Sociobiology 64(1): 57-68 (March, 2017) DOI: 10.13102/sociobiology.v64i1.1192

Sociobiology
An international journal on social insects

RESEARCH ARTICLE - BEES

Diversity of bees and their interaction networks with *Ludwigia sericea* (Cambessides) H. Hara and *Ludwigia peruviana* (L.) H. Hara (Onagraceae) flowers in a swamp area in the Brazilian Atlantic Forest

L Gonçalves, ML Tunes Buschini

Programa de Pós-Graduação em Biologia Evolutiva, Universidade Estadual do Centro-Oeste, Guarapuava-PR, Brazil

Article History

Edited by
Wesley Dátillo, Instituto de Ecología A.C., Mexico
Received 18 September 2016
Initial acceptance 25 October 2016
Final acceptance 27 February 2017
Publication date 29 May 2017

Keywords
Apis mellifera, Bombus, Floral resources, Food web, Pollen grains.

Corresponding author
Lia Gonçalves
Universidade Estadual do Centro-Oeste
Rua Saldanha Marinho 1604, apto 11
Centro, CEP: 85010-290.
Guarapuava-PR, Brasil
E-Mail: liagoncalves22@hotmail.com

Abstract

In Southern Brazil the great diversity of bees is due to the richness of ecosystems in the region and when studies attribute the processes for identification of the floral resources used by bees we can get important steps for the elaboration of management and conservation plans of the species involved. Based on this setting and considering that the study area is a "várzea" (swamp) with a large concentration of flowers of *Ludwigia sericea* and *Ludwigia peruviana*, important sources of resources for bees, the aim of this study was to find out about the floral visitor bees and through palynological studies and interaction networks, understand the role of these plants as providers of pollen grains to bees and how the bees interact with them and other plants, also found in this habitat. *Ludwigia sericea, Ludwigia peruviana* and the other plant species are presented as generalist in the interactions with the bee species, and the same occurs for most of the bee species in relation to these plants. Generalist bee species (*Bombus pauloensis, Apis mellifera, Augochlora amphitrite* and *Melissoptila paraguayensis*) tend to be more abundant and more resistant to disturbances than the specialist species. It was the first time that *Plebeia emerina*, *Centris varia*, *Mourella caerulea* and *Augochlorella ephyra* were recorded on the *Ludwigia* flowers in Brazil. Based on the results presented in this study, these plants are important for maintaining the bee community in the region of the Atlantic Forest in Southern Brazil, because they provide resources (nectar and pollen) to bee species that only occur in this region.

Introduction

The family Onagraceae consists of 17 genera and approximately 650 species distributed in subtropical and temperate regions (Hoch et al., 1993), and is predominant in the Americas (Cabrera, 1965). This family is divided into the subfamilies Ludwigioideae and Onagroideae. Ludwigioideae, according to the former classification, presented a single tribe – Jussieeae (Wagner et al., 2007). This tribe has been excluded and *Ludwigia* L. is the only genus (Wagner et al., 2007).

In fact *Ludwigia* is considered one of the largest and most diverse genera in the family Onagraceae, which has a generalized morphology and records of five species that are self-incompatible (*L. elegans* (Camb.) Hara, *L. irwinii* Ramamoorthy, *L. nervosa* (Poiret) H. Hara, *L. pseudonarcissus* (Chodat & Hassler) Ramamoorthy and *L. sericea*) (Ramamoorthy & Zardini, 1987).

Out of 82 species of the genus *Ludwigia* considered mesophytic (growing in humid areas), 45 occur in South America, mainly in Brazil, Argentina and Paraguay (Ramamoorthy & Zardini, 1987). In Brazil, species from the family Onagraceae are concentrated in the South and Southeast (Falkenberg, 1988), where the genus *Ludwigia* is known as "cruz-de-malta".

The place of origin of the family Onagraceae has not been determined precisely, but the region of South America has been suggested as the most probable (Raven & Axelrod,

ISSN: 0361-6525

1974; Raven 1988). According to some authors, *L. peruviana* originated in the Americas (Ramamoorthy & Zardini, 1987) and later introduced into wet areas in different regions, making it a dominant species in a short period of time and an important source of floral resources for pollinators, especially for bees (Jacobs et al., 1994).

