



Biota Neotropica
ISSN: 1676-0611
cjoly@unicamp.br
Instituto Virtual da Biodiversidade
Brasil

Biesmeijer, Jacobus C.; Slaa, E. Judith; Siqueira de Castro, Marina; Viana, Blandina Felipe; de M. P. Kleinert, Astrid; Imperatriz-Fonseca, Vera L.
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Biota Neotropica, vol. 5, núm. 1, 2005, pp. 85-93
Instituto Virtual da Biodiversidade
Campinas, Brasil

Available in: <http://www.redalyc.org/articulo.oa?id=199114288010>

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CONNECTANCE OF BRAZILIAN SOCIAL BEE – FOOD PLANT NETWORKS IS INFLUENCED BY HABITAT, BUT NOT BY LATITUDE, ALTITUDE OR NETWORK SIZE.

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Biota Neotropica v5 (n1) – <http://www.biotaneotropica.org.br/v5n1/pt/abstract?article+BN02605012005>

Date Received 11/8/2004

Accepted 01/02/2005

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Abstract

Several recent studies suggest that the level of generalization (measured as percentage connectance) of plant-pollinator networks has several ecological correlates, e.g. latitude and altitude. Here we report on levels of generalization in 27 two-mode networks of social bees and their food plants in various Brazilian habitats and urban environments. Social bees are generalist foragers and are among the most abundant flower visitors in Brazil. They probably account for 30-50% of all plant – flower visitor interactions. Connectance was significantly influenced by habitat. Cerrado forests showed lower connectance than the dry dune habitats, with Atlantic rain forest and urban sites taking intermediate position and arid Caatinga being similar to dunes. This shows that generalization in a plant – flower visitor community can be influenced by habitat even within a group of generalist flower visitors, in our case social bees. We show that the strength of the interactions is not different between Cerrado and semi-arid habitats (dunes and Caatinga) and discuss other explanations for our findings.

Key words: *Pollination, stingless bees, Meliponini, Apis, Bombus, food plants.*

Resumo

Vários estudos recentes mostram que o nível de generalização (medido como porcentagem de conectância) das redes plantas-polinizadores apresentam várias correlações ecológicas, como latitude e longitude. Neste trabalho, apresentamos os níveis de generalização em 27 redes de dois-modos de abelhas sociais e das plantas que lhes servem de alimento em vários habitats e ambientes urbanos brasileiros. As abelhas sociais são forrageiras generalistas e estão entre os visitantes florais mais abundantes no Brasil. Provavelmente, são responsáveis por 30 a 50% de todas as interações entre plantas e visitantes florais. A conectância é significativamente influenciada pelo habitat. Os cerrados apresentaram uma menor conectância do que as dunas, a Mata Atlântica e os ambientes urbanos ocuparam uma posição intermediária, e a caatinga árida apresentou um grau de conectância semelhante às dunas. Isso mostra claramente que a generalização nas comunidades de visitantes florais e plantas pode ser influenciada pelo habitat, mesmo em um mesmo grupo de visitantes, como, no nosso caso, as abelhas sociais. Nós provamos que a força das interações não é diferente entre o cerrado e os habitats semi-áridos (dunas e caatinga) e discutimos outras explicações para nossas interpretações.

Palavras-chave: *Polinização, abelhas sem ferrão, Meliponini, Apis, Bombus, recursos alimentares*

Introduction

Plant-pollinator networks have been suggested to show trends towards higher levels of generalization with decreasing species richness, with increasing latitude and in lowlands compared to highlands (Olesen and Jordano 2002). Two earlier reviews, however, concluded that the frequency of occurrence of specialized pollination syndromes is about the same at different latitudes (Kevan and Baker 1983, Kevan and Baker 1999). In addition, generalization seems lower for some pollinator taxa (stingless bee, euglossine bees, and fig wasps) than for others (hummingbirds and bumblebees) (Jordano 1987). How these findings relate to each other is not directly clear, because some groups of pollinators (and food plants) are largely temperate whereas others are exclusively tropical. Also, data from lowland tropical pollination networks are largely lacking, which Olesen and Jordano (2002) regard a serious shortcoming for their review.

