Journal of Pollination Ecology, 2(1), 2010, pp 1-6

A PRELIMINARY EARLY-SEASON FLOWER-VISITATION WEB FOR THE KIRINDY FOREST, MADAGASCAR

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This paper is dedicated to future Tropical Biology Association (TBA) students, who we hope will expand and refine the Kirindy pollination web.

Abstract—Tropical dry deciduous forest is an endangered ecosystem whose plant-pollinator relationships are little known. We characterised a portion of the web of interactions between flowering plants and flower visitors in the Kirindy Forest of the Menabe region of west-central Madagascar. Taking a plant-centered approach, we observed individuals of the 5 most abundant native plant species that were coming into flower at the end of the annual dry season, and recorded all identifiable flower-visitors. Taking a visitor-centered approach, we walked a network of established trails and listened for distinctive calls of a common flower-visiting bird, noting the plant species visited. The former approach revealed connections among the early-flowering species via birds and insects, whereas the latter confirmed these connections and added an additional plant species. Flowers of the 6 plant species were visited on average by 5.5 animal species, while 10 visitor species for which we had reasonable samples frequented on average the flowers of 3.3 plant species. These qualitative results resemble those reported from other temperate and tropical webs, in that interactions appeared to be relatively generalised by pollinator species and body plan (e.g., birds vs. bees). Also in agreement, the visitation web was significantly nested, with more-specialised species tending to interact with mutualistic partners that were themselves more generalised. In addition to documenting previously-unreported interactions, therefore, this preliminary web conforms to more widespread patterns emerging for pollination systems at the community level.

Keywords: Connectance, forest, generalisation, nestedness, pollination, tropical

INTRODUCTION

Studies of the mutualistic interaction between flowering plants and animal pollinators at the level of entire communities have a long history (e.g. Clements and Long 1923; Robertson 1929; Moldenke 1975), but recent advances in computational power and multivariate analyses have reinvigorated this approach. The newer methods allowed Memmott (1999) to visualise the first flower-visitation web (or network) for an entire ecological community, following an earlier investigation of fragments of such webs by Jordano (1987) and a prescient verbal description of an entire web by Petanidou and Ellis (1996).

In the decade since Memmott's paper, many additional flower-visitation webs have appeared for temperate and tropical communities, along with analysis of their properties. In general, these and other mutualistic ecological webs contain both specialists and generalists, and the frequency distribution of the degree of generalisation is long-tailed, with many relative specialists and moderate generalists and a few highly-generalised species (Jordano et al. 2003; Vázquez et al. 2009). Furthermore, more-specialised species tend to interact with subsets of the mutualistic partners with which their more-generalised brethren interact; that is, the webs are nested (Petanidou and Ellis 1996; Bascompte et al. 2003). The implication of this last pattern is that specialists usually interact with generalists, in contrast to a more classical expectation in pollination ecology that specialist visitors will interact with specialist flowers, and generalists with generalists.

In spite of the efflorescence of studies on flower-visitation webs, including those that estimate the relative importance of different visitors as pollinators (i.e., pollination webs in the true sense; see e.g. Alarcón 2009), more empirical work is welcome, especially for relatively unstudied community types. Here we present a portion of a flower-visitation web from a tropical dry forest in west-central Madagascar, coinciding with the end of the annual dry season and the very beginning of flowering of the first trees and lianas. We adopted both a plant-centered approach, in which we observed individuals of native plant species that were in early flower, and a visitor-centered approach, focused on a common flower-visiting bird. These complementary approaches suggest a pollination web that resembles those for other systems, with moderate average

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Received 13 July, accepted 13 August 2010

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generalisation on the part of both plants and flower visitors, and with significant nestedness.