Studies about interactions between the *Ludwigia* flowers and their visitors demonstrated the existence of important characteristics of both the flowers and the bees (the most important group of *Ludwigia* pollinators). Their flowers produce pollen grains in large tetrads (diameter > 100 μm), with the presence of viscin threads (Hesse, 1984), and only specialist bees with long rigid hairs and few branched in their scopa, and with rapid body and leg movements can be the potencial pollinators of these plants (Cruden, 1981; Gimenes, 1997). Schlindwein (2004), Michener (1979, 2000), Gimenes et al. (1993, 1996) and Gimenes (2003) observed an association between plants of the family Onagraceae, more specifically the genus *Ludwigia,* and oligoletic bees in the south and southeast of Brazil.

The Brazilian apifauna consists of five families (Andrenidae, Apidae, Colletidae, Halictidae and Megachilidae) and 1.600 species of described bees, however, approximately 3.000 species are estimated to exist in Brazil (Silveira et al., 2002). In the South, the great diversity of bees is due to the richness of ecosystems in the region, which is influenced by Andean elements from the temperate south and the dry west of the continent, as well as from subtropical components from the "cerrado" (Brazilian savanna) and the tropical forest to the north (Wittmann & Hoffman, 1990; Alves dos Santos, 1999).

Even presenting such diversity, the rate of exploitation of Brazilian ecosystems is alarming. High levels of richness and endemism, associated with past destruction, has definitively included the Atlantic Forest on a world scale as one of the 35 hotspots of biodiversity, as this biome is the fifth richest hotspot in endemism (Mittermeier et al., 2004). Its original area (in Brazil) is estimated to have covered between 1.300.000 km^2 to 1.500.000 km^2 and current data indicate that only 8.5% remains (Morellato & Haddad, 2000; Câmara, 2005).

Based on this setting and considering that the study area is a "várzea" (swamp) with a large concentration of *Ludwigia* the aim of this study was to find out about the floral visitor bees of the *Ludwigia sericea* and *Ludwigia peruviana* in this habitat and with palynological studies mapping their interactions and also know the other plants that interact to form the network.

Materials and methods

Study area

This study was carried out in the Parque Municipal das Araucárias (Araucárias Municipal Park), located in the municipality of Guarapuava (Paraná state) (25°21'06"S; 51°28'08"W) (Third Plateau of Paraná) (altitude = 1.120 m.a.s.l.).

The area of the park is approximately 104 ha, consisting of araucaria forest (43% of the area), gallery forest (10.09%), grasslands (6.8%), swamps (7.13%) and altered areas (33.23%) (Niesing, 2003). The swamp areas are located in the lower-altitude regions of the park and are composed of mainly grasses and members of the family Asteraceae (Buschini & Fajardo, 2010).

According to the Köppen classification, the climate in the region is humid mesothermal, with no dry season, and a moderate winter with frost. The average annual temperature is approximately 22°C.

Sample design

The studied species of *Ludwigia* were *L. sericea* and *L. peruviana*, both ones present in the swamp area of the park. Observations were carried out in the area beginning in August/2011 to accompany the start of the flowering of the species. After the commencement of flowering, the captures of bees were carried out three times per week from December/2011 to April/2012. The collection time was established after observation of floral receptivity, which occurred from 09h to 16h, totaling 176 hours. The flowering bushes of the two species of *Ludwigia* were used randomly in the collections, until the end of flowering or visitation by the bees.

In 20min per-hour intervals, all of the bees present in the flowers (chosen randomly in each bush) were collected using small sequentially-numbered transparent flasks. Posteriorly some bees separated in morphospecies for identification at Universidade Federal do Paraná (UFPR), by Gabriel A. R. Melo. The specimens are deposited in the Collection of Bees and Wasps of the Biology and Ecology Laboratory, of Universidade Estadual do Centro-Oeste (UNICENTRO).

Diversity and composition of bees species

The diversity of bees visiting *L. sericea* and *L. peruviana* flowers was calculated using the indices of Shannon-Wiener diversity *H'* (measures community diversity), Margalef richness *Dmg* (degree of species richness) and Pielou evenness *J'* (indicates if different species possess similar or divergent abundances). These indices were calculated using the program PAST© (version 1.98. Paleontological Statistics 1999-2010).

The frequency of occurrence (FO) and the species dominance were calculated for each bee species obtained. Frequency of occurrence is the percentage of the number of collections with a given species and was calculated as $FO = (F/N)\cdot 100$ (Silveira Neto et al., 1976), where "F" is the number of collections with the species and "N" is the total number of collections performed. The bee species were classified as primary (FO > 50%), secondary (FO = 25% -50%), or accidental (FO < 25%).

