analysis

Prior to all regression analyses data were ln-transformed. Fisher's PLSD-test was used to compare linkage level pair-wise between endemic, non-endemic native and introduced species of plants and pollinators from the two networks and subsequently probabilities for each category of species were combined using a technique suggested by Sokal & Rohlf (1995). In addition, we examined if interactions between introduced and native plant (endemic and non-endemic combined) species and native and introduced animal species were established at random (our null hypothesis). For each network, we made a two-way contingency table (see Table 5), where the two descriptors were pollinators and plants and each of these had two states: native and introduced species. Thus the table consisted of four cells. Each of these contained the number of observed species-species interactions, e.g. the

number of interactions in the cell defined by native visitors and introduced plants on Flores was five (see Table 2). The significance of the association between the two descriptors in the tables was tested using Pearson statistics  $\chi^2 = \Sigma(O - E)^2/E$ , where  $O$  and  $E$  are observed and expected numbers of species interactions, respectively (Legendre & Legendre, 1998). As no values of  $E$  were less than 1, and less than 20% of the expected values  $E$  were smaller than 5 it was not necessary to group any cells. Subsequently, we tested the significance of the difference between  $O$  and  $E$  in each cell using a correspondence analysis. If the statistic Freeman-Tukey deviate  $= \sqrt{O} + \sqrt{(O + 1)} - \sqrt{(4E + 1)}$  was larger than a criterion value  $= \sqrt{(\chi^2/\text{no. cells})}$ , it was concluded that the difference between  $E$  and  $O$  was significant (Legendre & Legendre, 1998). All data were statistically analysed using the JMP® 3.2.2, 1997, software package from SAS Institute Inc.

### RESULTS

The two networks are shown in Tables 1 and 2. Network size, connectance and average linkage levels of plants and pollinators were similar (Table 3). On Flores, all pollinator species were insects, whereas the Mauritian site had a pollinating day gecko, *Phelsuma ornata ornata* (Gray). The only species shared by the two sites were the honeybee *Apis mellifera* L. and the house fly *Musca domestica* L.

As observation quadrates were selected randomly, abundance of plant species determined the number of observation periods per plant species. Time spent making pollinator observations at plant species  $n$  influenced the count of pollinator individuals ( $a$ ) visiting  $n$  (linear regression analysis: Ile aux Aigrettes:  $\ln(a) = 2.5 + 0.8 \ln(\text{observation time})$ ,  $R^2 = 0.36$ ,  $F = 6.9$ ,  $P = 0.02$ ; Flores:  $\ln(a) = 1.3 + 1.3 \ln(\text{observation time})$ ,  $R^2 = 0.43$ ,  $F = 5.8$ ,  $P = 0.04$ ). By using the residuals of  $a$  from these two regression analyses we corrected for variation in observation time. Linkage level ( $L_n$ ) of  $n$  and the observation time-corrected abundance of its pollinators (residual- $a$ ) were significantly correlated (linear regression analysis: Ile aux Aigrettes:  $\ln(L_n) = 1.126 + 0.004 \text{ residual-}a$ ,  $R^2 = 0.29$ ,  $F = 4.8$ ,  $P = 0.049$ ; Flores:  $\ln(L_n) = 0.724 + 0.008 \text{ residual-}a$ ,  $R^2 = 0.99$ ,  $F = 732$ ,  $P = 0.001$ ). Thus 29% and 99% of the variation

**Table 1** Pollination network of the Mauritian Ile aux Aigrettes. Values are numbers of visitors seen during the total observation period