STUDY SITE AND METHODS

We worked in the Kirindy Forest (20° 03' S, 44° 39' E), ca. 60 km northeast of the city of Morondava in the Menabe region of west-central Madagascar. Kirindy is a tropical dry deciduous forest of some 12,000 ha, comprising one of the few remaining fragments of a forest type that was far more widespread ancestrally on Madagascar, and that is endangered worldwide (Dufils 2003). Kirindy is managed by the Centre National de Formation, d'Etudes et de Recherche en Environement et Forestiere (CNFEREF) of the Malagasy government. CNFEREF maintains a small field station in the forest that served as our base.

Plant-based sampling

In early November 2009 we accumulated 60 person-hours of observation of 5 plant species (Tab. 1), choosing individuals that grew within 1 km of the Kirindy field station. By walking trails in the forest within 2 km of the station we estimated that fewer than 10 species were beginning to flower at this time, as the end of the dry season grew near (first rain fell in Kirindy only on 21 November, almost 2 weeks after this study). The 5 species chosen were the most abundant and profusely flowering of these. Pairs of observers watched each species from 0600-0700 hr, 0800-0900 hr, and 1600-1700 hr on 8 November and from 0700-0800 hr on 9 November, using binoculars as needed. Flower visitors were identified to the lowest taxonomic level possible. Because flowers were borne at up to more than 10 m above the ground it was impractical in most cases to collect either flowers or visitors for closer examination; nor are reference collections or published taxonomic resources readily available at Kirindy (or in Madagascar more generally) for most animal groups.

An additional trio of observers simultaneously watched a treelet into which an individual of each of two liana species, *Combretum coccinea* and *Adenia olaboensis*, had climbed. This allowed them to compare flower preferences of 2 species of small native birds, common jerys (*Neomixis tenella*) and souimanga sunbirds (*Nectarinia souimanga),* which were frequent (but not the only, see Results) visitors of both plant species. Because no more than one bird visited at any time, and the birds were easy to follow as they foraged, there was no difficulty in determining that choices of flowers were being made by the same individual at any given time.

Visitor-based sampling

We also accumulated 20 person-hours of observation of flower visitors at the same time as the plant-based sampling just described. One pair and one trio of observers slowly walked separate trails within 2 km of the Kirindy field station. They listened for distinctive contact notes and alarm calls of souimanga sunbirds, which carried well in the largely-leafless forest and were loud enough for a trained ear to discern and to follow so as to discover what flowers an individual was visiting.

Analysis

We characterised the qualitative visitation web derived from our observations in terms of basic network statistics, and obtained a measure of nestedness with the ANINHADO program (http://www.guimaraes.bio.br/softwares.html; Guimarães and Guimarães 2006). This program calculates a "Temperature" (T) statistic ranging from 0° for a perfectly-nested matrix to 100° for a randomly-organised one. With perfect nesting the most generalised plant and pollinator species have links with all possible partner species in the community, and each successively more specialised species interacts with a proper subset of the partners of more generalised species. As a result, the partner of a species with only one partner will itself be the most generalised species (see Bascompte et al. 2003, Lewinsohn et al. 2006). The statistical significance of T is derived by a Monte Carlo procedure that generates 10,000 random matrices and their T values to compare with the actual T value. We used the CE null model, which limits the probability of observing an interaction between plants and pollinators as a function of their degree of specialisation (Bascompte et al. 2003; Guimarães and Guimarães 2006). We also followed Bascompte et al. (2003) in converting T to the Nestedness index N (N= (100-T)/100), which ranges from 0, when the network is randomly organised, to 1, when it is perfectly nested.

RESULTS

Qualitative visitation web

Our sampling yields a qualitative web that includes 10 bird and insect species visiting 6 plant species (Tab. 2). In addition to the 5 focal plant species, visitor-based sampling revealed souimanga sunbirds at the canopy tree *Hildegardia erythrosiphon* (Malvaceae), of which we found 3 individuals in flower within 2 km of the field station. With the exception of this last species, whose flowers are stiff red tubes ca. 20mm long, formed of fused sepals, with sex parts exserted ca. 15mm further, the flowers of the other species (Tab. 1) are relatively inconspicuous. Most flower visitors were clearly collecting either nectar or pollen. The common jery, usually described as insectivorous (although also as searching inside flowers for insects; Langrand 1990), appeared to visit older inflorescences of *Albizia* to hunt for insects. However, these small passerine birds were very distinctly probing younger *Albizia* flowers for nectar, and foraging for nectar at the other species we saw them visiting.