In this paper we take a slightly different approach that may extend our understanding of patterns of generalization in plant-pollinator networks. We do not aim at complete plant-pollinator networks, but restrict our analysis to a specific group of pollinators, social bees, in a restricted geographic area, Brazil. In this way our analyses are largely free of taxonomic biases, however, they do not address plant-pollinator networks in general.

Social bees of the subfamily Apinae (stingless bees, bumble bees, and honey bees) are the most abundant flower visitors in many tropical habitats (Heithaus, 1979, Roubik 1989, Bawa 1990). Their colony's life span surpasses the blooming period of most plant species, which partly explains their polylectic diet, i.e. use of multiple plant species as food source. They are generalist foragers (Roubik 1989) with wide niches and some extreme cases, e.g. honey bees, have been referred to as super generalists (e.g. Olesen et al. 2002). Therefore, although we analyze only a subset of all interactions, it comprises probably 30-50% of the complete plant-pollinator network (or more correctly flower-flower visitor network). Social bee food plant relationships have been studied extensively (reviewed in Roubik, 1989, Ramalho et al. 1990), but food web theory (e.g. Jordano 1987, Dunne et al. 2002) has rarely been used to study the characteristics of the two-mode network of social bees and their food plants. We analyzed 27 complete datasets of social bee-food plant interactions and examine (1) the patterns of generalization in these networks and (2) the influence of a series of ecological factors, altitude, latitude, habitat, on generalization levels.

2. Material and Methods

2.1 Dataset selection.

The datasets were selected according to the following criteria:

1) They had to be taxonomically well resolved. The two leading Brazilian social bee experts, Profs Padre Santiago Moure and João Camargo, identified bees in all studies and plants were identified by various leading botanical taxonomists.

2) Exhaustive sampling of a restricted area. All studies collected at least once a month for a year, but most sampled more intensively. Areas ranged from 0.3 ha to more than 200 ha, and was <100 ha in all but three studies.

3) Unrestricted sampling of bees and flowering plants. Note, however, than many studies under-sampled the higher strata of the forest.

4) Comparable sampling methods. Methodology was highly uniform among the studies. All used the Sakagami et al. (1967) sampling method or a variant of that method. In this method a fixed amount of time is spent at each flowering plant (or patch) and the coverage of transects is randomized in time, order, and direction.

5) Availability of interaction tables or raw data sheets. We compiled each data matrix from the interaction lists or raw data tables provided in the source. More than a dozen additional studies had to be excluded because they lacked sufficiently detailed information of bee-plant interactions in the published material. A complete list of the main features of all studies included is given in table 1. The studies that could not be included and the reason for their exclusion are given in table 2. Many datasets have been published only in student PhD- or MSc-theses about half of which were supervised by the latter two authors, but all are publicly available from the respective universities (for full references of all studies see Appendix 1).

2.2 Network properties

We followed methods of Jordano (1987) and Olesen and Jordano (2002). A two-way social bee – food plant network is defined as a matrix describing interactions between B flower-visiting social bees and P flowering plant species. Each cell of the matrix represents a single bee-plant interaction and can have a value of 0 if not observed or 1 if observed. Many studies gave actual numbers of bees collected from plants. All values >0 were set equal to 1 for connectance calculations, but real values were used in calculating interaction strengths (see below). Network size (M) is given by $M = BP$, where B and P are the number of interacting bees and plants in the habitat, respectively. M indicates the maximum possible number of interactions. As measures of generalization we use the number of observed interactions (I) and the connectance (C), where $C = I/M$. Connectance is thus the percentage of all possible interactions actually observed within a network.