The species dominance of bees (D) was calculated as $D = (d/n)\cdot 100$ (Palma 1975), where "d" is the abundance of a specific species and "n" the total abundance. The species were classified as dominant (D > 5%), accessory (D = 2.5% - 5%), or accidental (D < 2.5%). According to Palma (1975), the FO and D indices when used together group and determine the species as common, intermediary or rare.

Pollen collection

Pollen material was retrieved from floral visiting bee bodies washing them with 70% alcohol. From this material slides were elaborated for observation with a petrographic microscope based on the method proposed by Erdtman (1960).

Bees of the same species collected on the same day and time were grouped. The simultaneous removal of pollen from their bodies was performed for the preparation of only one slide to represent the occurrence of that species in that day and time.

Plants in a flowering state, or presenting flower buds that were found in the proximity, were collected for the elaboration of slides, which aided in the identification of pollen types found on the bees bodies.

After identifying each pollen type, the first 400 grains per slide were counted. The species and their respective authors were consulted on the botanical database site Tropicos® of the Missouri Botanical Garden.

The slides were labeled and deposited in the Palynotheca of the Department of Biology, Universidade Estadual do Centro-Oeste, Guarapuava (Paraná state), Brazil.

Interaction networks

The network of interaction was built between the bees found in *L. sericea* and in *L. peruviana* flowers and the pollen grains obtained from their bodies.

The network size was calculated through the formula $M = A \cdot P$ (where M is the maximum number of possible interactions; A is the number of bees and P is the number of pollen types).

Connectance ($C = E/(a \cdot p)$) measures the ratio between the number of observed interactions (E) and the number of possible interactions, given that p is the number of plants (pollen types), and a is the number of bees in the network.

To transform these values into percentages, results were multiplied by 100 (Jordano, 1987). The connectance is a qualitative measure of network specialization and also represents the density of interactions in a network. Thus, a highly specialized community presents a low value of connectance (Jordano, 1987; Blüthgen, 2010).

The specialization index (H'_2) was calculated from the weighted matrix (quantitative) (Blüthgen et al., 2006, 2008), and its result varies from 0 (maximum generalization) and 1 (maximum specialization) (Blüthgen et al., 2006). The network specialization index evaluates niche overlap among species. A highly specialized community has a high value of network specialization index (Blüthgen, 2010).

On the qualitative interaction networks (binary matrix), the average degree (k) was determined, which is the average number of observed connections for species of plants or bees (Blüthgen et al., 2006, 2008). The degree is possibly the simplest measure of specialization. A species can be described as a specialist if it reveals a low degree, compared with degrees of the other species in the network or the number of potential partners. Nevertheless, this interpretation is based on the premise that all interactions are equally possible (Olesen & Jordano, 2002).

The dependency of species was ascertained from frequency of floral visits, with quantitative pollen analysis (Bascompte & Jordano, 2007). In this way, for each interaction two dependency values were obtained from plant species to bee species, and vice versa.

From the adjacency matrix, built with data on the presence and absence of plant and bee species, Eulerian graphs were prepared, using software R, version 3.0.1. The evaluation of the network degree of nestedness based on the adjacency matrix, was performed using the *NODF* metric (Nestedness Metric Based on Overlap and Decreasing Fill), for more consistent statistical properties.

Nestedness was estimated using the ANINHADO 3.0 software (Guimarães & Guimarães, 2006). Nestedness is used in ecology to describe one of the possible distribution patterns of species among discrete environments (Atmar & Patterson,1993). In a nested network generalist species in general interact among themselves and with the specialists, but specialists rarely interact among themselves (Bascompte et al., 2003).

Results

The flowering period of *L. sericea* was different from that of *L. peruviana*, presenting a few months of overlap between them. *Ludwigia sericea* started to flower in December/2011, lasting until April/2012, with the flowering peak in February; whereas *L. peruviana* flowered between February/2012 and May/2012, with the flowering peak in March. No bee was collected in *L. peruviana* in May. During the period in which the two species were flowering, the quantity of *L. sericea* specimens was 5 times larger than the quantity of *L. peruviana* specimens (20 and 4 flowering plants respectively).