Flowers of the 6 plant species were visited on average by 5.5 animal species (median = 6.5, range = 1–7), whereas the 10 visitor species frequented on average the flowers of 3.3 plant species (median = 4, range = 1–6), for a total of 33 pairwise species interactions. This represents a web connectance (the percentage of the 60 possible interactions actually realised) of 55%.

TABLE 1. Characteristics of the five species on which plant-based censuses were focused

Plant Species	Family	Growth Form	Flower description
Adenia olaboensis	Passifloraceae	Liana	Miniature pale yellow-green 5-merous passion flower; partially reflexed sepals ca. 15mm long, unfused ‘tube’ of petals ca. 10mm long enclosing sex parts, bisexual
Albizia perrieri	Leguminosae	Tree	Pale yellow-green bisexual flowers clustered into heads; corolla ca. 8mm; sex parts exserted as brush ca. 15-20mm
Azadirachta indica	Meliaceae	Tree	Small 5-merous star of cream-white petaloid sepals with central corolla tube ca. 4mm long; sex parts at opening of tube; bisexual
Berchemia discolor	Rhamnaceae	Tree	Tiny greenish open 5-merous flower ca. 7mm across; bisexual with ovary half submerged in central nectary disc
Combretum coccinea	Combretaceae	Liana	Aggregated heads of ca. 10 flowers with green corollas ca. 10mm long; sex parts further exserted as a brush ca. 15mm long; filaments red

Examination of the qualitative web (Tab. 2) furthermore indicates a significant degree of nestedness (N = 0.785, P = 0.018), that is, the tendency for each more specialised plant or animal species (those associated respectively with fewer animal or plant partners) to associate with a subset of those used by more generalised species.

Preferences for Adenia *vs.* Combretum

Simultaneous observation of intertwined branches of *Adenia olaboensis* and *Combretum coccinea* (Fig. 1) suggested that souimanga sunbirds strongly preferred *Adenia* in the morning, and of these 2 species visited only *Combretum* in the afternoon. Common jerys exhibited an even stronger preference for *Adenia* in the morning, but did not visit either species at all during afternoon observations.

TABLE 2. The partial qualitative flower visitation web for Kirindy forest at the end of the dry season, 2009. *Nectarinia* are sunbirds, *Neomixis* is the common jery, *Xylocopa* a carpenter bee, *Liotrigona* a stingless bee (see Brooks and Michener 1988), *Apis* the honey bee, and the remainder are butterflies. The *Acraea* sp. has clear outer forewing and orange inner wings with black patches; the *Danaid* butterfly is likely *Danaus chrysippus*. Small insects that could not be identified more precisely were ignored of necessity, as we had no way to match them across plant species. The canopy tree *Hildegardia erythrosiphon* (Malvaceae) appears in the plant column, as visitor-based sampling detected visits by souimanga sunbirds.

PLANT	VISITOR										
	Nectarinia souimanga	*Xylocopa calens*	*Liotrigona* sp.	*Neomixis tenella*	*Heliconid* “cream”	*Acraea* sp.	*Nectarinia notata*	*Heliconid* “orange”	*Apis mellifera*	*Danaid butterfly*	TOTAL
Adenia	X	X	X	X	X	X	X				7
Berchemia	X	X	X	X	X	X			X		7
Combretum	X	X	X	X	X	X	X				7
Azadirachta	X	X	X		X	X				X	6
Albizia	X	X	X	X				X			5
Hildegardia	X										1
TOTAL	6	5	5	4	4	4	2	1	1	1	33

DISCUSSION

Any empirical web is in one important sense a fragment of the entire interaction web. Because there is turnover of species in space, and turnover in time due to seasonal phenology, extending the sample spatially or temporally will inevitably expand the web (e.g. Medan et al. 2006) and make difficult the definition of “entire”. In this context, the qualitative web reported here contains by our estimate more than half the plant species in flower close to the Kirindy field station at the time of sampling, and more specifically those that were most common or were flowering most profusely. Thus we probably succeeded in our aim of sampling the majority of floral resources available locally at the end of the dry season.