We used correlation to analyze relations among network properties (B+P, I, C) and multiple regressions to

analyze the relation between C and several study site features: latitude, altitude (mean of upper and lower limit for larger areas), and M. Four natural habitat types were represented in multiple studies (Table 1): Atlantic rain forest, Cerrado forest (dense, dry forest of medium height), Caatinga (arid woodland), and Dunes. In addition, urban environments (parks and university campus) were sampled in five studies. The habitats of the remaining studies comprised fields, shrubland, orchard, a mix of habitats, and highland Araucaria forest. We analyzed the relation between the common habitats (Rain forest, Cerrado, Caatinga, Dunes, Urban) and connectance by means of a Kruskal-Wallis test with posthoc multiple comparisons tests (MCT) (Siegel and Castellan, 1988).

In our effort to find an explanation for the difference in connectance among habitats, we calculated interaction strengths for the Cerrado studies (Table 1: studies 15, 16, 17, and 19) and pooled dry habitat studies, Caatinga (Table 1: study 14) and Dunes (Table 1: studies 25 and 26), that provided numbers of bees visiting each flowering plant. We follow Jordano (1987) and use dependence of bees on food plants as a measure of interaction strength. Dependence here is the proportion of all interactions of the bee occurring between a particular plant and this bee. Note that this measure does not indicate the quality of the interaction and for the social bees we consider here high values may occasionally present a single or few successful group foraging events.

3. Results

Twenty-seven datasets were included in the analysis (Table 1), whereas many other studies could not be included (Table 2). The included studies covered 72 social bee taxa (66 stingless bees, 5 bumble bees, and the introduced African honey bee), 1725 plant species and a total of 6588 bee-plant interactions. Individual datasets contained 6 to 27 bee species (mean 13.5, median 12; table 1) and sampled 20 to 230 plant species (mean 92.9, median 93). The number of interactions ranged from 34 to 932 (mean 235.3, median 174) and increased linearly with network size ($I = 0.16M + 13.6$; $F = 114.5$, $p < 0.001$, $R^2 = 0.81$). Connectance (C) ranged from 7.2% to 37.1% (mean 18.9%, median 17.6%) and was independent of the total number of species ($B + P$; $F = 0.64$, $df=1,25$, $p = 0.43$) in the dataset. A multiple regression analysis revealed that C was not significantly influenced by network size (M), latitude or altitude of the study site ($F = 0.66$, $df=3,19$, $p = 0.59$). However, C differed among the four natural habitats and the urban environments covered in the studies (Figure 1; KW-test: $X^2 = 13.2$, $p = 0.01$; 5 groups: Atlantic rain forest, Cerrado, Caatinga, Dunes, Urban). The MCT showed that Cerrado forest had significantly lower connectance than dunes, and that other combinations were not significantly different. If more Caatinga sites are sampled in the future it is possible that connectance in Caatinga will

become different from Cerrado as well (Figure 1). Data were not sufficient to detect within-habitat trends between connectance and other parameters.

The distribution of dependence values of bee-plant links was not different between Cerrado forest and the semi-arid habitats, Caatinga and dunes (two-sample KS-test: $D_{\max} = 0.6$, $Z = 0.82$, $p = 0.41$, $N_{\text{cerrado}} = 745$, $N_{\text{caatinga/dunes}} = 236$; Figure 2). This suggests (see Jordano 1987) that the lower C in Cerrado forest compared to that of dry habitats Caatinga and Dunes does not reflect differences in the strength of the interactions. In both cases weak interactions (dependence < 0.1) are vastly more numerous than strong interactions (dependence > 0.1).

4. Discussion

The average level of generalization ($C = 19\%$) in the social bee – food plant networks was higher than in complete plant-pollinator networks (11%; Olesen and Jordano 2002). This was expected because all social bees are generalists and they have broader food niches than do oligolectic bees and other non-social flower visitors. Generalization level was lower than in incomplete social bee – plant networks reported by Jordano (1987; average of 14 studies: $C = 28.1\%$), but higher than in the tropical social bee studies he reviewed (Engel and Dingemans-Bakels 1980: $C = 8.7$ and 15.7%), probably reflecting the different methods used in that study.

