



Pollination networks and functional specialization: a test using Lesser Antillean plant–hummingbird assemblages

Bo Dalsgaard, Ana M. Martín González, Jens M. Olesen, Allan Timmermann, Laila H. Andersen and Jeff Ollerton

B. Dalsgaard (bo.dalsgaard@biology.au.dk), J. M. Olesen, A. Timmermann and L. H. Andersen, Dept of Biological Sciences, Univ. of Aarhus, Ny Munkegade, Building 1540, DK-8000 Aarhus, Denmark. – A. M. Martín González, Unit of Ecology and Center for Ecological Research and Forestry Applications (CREAF), Autonomous Univ. of Barcelona, ES-08193 Bellaterra, Barcelona, Spain. – J. Ollerton, Landscape and Biodiversity Research Group, School of Applied Sciences, Univ. of Northampton, Park Campus, Northampton, UK, NN2 7AL.

Network analysis has in recent years improved our understanding of pollination systems. However, there is very little information about how functionally specialized plants and pollinators interact directly and indirectly in pollination networks. We have developed a parameter, Functional specialization index, to quantify functional specialization in pollination networks. Using this parameter, we examined whether different sized hummingbirds visit a distinct set of flowers in five hummingbird-pollinated plant assemblages from the Lesser Antilles, obtaining a simple relationship between hummingbird body size, network parameter and ecological function. In the Lesser Antilles, functionally specialized hummingbird pollination is distinct for plant species pollinated by the largest hummingbird species, whereas the pollination niche gradually integrates with the insect pollinator community as hummingbird body size decreases. The network approach applied in this study can be used to validate functional specialization and community-level interdependence between plants and pollinators, and it is therefore useful for evaluating and predicting plant resilience to pollinator loss, presently a global concern.

Knowledge of the interdependence between plant and pollinator species, especially at the community level, is crucial for an improved understanding of ecosystem functioning (Waser and Ollerton 2006) and health (Petanidou and Lamborn 2005). In recent years, plant–pollinator interactions have often been interpreted in the context of complex plant–pollinator networks (Dicks et al. 2002, Bascompte et al. 2003, Dupont et al. 2003, Memmott et al. 2004, Vázquez and Aizen 2004, 2006, Petanidou and Lamborn 2005, Bascompte et al. 2006, Olesen et al. 2007). This has substantially improved the knowledge of the structure of plant–pollinator assemblages, e.g. nestedness (Bascompte et al. 2003, Dupont et al. 2003), asymmetry (Vázquez and Aizen 2004, Bascompte et al. 2006) and compartments or modules (Dicks et al. 2002, Olesen et al. 2007), and thereby the understanding of plant–pollinator functioning, resilience and stability. Dicks et al. (2002) and Olesen et al. (2007) found compartments or modules in plant–pollinator webs which, to some extent, reflected underlying specialization on functional groups of pollinators. However, apart from this, not much attention has been paid to the identification of functional specialization in pollination assemblages, using the network approach.

Here we developed a simple method to quantify functional specialization in pollination networks (Fig. 1).

We use floral visitation data from which we construct traditional plant–pollinator interaction matrices (Fig. 1a) as used by, for example, Olesen et al. (2007). However, instead of analysing the data as traditional matrices, we propose depicting each plant–pollinator matrix as a two-mode plant–pollinator network (Fig. 1b), and then transforming it into a one-mode pollinator network containing only the animal species (Fig. 1c). In these networks, two animal species are linked if they share at least one plant species. In functionally specialized pollination systems, one would expect functionally similar animals to visit plant species with similar floral morphology and, hence, to be directly linked in one-mode pollinator networks. Conversely, if different pollinator types are linked directly in one-mode pollinator networks, the pollination systems are functionally less clear-cut. In order to measure functional specialization in pollination networks, we developed a parameter, Functional specialization index $\langle FS \rangle$, to calculate the linkage distance between pollinator types. The FS-index, inspired by the *k*-neighbours concept in social science (de Nooy et al. 2005), measures the topological distances from a focal node in one set of nodes, A, to each other node included in another particular set, B, in the network (Fig. 1d). Each of these sets of nodes, A and B, may represent different pollinator types. Hence, the smaller the FS values, the more directly type A species are