		<i>Gastonia mauritiana</i> Marais (Araliaceae)	Endem	<i>Dracaena concinna</i> Kunth (Agavaceae)	Endem	<i>Scaevola sericea</i> Vahl (Goodeniaceae)	nE nat	<i>Ipomoea macrantha</i> Roemer & Schultes (Convolvulaceae)	nE nat	<i>Pemphis acidula</i> J. R. & G. Forster (Lythraceae)	nE nat	<i>Hibiscus tiliaceus</i> L. (Malvaceae)	nE nat	<i>Suriana maritima</i> L. (Surianaceae)	nE nat	<i>Argusia argentea</i> (L. f.) Heine (Boraginaceae)	nE nat	<i>Thespesia populnea</i> (L.) Soland. ex Correa (Malvaceae)	nE nat	<i>Morinda citrifolia</i> L. (Rubiaceae)	Intro	<i>Leucaena leucocephala</i> (Lam.) de Wit (Mimosaceae)	Intro	<i>Passiflora suberosa</i> L. (Passifloraceae)	Intro	<i>Stachytapheta jamaicensis</i> (L.) Vahl (Verbenaceae)	Intro	<i>Turnera angustifolia</i> Miller (Turneraceae)	Intro	Total visitor species abundance
Endem	<i>Phelsuma ornata</i> (Gray) (Gekkonidae)	30	33	19				21		28					12	14	23	9	7											196
nE nat	<i>Phalantha phalantha</i> Drury (Nymphalidae)							117																		26				143
nE nat	Stratiomyidae sp.	16						11									7		5						2	1				42
nE nat	<i>Xylocopa fenestrata</i> (Fabr.) (Anthophoridae)			15				16																			2			33
nE nat	<i>Megachile</i> sp. (Megachilidae)			15										13													2			30
nE nat	<i>Protaetia aurichalcea</i> Vinson (Scarabaeidae)	15																												15
nE nat	<i>Leptotes pirithous</i> L. (Lycaenidae)	2						1						1						2						1				7
nE nat	<i>Borbo borbonica</i> Boisduval (Hesperiidae)																2				2				1	1				4
Intro	<i>Apis mellifera</i> L. (Apidae)	149	11	92	126	103	138	23	57	69	115	46	34																	963
Intro	<i>Musca domestica</i> L. (Muscidae)	16														6														22
Intro	Syrphid sp. (Syrphidae)		17													6										2				25
Intro	<i>Lucilia</i> sp. (Calliphoridae)	16																												16

**Table 1** *continued*.

Intro	<i>Ornidia obesa</i> (Fabr.) (Syrphidae)	16														16
	Total visitor abundance	260	61	141	126	269	166	37	81	92	140	60	41	32	6	1512
	Relative plant species abundance	51	54	23	43	27	47	16	8	12	35	39	31	19	4	
	Observation period (h)	21	23	11	22	11	19	7	3	5	12	14	13	10	2	
	<i>Gastonia mauritiana</i> Marais (Araliaceae)	Endem														
	<i>Dracaena concinna</i> Kunth (Agavaceae)	Endem														
	<i>Scaevola sericea</i> Vahl (Goodeniaceae)	nE nat														
	<i>Ipomoea macrantha</i> Roemer & Schultes (Convolvulaceae)	nE nat														
	<i>Pemphis acidula</i> J. R. & G. Forster (Lythraceae)	nE nat														
	<i>Hibiscus tiliaceus</i> L. (Malvaceae)	nE nat														
	<i>Suriana maritima</i> L. (Surianaceae)	nE nat														
	<i>Argusia argentea</i> (L. f.) Heine (Boraginaceae)	nE nat														
	<i>Thespesia populnea</i> (L.) Soland. ex Correa (Malvaceae)	nE nat														
	<i>Morinda citrifolia</i> L. (Rubiaceae)	Intro														
	<i>Leucaena leucocephala</i> (Lam.) de Wit (Mimosaceae)	Intro														
<i>Passiflora suberosa</i> L. (Passifloraceae)	Intro															
<i>Stachytapheta jamaicensis</i> (L.) Vahl (Verbenaceae)	Intro															
<i>Turnera angustifolia</i> Miller (Turneraceae)	Intro															
Total visitor species abundance																

Endem: endemic species. nE nat: non-endemic native species. Intro: introduced species. Relative plant species abundance is total number of flowering plants observed for flower visitors.