During the collections, 908 bees (837 in *L. sericea* and 71 in *L. peruviana*) were captured belonging to 24 species and five families (Andrenidae, Apidae, Colletidae, Halictidae and Megachilidae). *Apis mellifera* was the most abundant species in the two species of *Ludwigia* (n = 317 in *L. sericea* and n = 28 in *L. peruviana*), followed by *Augochlora amphitrite* (n = 105) and *Bombus pauloensis* (n = 93) in *L. sericea* and *Melissoptila marinonni* (n = 14) and *Tetraglossula amphitrite* (n = 7) in *L. peruviana* (1).

Diversity and composition of bees species

The values of the indices of richness (*Dmg*) and diversity (*H'*) for *L. sericea* (*Dmg* = 2.972; *H'* = 2.043) were superior compared to those obtained for *L. peruviana* (*Dmg*

= 2.815; *H'* = 1.906). On the other hand, the index of Pielou evenness was higher for *L. peruviana* (*J'* = 0.743) than for *L. sericea* (*J'* = 0.671).

Uniting the results of the indices of frequency of occurrence (*FO*) and dominance (*D*) in *L. sericea*, only *A. mellifera* (*FO* = 54%; *D* = 38%) was considered a common species, eight species (*B. pauloensis*, *M. marinonii*, *M. paraguayensis*, *P. emerina*, *T. diversipes*, *T. spinipes*, *T. anthracina* and *A. amphitrite*) were considered intermediate (*FO* = 36.3% to 48.5%; *D* = 2% to 12%) and the others rare. As regards *L. peruviana*, no species was classified as common, six (*A. mellifera*, *B. pauloensis*, *M. marinonii*, *M. paraguayensis*, *T. anthracina* and *M. fiebrigi*) were intermediate (*FO* = 9.09% to 30.3%; *D* = 4% to 39%) and the others rare (1).

Bee-plant interaction networks

The interaction network established in the area of study consisted of 15 bee species (*a*) and 49 plant species (*p*), and 735 interactions (*M*) were theoretically possible (Fig 1). However, among these interactions only 194 were observed (*E*) (*C* = 0.26; 26.3%).

Ludwigia sericea was visited by 15 bee species, while *L. peruviana* by 10 species. Nine bee species were common to the two species of *Ludwigia*. In this interaction network, some plant species were visited by almost all the bee species that visited the *Ludwigia species*, for example, *Polygonum punctatum* (12 bee species), *Cinnamomum amoenum* (11 species) and *Styrax leprosum* (10 species).Out of the 49 plant species that made up the network, 30 maintained interaction with only 3 or less bee species. In the interaction network, the average degree of interactions with the plant species observed, was relatively low (*K*= 3.95), as a heterogeneous distribution, i.e., having few species with many interactions and many species with few interactions (Fig 2A).

The bees present the average degree of interaction (*K*= 12.93), higher than that observed for the plants. The level distribution, as well as for the plants, was also heterogeneous (Fig 2B).