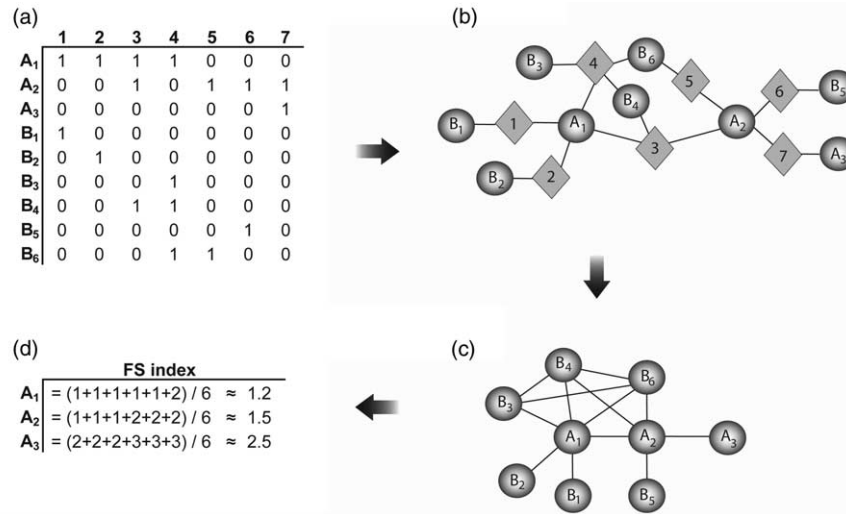


Fig. 1. Method for the calculation of the Functional specialization index $\langle FS \rangle$: (a) plant–pollinator interaction matrix. Columns are plant species (1–7) and rows two types of animal species (type A: A1-A3 and type B: B1-B6). Interactions known to occur are represented by 1s, 0s indicate absent interactions; (b) two-mode plant–pollinator network representation of the plant–pollinator interaction matrix; diamonds symbolize plant species, circles animal species and links between nodes recorded interactions; (c) one-mode pollinator network; animals are linked if they share at least one plant species; and (d) calculation of FS-values for each hummingbird species.

linked with type B species in the pollinator network, and the less strict is the functional specialization. We illustrate the proposed method by testing whether functionally specialized ornithophily exists in plant–hummingbird assemblages in the Lesser Antilles, or conversely whether hummingbirds and insects visit the same flowers. Specifically, we: 1) calculated the network distances from different-sized hummingbirds to all insect species in plant–hummingbird assemblages in five Lesser Antillean networks; 2) examined whether small hummingbirds were closer than large hummingbirds to insect species, i.e. whether the ornithophilous functional group was distinct for plant species pollinated by large hummingbirds only; 3) tested whether the difference in hummingbird body size is a good predictor of the difference in FS-values between hummingbird pairs; and finally 4) discuss the use of pollination networks to assess the presence of other functionally specialized pollination systems.

Methods

Study area and species

The study was carried out in two 400×5 m plots in the southwestern part of the Lesser Antillean island of Dominica ($15^{\circ}25'N$, $61^{\circ}20'W$) and in three 200×5 m plots in Grenada ($12^{\circ}07'N$, $61^{\circ}40'W$) at different altitudes and in different vegetation types. In order to include all five species of hummingbirds present in the Lesser Antilles, we observed pollination interactions both in coastal dry scrub woodland (3–15 m a.s.l.) and in montane thicket-elfin woodland (779–847 m a.s.l.) in Dominica, and in coastal dry scrub woodland (30–45 m a.s.l.), rainforest (495–505 m a.s.l.) and montane thicket-elfin woodland (695–715 m a.s.l.) in Grenada. In Dominica, the fieldwork was conducted from 10 April to 17 July 2005 and in Grenada from 10 March to 25 June 2006.