**Table 2** Pollination network of the Azorean Flores. Values are numbers of visitors seen during the total observation period

		Endem	nE nat	nE nat	nE nat	nE nat	nE nat	nE nat	Intro	Intro	Intro	
		<i>Azorina vidualii</i> (Watson) Feer (Campanulaceae)										
		<i>Crithmum maritimum</i> L. (Apiaceae)										
		<i>Solidago sempervirens</i> L. (Asteraceae)										
		<i>Beta vulgaris</i> ssp. <i>maritima</i> (L.) Arcangeli (Chenopodiaceae)										
		<i>Daucus carota</i> L. (Apiaceae)										
		<i>Silene vulgaris</i> (Moench) Garcke (Caryophyllaceae)										
		<i>Chamomilla suaveolens</i> (Pursh) Rydb. (Asteraceae)										
		<i>Lotus corniculatus</i> L. (Fabaceae)										
		<i>Freesia refracta</i> (Jacq.) Ecklon ex Klatt (Iridaceae)										
		<i>Reseda luteola</i> L. (Resedaceae)										
		Total visitor species abundance										
End	<i>Halictus</i> sp. nov. (Halictidae)	98		141		11	7	21			11	289
nE nat	<i>Sepsis thoracica</i> Rob.-Desv. (Sepsidae)	51	87		8		30					176
nE nat	<i>Agrotis ipsilon</i> (Hufnagel) (Noctuidae)			22								22
nE nat	<i>Bombus ruderatus</i> (Müller) (Apidae)	9							47	11		67
nE nat	<i>Colias crocea</i> (Fourcroy) (Pieridae)	9							21	12		42
Intro	<i>Musca domestica</i> L. (Muscidae)	23	83			102		42				250
Intro	<i>Apis mellifera</i> L. (Apidae)	89							9		9	107
Intro	<i>Lucilia sericata</i> Meig. (Calliphoridae)		93			8						101
Intro	<i>Lasius niger</i> (L.) (Formicidae)	37										37
Intro	<i>Anthomyia pluvialis</i> L. (Muscidae)							23				23
Intro	<i>Calliphora vomitoria</i> L. (Calliphoridae)	13										13
Intro	<i>Eristalis tenax</i> L. (Syrphidae)		12									12
	Total visitor abundance	329	275	163	8	121	37	86	77	23	20	1139
	Relative plant species abundance	152	137	76	30	30	15	15	30	15	15	
	Observation period (h)	20	22	20	12	10	6	6	8	5	4	

Endem: endemic species. nE nat: non-endemic native species. Intro: introduced species. Relative plant species abundance is total number of flowering plants observed for flower visitors.

in linkage level of plant species was determined by total abundance of their pollinator fauna.

Pollinators and plants were categorized into endemic, non-endemic native and introduced species. Linkage levels of plants and pollinators of the three categories are given in Table 4. In

general, linkage level of endemic species was significantly higher than that of non-endemic native and introduced species, whereas linkage level of the two latter categories did not differ significantly from each other (Fisher's PLSD-test:  $P < 0.05$  for both comparisons).

**Table 3** Parameter values for the two island pollination networks. *A*, size of community of pollinator species, i.e. number of pollinator species within the study site. *P*, size of community of flowering-plant species, i.e. number of flowering plant species within the study site.  $M = A \times P$ , pollination network size. *I*, number of species interactions between *P* and *A* within study site and period.  $C = I/M$ , network connectance, i.e. fraction of all possible interactions in the network being realised.  $L_m$ , linkage level or generalisation level of pollinator species *m*, i.e. number of plant species visited by pollinator species *m*.  $L_n$ , linkage level or generalisation level of plant species *n*, i.e. number of pollinator species visiting plant species *n*

	Flores	Ile aux Aigrettes
<i>A</i>	12	13
<i>P</i>	10	14
<i>M</i>	120	182
<i>I</i>	30	52
<i>C</i> (%)	25.0	28.6
$L_m$	2.5	4.0
$L_n$	3.0	3.7

Combining the three categories of pollinators and plants we get nine interaction types in all. Observed frequencies of each pair of the nine interaction types of the two islands were very similar (paired *t*-test:  $t < 0.001$ ,  $P = 0.99$  for all nine comparisons).