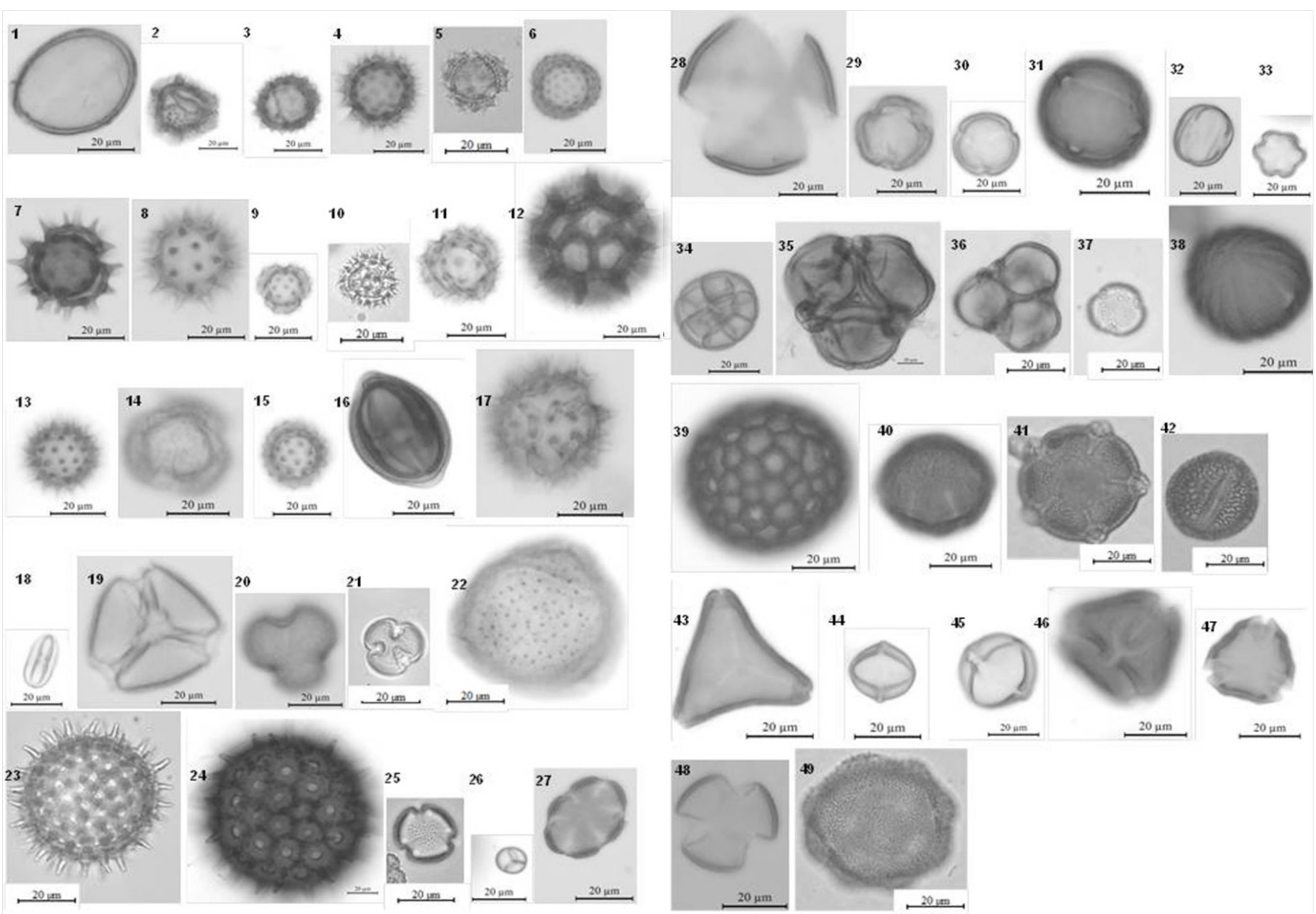

Fig 1. Pollen types observed during pollen analysis of floral visitor bees of *Ludwigia sericea* and *Ludwigia peruviana*: 1-Arecaceae sp; 2-Asteraceae sp1; 3-Asteraceae sp2; 4-Asteraceae sp3; 5-Asteraceae sp4; 6-Asteraceae sp5; 7-Asteraceae sp6; 8-*Baccharis anomala*; 9-*Baccharis microdonta*; 10-*Baccharis* sp; 11-*Campovassouria cruciata*; 12-*Chrysolaena platensis*; 13-*Enechtites valerianifolius*; 14-*Gochnatia polymorpha*; 15-*Stevia tenus*; 16-*Trixis* sp; 17-*Vernonanthura westiniana*; 18-*Begonia cucullata*; 19-*Senna araucarietorum*; 20-*Lobelia camporum*; 21-*Lobelia* sp; 22-*Lonicera japonica*; 23-*Ipomoea grandifolia*; 24-*Ipomoea purpurea*, 25-*Erythroxylum deciduum*; 26-*Mimosa flocosa*; 27-*Lycopus* sp; 28-*Tectona grandis*; 29-*Cinnamomum amoenum*; 30-*Heimia myrtifolia*; 31-*Janusia guaranitica*; 32-*Leandra* sp; 33-*Tibouchina cerastifolia*; 34-*Acacia recurva*; 35-*Ludwigia peruviana*; 36-*Ludwigia sericea*, 37-*Phytolacca dioica*; 38-*Polygala* sp; 39-*Polygonum punctatum*; 40-*Galianthe dichasia*; 41-*Rubiaceae* sp; 42-*Citrus* sp; 43-*Serjania* sp; 44-*Solanum americanum*; 45-*Solanum variabile*; 46-*Styrax leprosum*; 47-*Vochysia ferruginea*; 48-Indet1; 49-Indet.

Table 1. Species of bees collected in the flowers of *L. sericea* and *L. peruviana* in a "várzea" (floodplain) area in Parque Municipal das Araucárias (Guarapuava state of Paraná) and their indices: Frequency of occurrence (*FO*), Dominance index (*D*) and Dominance classification.