Visitation by hummingbirds was monitored for all flowering plant species in 30-min periods (a total of 815 h) from a distance of approximately 10 m. Observations were conducted during dry and calm weather between 06–18 h (Dominica) and 06–14 h (Grenada). Additional plant–hummingbird interactions observed between the 30-min observation periods were also included in the dataset. Only plant species visited and regarded as pollinated by hummingbirds are reported in this study, i.e. our focus was the plant–hummingbird compartment. All these plant species were identified and censused for insect visitation. Visitation by insects was observed in 10-min observation periods (a total of 87 h) in dry and calm weather between 10–16 h (Dominica) and 6–14 h (Grenada). Only visits where insects touched either anthers or stigma were included. Insects were caught for later identification and assignment to distinct morphospecies at family level using Triplehorn and Johnson (2005) and Michener (2000). Vouchers are kept at the Univ. of Aarhus, Denmark.

Data analysis

Following the above described procedure, we created one-mode pollinator networks and calculated FS-values, focusing on the linkage pattern between different sized hummingbirds and insect species. If $FS = 1$ then the hummingbird and the insect species were directly linked by visiting at least one of the same plant species. If $FS = 2$ the hummingbird and insect were only indirectly linked, via another animal (hummingbird or insect species), that was directly linked with both the focal hummingbird and the insect species. If $FS = 3$ the hummingbird and insect were only indirectly linked, via two other animals (hummingbird or insect species), linking the focal hummingbird and the insect species. Hence, the smaller the FS-values, the more directly the hummingbird species was linked with insect

Table 1. Network parameter values for each of the five plant–hummingbird assemblages. Plant, number of hummingbird-pollinated plant species. Hummingbird, number of hummingbird species. Insect, number of insect morphospecies. I, number of interactions between plants and animals (hummingbirds and insects).

	Dominica lowland	Dominica highland	Grenada lowland	Grenada rainforest	Grenada highland
Plant	11	12	3	7	7
Hummingbird	2	3	1	3	2
Insect	51	12	12	8	17
I	99	36	17	22	33

species in the pollinator network and the less strict the functionally specialized ornithophily was. First, we calculated the FS-values for each hummingbird species in each network, and examined whether they varied between different-sized hummingbirds. Secondly, we tested whether body size difference between pairs of hummingbirds in each network was a good predictor of their difference in mean FS distance. As both difference in hummingbird body size and FS-values were normally distributed (Kolmogorov–Smirnov test), we examined the relation between difference in hummingbird body size and difference in FS by Pearson correlation analysis using JMP 6.0. We used PAJEK 1.15 <<http://vlado.fmf.uni-lj.si/pub/networks/pajek/>> for all calculations of network properties.

Results

The Lesser Antillean hummingbird-pollinated plant data set comprised a total of 207 interactions between 36 plant species, five species of hummingbirds and 84 insect morphospecies, with some species occurring in more than one network (Table 1, 2).

Hummingbirds were the exclusive visitors of only seven plant species (19%) – the remaining 29 plant species (81%) were visited by both hummingbird and insect species. FS-values of hummingbirds ranged between 1 (direct linkage with insect species) and 3 (indirect linkage via two other pollinators). The proportional distribution of FS varied considerably between hummingbird species (Table 2). The smallest hummingbird species (Antillean crested hummingbird *Orthorhyncus cristatus*) was most frequently linked directly with insect species, $FS = 1.0 \pm 0.00$ SD 1.17 ± 0.39