At both sites, the numbers of interactions between native (including endemics and non-endemics) and introduced pollinator species and native and introduced plant species differed significantly from random expectations ( $\chi^2 = 3.9$  and 3.7 for Ile aux Aigrettes and Flores, respectively, and for 1 degree of freedom,  $P = 0.05$  in both cases, Table 5). The cell that accounted for the

significant relationship in the Ile aux Aigrettes network was the one defined by introduced pollinators and introduced plants where the number of observed interactions were significantly lower than expected by chance alone. At Flores, two of the four cells accounted for the significant relationship. The number of observed interactions between native pollinators and native plants was larger than expected by chance and the number of observed interactions between introduced pollinators and introduced plants was lower than expected. Thus in both networks, the number of interactions between introduced animals and introduced plants was lower than expected by chance. Thus we found no evidence to support the existence of invasional complexes.

## DISCUSSION

### Other island networks

To some extent, information like that obtained by our study can be extracted from other sources as well. McMullen (1993) studied pollination in the Galápagos flora. He listed interactions between plants and insects from several islands. On the Canarian island of Gomera, Forfang & Olesen (1998), Olesen *et al.* (1998a), and Olesen *et al.* (2002) studied pollination of all flowering plants in a plot of laurel forest. Finally, on Tenerife, Olesen *et al.* (2002) studied pollination of all flowering plants in a plot of *Euphorbia* desert. Proportions of interactions between native and introduced species vary among these networks and the two in this study, e.g. interactions between endemic species, are much more frequent in the Canaries than on the other islands. The reason is the very high numbers of endemic plants in the laurel forest and in the *Euphorbia* desert. Values

**Table 4** Linkage level of endemic, non-endemic native and introduced pollinators and plants from two island pollination networks. Linkage level for, say endemic pollinators refers to the interactions to all plants, whether or not native or introduced

	Flores		Ile aux Aigrettes	
	Pollinator	Plant	Pollinator	Plant
Endemic	6.0	8.0	6.5	5.0
Non-endemic native	2.8	2.5	3.3	3.3
Introduced	1.9	2.3	3.8	4.0



**Table 5** Two-way contingency tables used in  $\chi^2$  tests. Values are numbers of species interactions (for details, see text)

## Flores

		10 plant species		
		7 native	3 introduced	
12 pollinator species	5 native	12	5	Observed
		8.8*	3.8	Expected
	7 introduced	11	2	Observed
		12.3	5.3	Expected

## Ile aux Aigrettes

		14 plant species		
		9 native	5 introduced	
13 pollinator species	8 native	20	13	Observed
		20.6	11.4	Expected
	5 introduced	15	4	Observed
		121.9	7.1	Expected

\* Example:  $(5/12) \times (7/10) \times 30 = 8.8$ .