	Ludwigia sericea				***Ludwigia peruviana***			
Subfamily of bees/Bee species	Number of individuals	*FO*	*D*	Classification	Number of individuals	*FO*	*D*	Classification
Andrenidae								
Rhophitulus flavitarsis (Schlindwein & Moure 1998)	6	18	0.7	Rare	-	-	-	-
Apidae								
Apis mellifera (Linnaeus 1758)	317	54	38	Common	28	30.3	39	Intermediate
Bombus (fervidobombus) pauloensis (Friese 1913)	93	48	11	Intermediate	5	18.2	7	Intermediate
Centris (Centris) varia (Erichson 1849)	2	6.06	0.2	Rare	-	-	-	-
Exomalopsis analis (Spinola 1853)	1	3.03	0.1	Rare	-	-	-	-
Melissoptila marinonii (Urban 1998)	50	39.3	6	Intermediate	14	18.2	20	Intermediate
Melissoptila paraguayensis (Brèthes 1909)	87	48.5	10	Intermediate	6	18.2	8	Intermediate
Mourella caerulea (Friese 1900)	4	9.09	0.5	Rare	-	-	-	-
Paratetrapedia volatilis (Smith 1879)	2	3.03	0.2	Rare	-	-	-	-
Plebeia emerina (Friese 1900)	15	36.3	2	Intermediate	2	6	3	Rare
Tetrapedia diversipes Klug 1810	44	42.4	5	Intermediate	-	-	-	-
Trigona spinipes (Fabricius 1793)	51	42.4	6	Intermediate	1	3.03	1.4	Rare
Colletidae								
Tetraglossula anthracina (Michener 1989)	40	36.4	5	Intermediate	7	15.1	10	Intermediate
Halictidae								
Augochlora (Augochlora) amphitrite (Schrottky 1909)	105	42.4	12	Intermediate	-	-	-	-
Augochlorella ephyra (Schrottky 1910)	1	3.03	0.1	Rare	-	-	-	-
Dialictus micheneri (Moure 1956)	1	3.03	0.1	Rare	-	-	-	-
Pseudogapostemon pruinosus (Moure & Sakagami 1984)	6	9.09	0.7	Rare	-	-	-	-
Megachilidae								
Coelioxys cfr. chacoensis (Holmberg 1903)	-	-	-	-	1	3.03	1.4	Rare
Coelioxys tolteca (Cresson 1878)	-	-	-	-	1	3.03	1.4	Rare
Megachile aff. brasiliensis (Dalla Torre 1896)	-	-	-	-	1	3.03	1.4	Rare
Megachile (Austromegachile) facialis (Vachal, 1909)	1	3.03	0.1	Rare	1	3.03	1.4	Rare
Megachile (Austromegachile) fiebrigi (Schrottky 1908)	1	12.1	0.1	Rare	3	9.09	4	Intermediate
Megachile (Moureapis) maculata (Smith 1853)	8	21.2	1	Rare	1	3.03	1.4	Rare
Megachile (Moureapis) pleuralis (Vachal 1909)	2	6.06	0.2	Rare	-	-	-	-
Total number of individuals	837				71			
Total number of species	21				13			

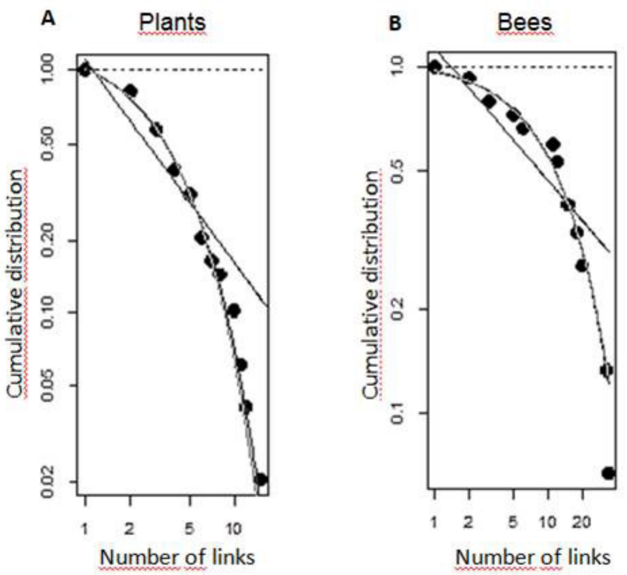

Fig 2. Average degree distribution of the connections on plant species (A) and bee species (B). The *line* represents the expected decline if the distribution follows a power law. The *horizontal axis* represents the number of connections of each point in a network. The *vertical axis* represents the probability of a point in the network to have a number "k" or more of connections.