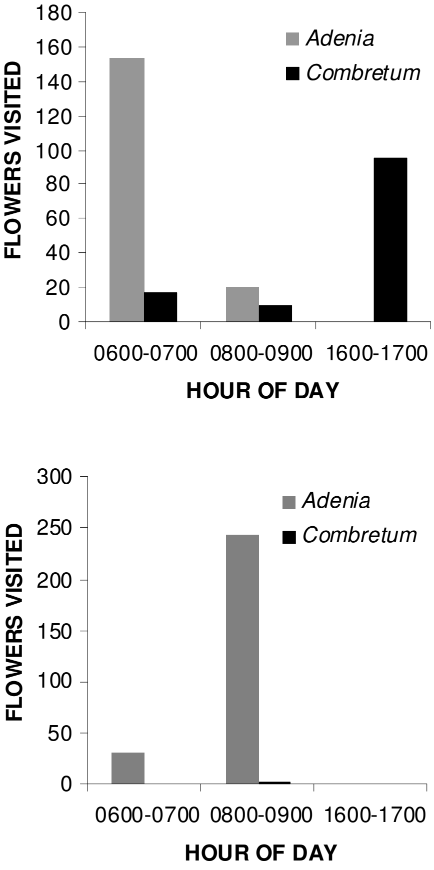

FIG.1. Preferences of souimanga sunbirds (top) and common jerys (bottom) visiting intertwined branches bearing flowers of *Adenia olaboensis* and *Combretum coccinea* at different times of day on 8 November 2009. Jerys visited no flowers on these plants between 1600 and 1700 hours.

To be sure, our preliminary web still is a fragment of the entire web, insofar as it ignores some species that were beginning to flower but that we did not detect in walking trails, and a number of insect visitors to flowers that we could not identify (and indeed whose identity often may be unknown even if they were in the hand). Furthermore, we were unable to measure the value of visitors in transporting pollen. In contrast, published webs are increasingly appearing that are more complete and that include estimates of relative value of visitors as pollinators (i.e., quantitative rather than qualitative webs; see for example Alarcón et al. 2008; Kaiser-Bunbury et al. 2009), and that recognise the potential for the network to change through time and space (e.g. Petanidou et al. 2008; Alarcón et al. 2008). Nonetheless, the information presented here is of value, because of the extreme paucity of knowledge about this tropical dry forest (and others). Thus we will proceed to compare our results with those from other qualitative studies, noting appropriate caveats.

The most striking result is the relative generalisation of both plants and flower visitors: species at both trophic levels tended to interact with multiple species at the other level, representing more than a single morphological type (compare to Ratsirarson and Silander 2003). The values for mean visitor species per flower and for floral diet breadth per visitor seem to be in keeping with those from other published pollination webs of small to moderate size. Jordano (1987) gives means of 4.1 visitor species per plant species and 5.3 plant species per visitor species from fragments of pollination webs, similar to our means of 5.5 and 3.3 (albeit his values apparently were taken from studies with either plant-centered focus or animal-centered focus, rather than both). In a larger and more complete web derived from Clements and Long (1923; see Waser et al. 1996), flowers of 94 plant species were visited by a mean of 9.8 animal species, not quite twice the Kirindy value, whereas the 268 animal species visited a mean of 3.3 plant species, identical to the Kirindy value. Connectance (C) of 55% in the Kirindy web may at first seem surprisingly high, but estimates of C have been shown to be inversely related to species number in empirical webs. Jordano (1987) derived the formula $C = 0.4994 \exp [-0.017S]$ for pollination webs, where S is the combined number of plant and pollinator species. This yields a predicted connectance of 38% for $S = 16$, as in the Kirindy web. Thus the actual connectance we estimated appears to be slightly but not grossly above values for other webs of similar size.