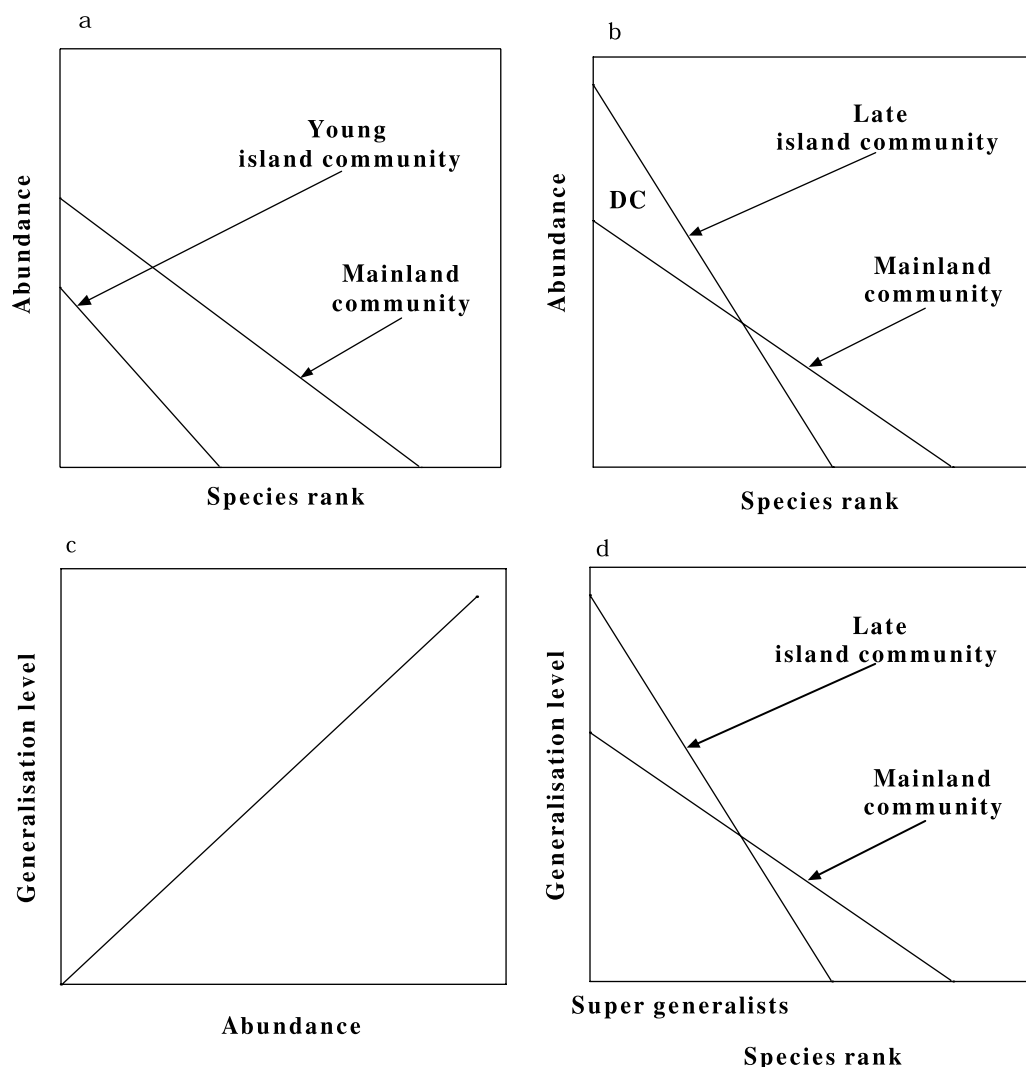
**Table 6** Endemic (or non-endemic native for *Cordia lutea*) super generalists on five oceanic islands. These species are the most generalized plants and pollinators of all species in their community. *C*, species connectance, i.e. actual number of interactions made by a species divided by total number of potential species interactions; for example, the gecko *P. ornata* visits 10 plant species and the total Ile aux Aigrettes plant community consists of 14 species ( $C = 71\%$ )

Island	Pollinator	<i>C</i>	Plant	<i>C</i>	Reference
Ile aux Aigrettes,	<i>Phelsuma ornata</i> ,	10/14	<i>Gastonia mauritiana</i> ,	8/13	This study; Nyhagen <i>et al.</i> (2001)
Mauritius	Geckonidae	(71%)	Araliaceae	(62%)	
Flores, the	<i>Halictus</i> sp.,	6/10	<i>Azorina vidalii</i> ,	8/12	This study
Azores	Halictidae	(60%)	Campanulaceae	(75%)	
Galapagos	<i>Xylocopa darwini</i> ,	64/83	<i>Cordia lutea</i> ,	17/38	McMullen (1993)
	Anthophoridae	(77%)	Boraginaceae	(45%)	
Tenerife, the	<i>Anthophora allouardii</i> ,	6/13	<i>Aeonium holochrysum</i> ,	16/20	Olesen <i>et al.</i> (2002)
Canaries	Anthophoridae	(46%)	Crassulaceae	(80%)	
Gomera, the	<i>Bombus canariensis</i> ,	14/29	<i>Cedronella canariensis</i> ,	24/54	Olesen (1985); Olesen <i>et al.</i> (1998a); Forfang & Olesen (1998); Olesen <i>et al.</i> (2002)
Canaries	Apidae	(48%)	Lamiaceae	(44%)	