Bombus (Fervidobombus) pauloensis was the most generalist species, visiting 34 plant species, including the two species of *Ludwigia*. The plants used by *B. pauloensis*, corresponded to 69.39% of the total number of plant species which comprise the network and 17.53% of all the network interactions. *Apis mellifera* was the second most generalist bee species, visiting 33 plant species, 67% of the total number of plants and 17.01% of all the interactions, followed by *Augochlora (Augochlora) amphitrite* and *Trigona spinipes* (20 plant species, 40.82% of the total number of plants; 10.31% of all the interactions) and *Megachile (Moureapis) maculata* (18 plant species; 36.73% of the total number of plants; 9.28% % of the total number of interactions).

The interaction network *Ludwigia*-visitors presented a nested pattern (*NODF*= 37.06; p< 0.001), with asymmetry shown in the split graphical representation.

When the diversity of interaction is analyzed considering the weighted matrix, the value of the specialization index was low (H_2'= 0.26), showing that most of the species maintain, in general, few interactions in relation to the proportion of possible interactions (connectance).

Concerning the dependence of the species of this network, it can be said that most of the bee species that visited the two species f *Ludwigia,* collected flower resources preferentially in *L. sericea*, presenting between 78% (*Megachile maculata*) to 100% (*Rhophitulus flavitarsis* x *Megachile (Moureapis) pleuralis*) of dependence, according to the quantitative analyses of the pollen grains in the samples. From the bees that visited the two species of *Ludwigia*, only *Plebeia emerina* presented pollen grains dominant from another plant species, *Cinnamomum amoenum* (52%) (Fig 3A).

When the dependence of the plants by bees was analyzed, 18 out of the 49 plant species presented dependence by some bee species, ranging between 72% for *Vernonanthura westiniana* x *Megachile maculata* to 99% for *Baccharis* sp. x *A. mellifera*. The rest of the plant species (n=31) were more generalist (Fig 3B).

Discussion

A variation in the flowering period of species of the genus *Ludwigia* has been verified, according to the region of Brazil. In this study, the flowering periods observed were from December to April for *L. sericea* and from February to April for *L. peruviana*. In the São Paulo state region, *L. elegans* (Camb.) Hara flowered practically the whole year (except in the cold months from August to October), with its flowering peak in February and March (Gimenes, 2003; Gimenes et al., 1993). *Ludwigia tomentosa* also flowered almost the whole year (except in the very dry months from June to August) in the Mato Grosso do Sul state region (Pott & Pott, 2000). In Minas Gerais state, *Ludwigia suffruticosa* (L.) Gomez had its flowering peak in June (Martins & Antonini, 1994).

The fact that the region of Guarapuava (Paraná state) possesses well-defined seasons, with cool summers (average temperature of 22ºC) and winters with frequent severe frosts, and an average temperature superior to 3ºC and inferior to 18ºC (Maack, 1981), emphasizes the results presented here, where, during the hot months, the flowering period of the studied species occurred, as well as the foraging activity of the collected bees. According to Bazilio (1997) and Mendes and Rêgo (2007), the seasonal pattern of the activities of various species of bees in subtropical climate regions is associated with the flowering of angiosperms.

In the present study, the indices of diversity and richness of the apifauna were higher for *L. sericea*. A high value for these indices indicates, in most cases, a well-structured community, with many rare species (Costa et al., 1993). The fact that *L. sericea* had flowered before, for more time and with more specimens than *L. peruviana*, may explain the result of the indices of diversity and richness of the bees collected in these plants.

Both the diversity and the richness of the species of bees visiting the flowers of the genus *Ludwigia* in the Guarapuava region were higher than those recorded in the Southeast and Midwest of Brazil (Gimenes, 2003; Steiner et al., 2010; Ruim et al., 2011; Carvalho et al., 2012). In addition, in these studies, the richness of solitary species was higher than social species. The fact that the diversity of solitary bees is greater in the South than in other regions of Brazil (Michener, 2000; Silveira et al., 2002; Santos, 2002; Buschini, 2005) is possibly one of the factors that makes the diversity of bees in the flowers of *Ludwigia* in Guarapuava greater than the diversity in other studied regions of the country. This result deserves to be highlighted, because it shows the importance of solitary species in the pollination of the some plants in Southern of Brazil.