Relative generalisation in Kirindy on the side of both plants and pollinators may be understandable in mechanistic terms. From the plant perspective, the common presentation of an exserted "brush" of sex parts by flowers in this part of the Kirindy flora should increase the chances that a diversity of visitors will transfer pollen, i.e., that they are true pollinators (see Stiles 1981; Sazima et al. 1999). From the animal side, brush flowers and relatively short corolla tubes may increase the chances that pollen or nectar are accessible, i.e., that flowers are rewarding and thus worth visiting. Although we could not determine whether individual birds or insects included multiple plant species in their foraging itineraries, except in the case of individual souimanga sunbirds and jerys that visited the intertwined patch of *Combretum* and *Adenia* flowers, this seems likely in general from the perspective of foraging efficiency. Generalisation on the part of visitors certainly makes sense in a system in which flowers are relatively scattered (see Pyke 1984; Chittka et al. 1999), as is true for this season in Kirindy. Furthermore, expanding the sample in space or time would probably increase the estimate of mean generalisation, along with increasing the size of the "complete" web (Waser et al. 1996).

The Kirindy nestedness value of $N = 0.785$ resembles those in other recently-reported pollination webs. For example, Bascompte et al. (2003) report a mean ± SE of 0.837 ± 0.029 from 29 pollination webs, with a range of 0.594-0.975. To be sure, apparent nestedness might derive in part from an incomplete sample. In other words, species that were not observed systematically (such as *Hildegardia* among the plants) logically will reveal only a subset of their interactions, leading to an impression of relative specialisation; and if (as with *Hildegardia*) they are included precisely because of a tie to the rest of the web (here through souimanga sunbirds), the apparent specialisation will necessarily appear nested. On the other hand, estimates of nestedness have been shown to be fairly insensitive to sampling biases (Nielsen and Bascompte 2007). And there are real biological causes of nestedness. For example Stang et al (2007) explore how nestedness derives from simple considerations such as the morphological match of flower and pollinator and the relative abundances of species. In summary, and as with other Kirindy metrics, nestedness appears to resemble values from other webs, lending confidence that the estimate is robust.

Finally, the preference of souimanga sunbirds and common jerys for *Adenia* relative to *Combretum* flowers in the morning suggests superior nectar reward of the former flowers at that time. *Adenia* flowers appeared to change shape in the afternoon, with sepals no longer strongly reflexed, perhaps indicating senescence, at which time sunbirds preferred *Combretum*. Because we were unable to gain access to flowers, however, we could not characterise their individual phenologies or nectar rewards. All plants that we watched had finished flowering by November 15, six days after our last observations.

ACKNOWLEDGEMENTS

For assistance and support in the field we thank Drs. H. Rakotomamana and E. Rabakonandrianina, and the staff of the CNFEREF Kirindy field station. Ruben Alarcón kindly calculated the nestedness statistic; he, Jens M. Olesen, and Christopher Kaiser-Bunbury made valuable comments on the manuscript. We are grateful to the British Ecological Society for scholarship support for Tropical Biology Association students on the Kirindy 09/4 course.

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REFERENCES

Alarcón R (2009) Congruence between visitation and pollen-transport networks in a California plant–pollinator community. Oikos 119:35-44

Alarcón R, Waser NM, Ollerton J (2008) Annual variation in the topology of a plant-pollinator interaction network. Oikos 117:1796-1807

Bascompte J, Jordano P, Melián CJ, Olesen JM (2003) The nested assembly of plant-animal mutualistic networks. Proceedings of the National Academy of Sciences (USA) 100:9383–9387

Brooks RW, Michener CD (1988) The Apidae of Madagascar and nests of *Liotrigona* (Hymenoptera). Sociobiology 14:299-323

Chittka L, Thomson JD, Waser NM (1999) Flower constancy, insect psychology, and plant evolution. Naturwissenschaften 86:361-377

Clements RE, Long FL (1923) Experimental pollination: An outline of the ecology of flowers and insects. Carnegie Institution of Washington, Washington, DC.