SD, and gradually FS changed towards more indirect linkages as the hummingbird species' body size increased (blue-headed hummingbird *Cyanophaea bicolor*, green-throated carib *Eulampis holosericeus* and rufous-breasted hermit *Glaucis hirsuta*), and finally with mostly indirect linkages, $FS = 2.17 \pm 0.83$ SD, for the largest hummingbird species (purple-throated carib *Eulampis jugularis*). Hence, the average FS-value decreased consistently with decreasing hummingbird size, and species occurring in more than one network had similar FS-values among networks (Table 2). The only apparent exception was the green-throated carib in the Grenada highland network which had lower FS-values (1.24 ± 0.44 SD) than the smaller blue-headed hummingbird in the Dominica highland network (1.42 ± 0.51 SD). However, within the Grenada highland network, the green-throated carib had larger FS-values than the coexisting smaller Antillean crested hummingbird, and it was therefore not an exception to the overall trend of increased FS-values as body size increased (Table 2). Indeed, when analysing the FS-values as contrasts between pairs of different sized hummingbirds within each network, body size difference was a good predictor of the difference in FS-value ($r^2 = 0.80$, $p < 0.01$; Fig. 2).

Discussion

This study complements previous work on the largest hummingbird in the Lesser Antilles, the purple-throated carib, which has been reported to be tightly co-evolved with its preferred food plants, *Heliconia caribbea* and *H. bihai* (Temeles et al. 2000, Temeles and Kress 2003). Our results confirm that distinct functionally specialized ornithophilous

Table 2. For each hummingbird species, the mean FS-value \pm SD in each pollination network is presented. The data are arranged by increasing hummingbird body mass as given in Brown and Bowers (1985) and, for species occurring in several pollination networks, by increasing FS-values.

Hummingbird species		Body mass (g)	Pollination network	FS-value (mean \pm SD)
Common name	Scientific name			
Antillean crested hummingbird	<i>Orthorhyncus cristatus</i>	2.71	Grenada lowland	1.00 \pm 0.00
			Grenada rainforest	1.00 \pm 0.00
			Grenada highland	1.00 \pm 0.00
			Dominica lowland	1.08 \pm 0.27
			Dominica highland	1.17 \pm 0.39
Blue-headed hummingbird	<i>Cyanophaea bicolor</i>	4.55	Dominica highland	1.42 \pm 0.51
			Grenada highland	1.24 \pm 0.44
Green-throated carib	<i>Eulampis holosericeus</i>	5.60	Dominica lowland	1.63 \pm 0.49
			Grenada rainforest	1.75 \pm 0.46
			Grenada rainforest	1.75 \pm 0.46
Rufous-breasted hermit	<i>Glaucis hirsuta</i>	6.82	Grenada rainforest	1.75 \pm 0.46
Purple-throated carib	<i>Eulampis jugularis</i>	8.67	Dominica highland	2.17 \pm 0.83

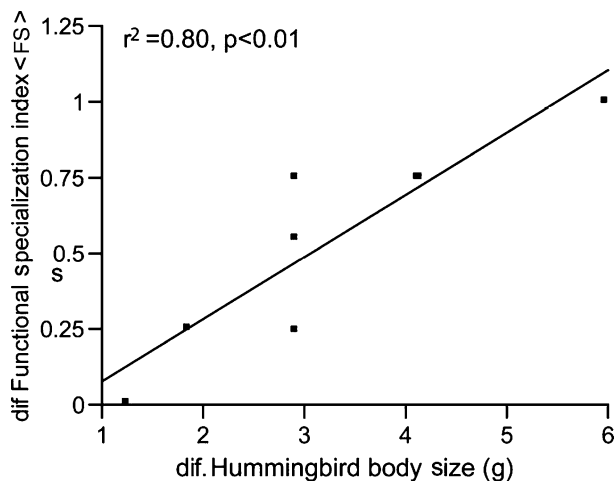


Fig. 2. The relationship between difference in hummingbird body size (g) and mean Functional specialization index $\langle FS \rangle$ for all possible species pairs in the five pollination networks. Hummingbird body mass as given in Brown and Bowers (1985).