of network parameters can also be extracted from these data. In all three studies, linkage level of endemic species was higher than that of non-endemic native and introduced species, as we observed in Ile aux Aigrettes and Flores. This is explained to some extent, but not entirely, by the presence of super-generalized plants and pollinators.

### Super generalists

According to Table 6, a super generalist is an endemic (or non-endemic native) species with a much higher linkage level than the remaining species in its community. Pollination networks on each of the five oceanic islands have their own



**Fig. 1** Sequence of events leading to super generalization. (a) Island communities have a lower species density than an the adjacent mainland and island population density is initially also lower. (b) Low species density leads to low interspecific competition and, in some taxonomic and trophic groups, to density compensation (DC, e.g. Case, 1982). We have complete DC when the areas of the two triangles become equal in size. (c) Generalization level and abundance are expected to be positively correlated in pollination networks (J.M. Olesen, unpublished data; and this study). (d) Because of (b) and (c), a rank-generalization diagram mirrors a rank-abundance diagram, as seen in (b). Species being super generalists will thus to some extent also be density-compensating species.

super-generalist pollinators and plants. Such species seem to respond to the reduced interspecific competition on islands by showing ecological release and in some cases density compensation (Fig. 1; Diamond, 1975; Case, 1982). Such highly

abundant species will, all other things being equal, become very generalized according to the principle of equal opportunity (*sensu* MacArthur, 1972). Hence, super generalists are widespread and very common species with many pollination

interactions. They may also act as keystone species. Richardson *et al.* (2000) referred to the honey bee as a super generalist, which was also seen in our study at Ile aux Aigrettes. The high generalization level of the Ile aux Aigrettes honeybees is due to a high density of bee hives on the adjacent mainland coast (personal observation).

In general, endemics tend to be more generalized than native and introduced species. Palaeoendemics may have survived extensive periods on isolated islands by being generalized, and neo-endemics may have evolved from non-endemic native or introduced species, i.e. from being more specialized towards being more generalized, as has been observed in one pollination case study from Madagascar (Armbruster, 1998).

### Invader complexes

This study suggests that introduced species do not preferentially establish interactions with other introduced mutualists. This is somewhat in line with the conclusions reached by Simberloff & von Holle (1999). They too did not find any clear evidence for facilitation between introduced species. On the contrary, endemic super generalists include newcomers in their niche. Our data set indicates that super generalists do not discriminate between native and introduced species when they establish their interactions. Mixed interactions are a well-known 'problem' among conservationists. Animal conservationists who aim to eradicate introduced animal species are often opposed by plant conservationists who see their endemic plants as having vital interactions with introduced pollinators and fruit dispersers and vice versa. The extremely rare Mauritian endemic plant *Nesocodon mauritanus* has the introduced bird the bulbul (*Pycnonotus jocosus*) as its sole pollinator (Olesen *et al.*, 1998b). Also in Mauritius, the endemic pink pigeon (*Nesoenas mayeri*) and echo parakeet (*Psittacula echo*) eat fruit of several introduced and very abundant fleshy-fruited plants, f. ex. *Psidium guajava* L. (J.M. Olesen, personal observation). Some of these mixed interactions are established between endemic super generalists and introduced species.

### CONCLUSIONS

We suggest that low species density on islands compared to adjacent mainland causes a widening

of the feeding niche of some flower-visiting animals and of the reproductive niche of some flowering plants. These species, here termed super generalists, then include new invaders in their niche and thus facilitate their future establishment on islands.

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