Neither latitude (4°N – 30°S) nor altitude (0–1050m) affected the generalization level. This corresponds to findings by Olesen and Jordano (2002) who show a general effect of both factors, but no clear relationships within the ranges included in our analysis (see their Fig. 2). The lack of a relationship between network size and C in our study is in contrast to both Olesen and Jordano (2002) and Jordano (1987). This may result from the taxonomic heterogeneity of the datasets analyzed by them compared to our datasets that are restricted to tropical social bees. More importantly, habitat significantly influenced the level of generalization in our analysis. The Cerrado forest habitat had lowest C levels at intermediate levels of network size and number of species (Fig. 1) and variance of C among habitats was high at low and intermediate network sizes. Olesen and Jordano (2002) report marginally different levels of generalizations among biogeographic regions. They report lowest connectance (residual values after controlling for species richness) for tropical and alpine networks and highest connectance for Mediterranean networks. Here we refine that result and show that among tropical habitats levels of generalization varies significantly. Interestingly, in both studies networks in the driest region, the Mediterranean (Olesen and Jordano 2002) and Dunes and Caatinga (our study), had highest levels of connectance. Cerrado forest is, however, much drier than rain forest and urban habitats but had lower connectance.

Why generalization levels in Cerrado forest are greatly lower than in the arid Dunes and Caatinga is not clear. First, whereas three of four of the arid studies have low species richness, overall connectance is not dependent on species richness. Second, the strength of the interactions of bees with their food plants, measured as dependence, is not different among these habitats (Fig. 2) suggesting that the bees' diets are not generally broader in the arid habitats. Third, the species composition is highly homogeneous among the habitats, the same genera of stingless bees occur in most habitats and several species were reported in all habitats. A more detailed analysis of the interactions and the floristic and faunistic composition may reveal why these habitats have intrinsically different levels of generalization.

In summary, our results indicate that 1) generalization level of a social bee – food plant network is affected by habitat; 2) Social bee foragers are not always extreme generalists; and 3) study of a homogeneous compartment of a network may reveal other patterns than study of a more heterogeneous 'complete' network. This analysis of a unique dataset of tropical bee-food plant networks adds to our incomplete understanding of lowland tropical plant – (potential) pollinator networks.

Information on properties of social bee – food plant networks is also fundamental in conservation and management of habitat for native pollinators (e.g. various contributions in Kevan and Imperatriz-Fonseca 2002, Kearns *et al.* 1998). The level of connectance of interactions in a food web may influence how the system changes following disturbance. In addition, complete information on the interactions between plants and pollinators may allow for more efficient management of biodiversity (Waser *et al.* 1996, Kearns *et al.* 1998, Pinheiro-Machado *et al.* 2002), e.g. concentration on specific groups of food plants to conserve a target pollinator species or vice versa concentration on specific pollinators to improve pollination in threatened native plant species. Finally, the construction and in-depth analysis of networks of pollinators and their food plants would allow for a detailed analysis of the influence of non-native species of plants and pollinators on the relation among native species (e.g. Olesen *et al.* 2002, Memmott & Waser 2002). It is known that introduction of super-generalist pollinators, such as the honey bee *Apis mellifera*, may adversely affect some native plant-pollinator interactions (e.g. Butz-Huryn 1997, Gross & Mackay 1998), because they readily incorporate native food plants in their diet. On the other hand, invasive plants that provide ample reward to pollinators, e.g. *Impatiens glandulifera*, may disturb the pollination market and attract native pollinators away from the native plants they used to visit (Chittka & Schurkens 2001). In conclusion, we feel that food web theory is a valuable tool in analyzing patterns and monitoring change in ecological communities.

5. Acknowledgements

We thank Isabel Alves dos Santos and two anonymous referees for helpful suggestions for improvement. FAPESP provided financial support for this study for which we are very grateful. JCB and EJS like to thank the members of the Bee laboratory of USP for their hospitality during their stay.

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Title: Connectance of Brazilian social bee – food plant networks is influenced by habitat, but not by latitude, altitude or network size.