pollination systems exist for plant species pollinated by the largest hummingbird species ($FS \approx 2$), but become more obscure with decreasing hummingbird size ($FS \approx 1$) with body size difference explaining 80% of the difference in FS -values among hummingbird pairs (Table 2, Fig. 2). Plant species pollinated by small hummingbird species were therefore more functionally generalized (sensu Ollerton et al. 2007) than those pollinated by large hummingbirds, i.e. they were visited by an array of insect species in addition to small hummingbirds. Whereas the pollination niche of large hummingbirds was practically separated from insect species in the pollinator community, the smallest hummingbird species functionally grouped with insects (sensu Fenster et al. 2004). This position of small hummingbirds in the pollinator community might affect the evolution of their body size, since they have to be small enough to make foraging on primarily insect-pollinated flowers energetically profitable (Snow and Snow 1972). From the plant's perspective, using such a wide suite of pollinators make them less sensitive to fluctuations in pollinator abundance, e.g. caused by environmental disturbances (Linhart and Feinsinger 1980, Stiles 1981, Waser et al. 1996, Fumero-Cabán and Meléndez-Ackerman 2007) such as hurricanes (Rathcke 2000, Rivera-Marchand and Ackerman 2006) or volcanic eruptions (Dalsgaard et al. 2007). This might especially be important in insular (Linhart and Feinsinger 1980, Spears 1987, Rivera-Marchand and Ackerman 2006, Fumero-Cabán and Meléndez-Ackerman 2007), stochastic (Waser et al. 1996, Rivera-Marchand and Ackerman 2006, Fumero-Cabán and Meléndez-Ackerman 2007) and fragmented (Rathcke and Jules 1993) environments.

With the global concern of pollinator decline (Allen-Wardell et al. 1998, Kearns et al. 1998) and linked plant extinctions (Biesmeijer et al. 2006), there is an urgent need to understand the level of interdependence between plant and pollinator species (Johnson and Steiner 2000) affecting ecosystem functioning and stability (Ollerton 1998). Despite pollination network studies having flourished in recent years, no network parameter has been proposed for

identifying functional specialization among plant–pollinator interactions. The Lesser Antillean hummingbirds and their flowers provide a simple relationship between hummingbird body size, a network parameter and ecological function. Such multidisciplinary approaches are needed to understand plant–pollinator interactions (Ollerton et al. 2007), and future examination of functional specialization could benefit from a similar network approach.

Acknowledgements – We are grateful to the Forestry and Wildlife Division, Dominica and Dept of Forestry and National Parks, Ministry of Agriculture, Grenada for research permission. We thank Elvis Stedman (Dominica Rainforest Aerial Tram) and Dean Jules (Nat'l Forestry Dept, Grenada) for help identifying the plants, Nancy G. L. Osler (Archbold Tropical Research and Education Centre at Springfield Plantation, Dominica), David Stemple and the Matthew family for help and advice. Also thanks to Jennifer A. Dunne who provided comments and ideas which greatly improved the manuscript. The project was financed by the Faculty of Natural Sciences at Aarhus Univ. (BD, AMMG, AT and LHA), the Danish National Science Research Council and WWF-Denmark/Novozymes (JMO).

References

- Allen-Wardell, G. et al. 1998. The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. – *Conserv. Biol.* 12: 8–17.
- Bascompte, J. et al. 2003. The nested assembly of plant–animal mutualistic networks. – *Proc. Natl Acad. Sci.* 100: 9383–9387.
- Bascompte, J. et al. 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. – *Science* 312: 431–433.
- Biesmeijer, J. C. et al. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. – *Science* 313: 351–354.
- Brown, J. H. and Bowers, M. A. 1985. Community organization in hummingbirds: relationship between morphology and ecology. – *Auk* 102: 251–269.
- Dalsgaard, B. et al. 2007. Impacts of a volcanic eruption on the forest bird community of Montserrat, Lesser Antilles. – *Ibis* 149: 298–312.
- de Nooy, W. et al. 2005. Exploratory social network analysis with Pajek. – Cambridge Univ. Press.
- Dicks, L. V. et al. 2002. Compartmentalization in plant–insect flower visitor webs. – *J. Anim. Ecol.* 71: 32–43.
- Dupont, Y. et al. 2003. Structure of a plant–flower–visitor network in the high altitude sub-alpine desert of Tenerife, Canary Islands. – *Ecography* 26: 301–310.
- Fenster, C. B. et al. 2004. Pollination syndromes and floral specialization. – *Annu. Rev. Ecol. Evol. Syst.* 35: 375–403.
- Fumero-Cabán, J. J. and Meléndez-Ackerman, E. J. 2007. Relative pollination effectiveness of floral visitors of *Pitcairnia angustifolia* (Bromeliaceae). – *Am. J. Bot.* 94: 419–424.
- Johnson, S. D. and Steiner, K. E. 2000. Generalization versus specialization in plant pollination systems. – *Trends Ecol. Evol.* 15: 140–143.
- Kearns, C. A. et al. 1998. Endangered mutualisms: the conservation of plant–pollinator interactions. – *Annu. Rev. Ecol. Syst.* 29: 83–112.
- Linhart, Y. B. and Feinsinger, P. 1980. Plant–hummingbird interactions: effects of island size and degree of specialization on pollination. – *J. Ecol.* 68: 745–760.
- Memmott, J. et al. 2004. Tolerance of pollination networks to species extinctions. – *Proc. R. Soc. Biol.* B 271: 2605–2611.