Dufils J-M (2003) Remaining forest cover. In: Goodman SM, Benstead JP (eds) The natural history of Madagascar. The University of Chicago Press, Chicago, pp 88-96

Guimarães PR, Guimarães P (2006) Improving the analyses of nestedness for large sets of matrices. Environmental Modelling & Software 21:1512-1513

Jordano P (1987) Patterns of mutualistic interactions in pollination and seed dispersal–connectance, dependence asymmetries, and coevolution. American Naturalist 129:657–677

Jordano P, Bascompte J, Olesen JM (2003) Invariant properties in coevolutionary networks of plant-animal interactions. Ecology Letters 6:69–81

Kaiser-Bunbury CN, Memmott J, Müller CB (2009) Community structure of pollination webs of Mauritian heathland habitats. Perspectives in Plant Ecology, Evolution and Systematics 11:241-254

Langrand O (1990) Guide to the birds of Madagascar. Yale University Press, New Haven

Lewinsohn TM, Prado PI, Jordano P, Bascompte J, Olesen JM (2006) Structure in plant-animal interaction assemblages. Oikos 113:174-184

Medan D, Basilio AM, Devoto M, Bartoloni NJ, Torretta JP, Petanidou T (2006) Measuring generalization and connectance in temperate, year-long active systems. In: Waser NM, Ollerton J (eds) Plant-pollinator interactions: From specialization to generalization. The University of Chicago Press, Chicago, pp 245–259

Memmott J (1999) The structure of a plant–pollinator food web. Ecology Letters 2:276–280

Moldenke AR (1975) Niche specialization and species diversity along a California transect. Oecologia 21:219-242

Nielsen A, Bascompte J (2007) Ecological networks, nestedness and sampling effort. Journal of Ecology 95:1134-1141

Petanidou T, Ellis WN (1996) Interdependence of native bee faunas and floras in changing Mediterranean communities. In: Matheson A, Buchmann SJ, O'Toole C, Westrich P, Williams IH (eds) The conservation of bees. Academic Press, London, pp 201–226

Petanidou T, Kallimanis AS, Tzanopoulos J, Sgardelis SP, Pantis JD (2008) Long-term observation of a pollination network: Fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. Ecology Letters 11:564-575

Pyke GH (1984) Optimal foraging theory: A critical review. Annual Review of Ecology and Systematics 15:523-575

Ratsirarson J, Silander JA Jr (2003) Pollination ecology of plant communities in the dry forests of the southwest. In: Goodman SM, Benstead JP (eds) The natural history of Madagascar. The University of Chicago Press, Chicago, pp 272-275

Robertson C (1929) Flowers and insects: Lists of visitors to four hundred and fifty–three flowers. C Robertson, Carlinville.

Sazima, M, Buzato S, Sazima I (1999) Bat-pollinated flower assemblages and bat visitors at two Atlantic forest sites in Brazil. Annals of Botany 83:705-712

Stang, M, Klinkhamer P, Waser N, van der Meijden E (2007). Both constraints and abundance are needed to explain the topology of mutualistic networks. PLoS Biology http://biology.plosjournals.org/perlserv?request=read-response & doi=10.1371/journal.pbio.0050031#r1695>

Stiles FG (1981) Geographical aspects of bird-flower coevolution, with particular reference to Central America. Annals of the Missouri Botanical Garden 68:323-351

Vázquez DP, Blüthgen N, Cagnolo L, Chacoff NP (2009) Uniting pattern and process in plant-animal mutualistic networks: A review. Annals of Botany 103:1445-1457

Waser NM, Chittka L, Price MV, Williams N, Ollerton J (1996) Generalization in pollination systems, and why it matters. Ecology 77:1043-1060