Authors: Biesmeijer, J.C.; Slaa, E.J.; Castro M.S.; Viana, B.F.; Kleinert A.M. P. and Imperatriz-Fonseca, V.L.

Biota Neotropica, Vol. 5 (number 1): 2005
<http://www.biotaneotropica.org.br/v5n1/pt/abstract?article+BN02605012005>

Date Received 11/8/2004

Accepted 01/02/2005

ISSN 1676-0611

Table 1. Summary of the network characteristics of the studies included in our analysis. For complete references of the studies see appendix I. B-number of bee species, P-number of plant species, M-network size, I-number of interactions recorded, C-connectance value.

Study	Habitat	B	P	M	I	C
1. Aguilar (1998)	Atlantic Rain Forest	18	96	1728	245	14.18
2. Alves (1996)	Atlantic Rain Forest	15	113	1695	193	11.39
3. Barbola (1993)	Open fields	9	60	540	111	20.56
4. Campos (1989)	Cerrado	12	39	468	69	14.74
5. Carvalho (1990)	Cerrado	13	75	975	117	12.00
6. Castro (2001)	Caatinga	10	101	1010	350	34.65
7. Castro (unpubl.) Almeida	Atlantic Rain Forest	6	40	240	36	15.00
8. Castro (unpubl.) Orchard	Orchard	17	20	340	89	26.18
9. Cortopassi-Laurino (1982)	Urban	11	190	2090	414	19.81
10. Faria (1994)	Rupestrian fields	10	38	380	61	16.05
11. Harter (1999)	Araucaria Forest	14	185	2590	400	15.44
12. Hoffmann (1990)	Mixed habitats	6	108	648	130	20.06
13. Knoll (1990)	Urban	12	154	1848	539	29.17
14. Martins (1990) Casa Nova	Caatinga	9	39	351	68	19.37
15. Martins (1990) Lencois	Cerrado	10	81	810	131	16.17
16. Mateus (1998)	Cerrado	25	73	1825	264	14.47
17. Pedro (1992)	Cerrado	22	139	3058	285	9.32
18. Ramalho (1995)	Atlantic Rain Forest	20	106	2120	369	17.41
19. Rego (1998)	Cerrado	22	33	726	128	17.63
20. Schlindwein (1995)	Shrubland	9	131	1179	242	20.53
21. Silveira (1989)	Cerrado	22	106	2332	326	13.98
22. Sofia (1996) UEL	Urban	14	93	1302	197	15.13
23. Sofia (1996) USP-RP	Urban	27	106	2862	528	18.45
24. Taura (1990)	Urban	7	93	651	155	23.81
25. Viana (1999)	Dunes	6	48	288	71	24.65
26. Viana (unpubl.) Ibiraba	Dunes	8	35	280	104	37.14
27. Wilms (1995)	Atlantic Rain Forest	21	230	4830	932	19.30

Table 2. Studies not included in our analyses and the reason for exclusion.

Study	Reason for exclusion
28. Aguiar (2001)	No systematic data about visited plants
29. Kaminski (2001)	Visitors of only three plant species
30. Laroca (1974)	No list of visited plants per bee species (lumped per bee and plant family)
31. Orth (1983)	No list of visited plants per bee species (lumped per bee genus)
32. Machado (2002)	No systematic data about visited plants
33. Zanella (1991)	No list of visited plants per bee species (lumped per bee and plant family)
34. Schwartz Filho (1993)	No list of visited plants per bee species (lumped per bee and plant family)
35. Hakim (1983)	No list of visited plants per bee species (lumped per bee and plant family)
36. Albuquerque (1998)	No eusocial bees found on flowers (only <i>Apis mellifera</i>)
37. Knoll (1985)	Only data on visits by one species (<i>Tetragonisca angustula</i>)
38. Antonini (2002)	Only data on visits by one species (<i>Melipona quadrifasciata</i>)
39. Castro (1994)	Same data as Martins (1990) (Table 1, study 14)
40. Viana (1992)	Same data as Martins (1990) (Table 1, study 15)
41. Lorenzon et al. (2004)	Data of two separate sites are pooled in tables
All palynological studies	Methodology used is very different