- Michener, C. D. 2000. The bees of the world. – The Johns Hopkins Univ. Press.
- Olesen, J. M. et al. 2007. The modularity of pollination networks. – Proc. Natl Acad. Sci. USA 104: 19891–19896.
- Ollerton, J. 1998. Sunbird surprise for syndromes. – Nature 394: 726.
- Ollerton, J. et al. 2007. Multiple meanings and modes: on the many ways to be a generalist flower. – Taxon 56: 717–728.
- Petanidou, T. and Lamborn, E. 2005. A land for flowers and bees: studying pollination ecology in Mediterranean communities. – Plant Biosyst. 139: 279–294.
- Rathcke, B. J. 2000. Hurricane causes resource and pollination limitation of fruit set in a bird-pollinated shrub. – Ecology 81: 1951–1958.
- Rathcke, B. J. and Jules, E. S. 1993. Habitat fragmentation and plant-pollinator interactions. – Curr. Sci. 65: 273–277.
- Rivera-Marchand, B. and Ackerman, J. D. 2006. Bat pollination breakdown in the Caribbean columnar cactus *Pilosocereus royerii*. – Biotropica 38: 635–642.
- Snow, B. K. and Snow, D. W. 1972. Feeding niches of hummingbirds in a Trinidad Valley. – J. Anim. Ecol. 41: 471–485.
- Spears, E. E. Jr. 1987. Island and mainland pollination ecology of *Centrosema virginianum* and *Opuntia stricta*. – J. Ecol. 75: 351–362.
- Stiles, F. G. 1981. Geographical aspects of bird-flower coevolution, with particular reference to Central America. – Ann. Miss. Bot. Gard. 68: 323–351.
- Temeles, E. J. and Kress, W. J. 2003. Adaptation in a plant–hummingbird association. – Science 300: 630–633.
- Temeles, E. J. et al. 2000. Evidence for ecological causation of sexual dimorphism in a hummingbird. – Science 289: 441–443.
- Triplehorn, C. A. and Johnson N. F. 2005. Borror and DeLong's introduction to the study of insects. – Thomson Brooks/Cole.
- Vázquez, D. P. and Aizen, M. A. 2004. Asymmetric specialization: a pervasive feature of plant–pollinator interactions. – Ecology 85: 1251–1257.
- Vázquez, D. P. and Aizen, M. A. 2006. Community-wide patterns of specialization in plant–pollinator interactions revealed by null models. – In: Waser, N. M. and Ollerton, J. (eds), Plant–pollinator interactions: from specialization to generalization. Univ. Chicago Press, pp. 200–219.
- Waser, N. M. and Ollerton, J. (eds) 2006. Plant–pollinator interactions: from specialization to generalization. – Univ. Chicago Press.
- Waser, N. M. et al. 1996. Generalization in pollination systems, and why it matters. – Ecology 77: 1043–1060.