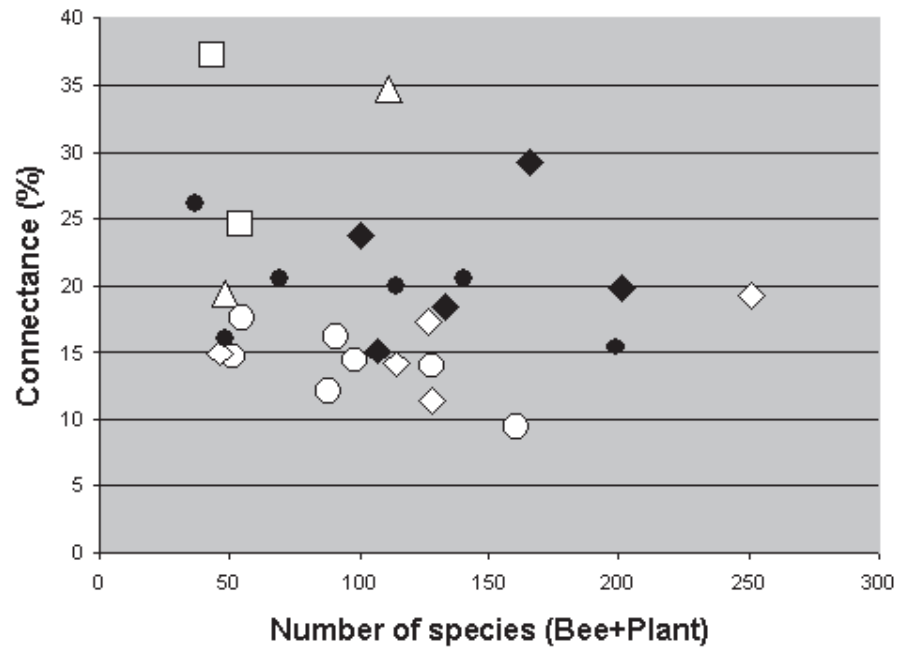


Figure 1 - Connectance calculated from each of the studies in relation to the number of species in the community. Open diamonds: Atlantic rain forest; Closed diamonds: Urban environments; Open triangles: Caatinga; Open squares: Dunelands; Open circles: Cerrado forest; Closed circles: other habitats (Orchard, shrubland, mixed habitats and open fields).

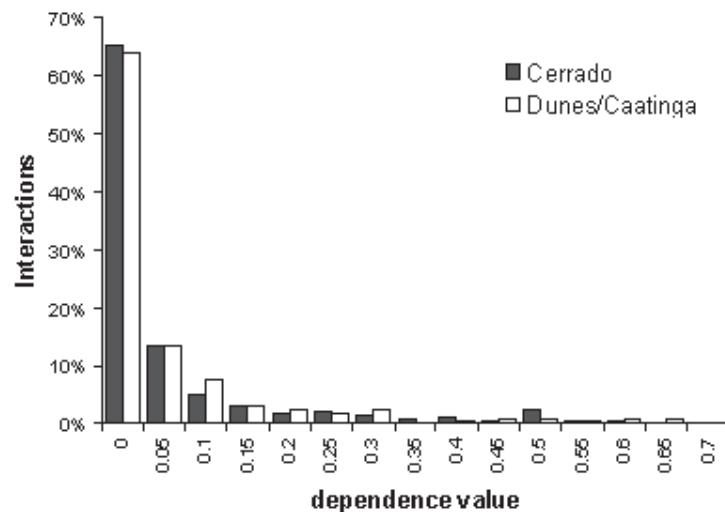


Figure 2. Frequency distribution of dependence values in Cerrado studies (four studies pooled: N = 745 links) and studies of dunes and Caatinga (three studies pooled: N = 236 links).

Appendix 1: References of all studies included in and excluded from our analysis. Numbers correspond to those given in tables 1 and 2.

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