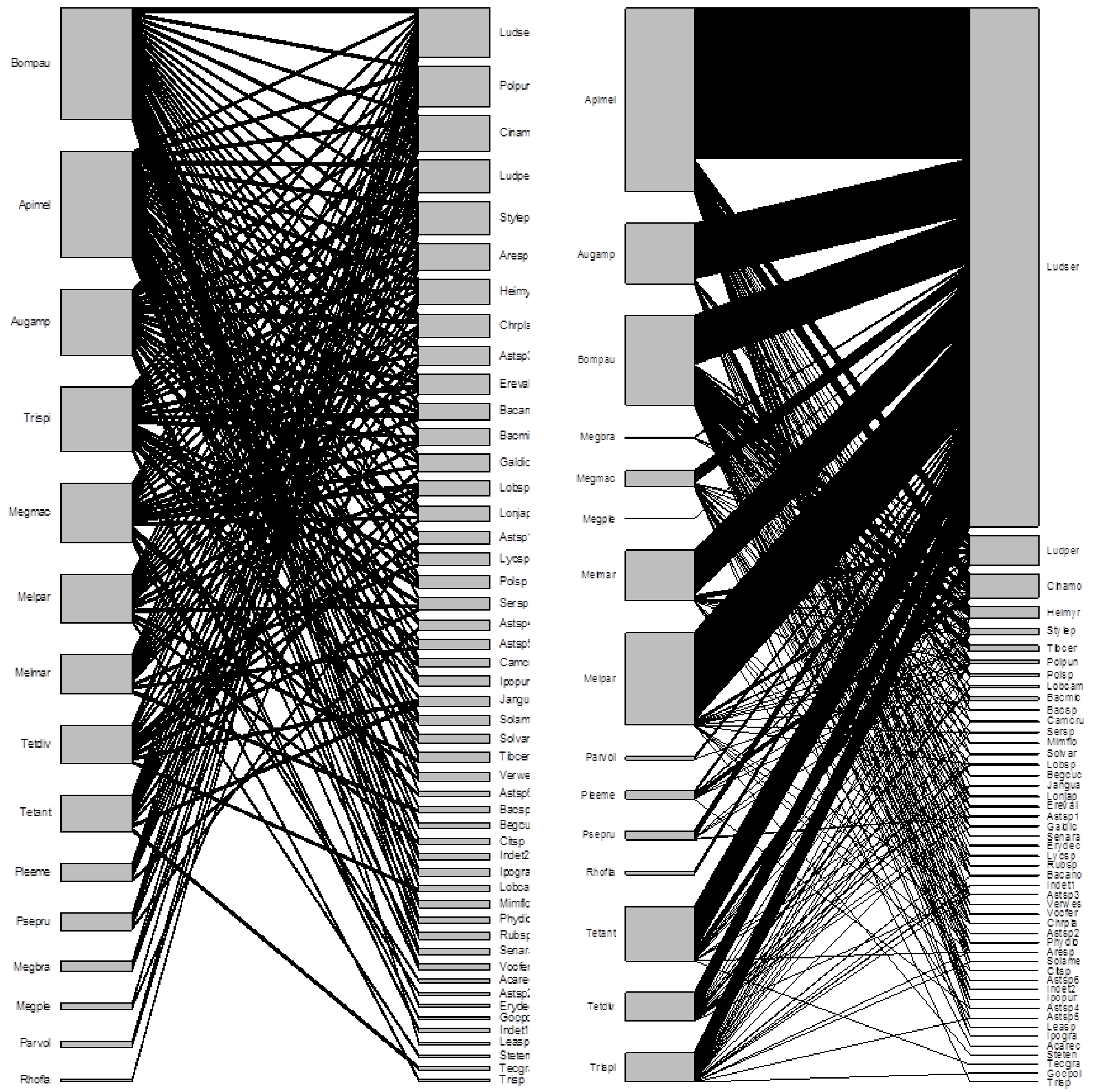

Fig 3. Interaction network between pollen types (right) and floral visitor bees *Ludwigia sericea* and *Ludwigia peruviana.* The binary matrix (A) qualitatively demonstrates the interactions between species. The weighted matrix (B) represents quantitatively interactions. The width of the lines in the weighted matrix indicates total interactions frequency between one pair of species. Abbreviations: see Table 2.

The nested standard presented in this study as in other studies (Bascompte & Jordano, 2007; Hernández-Yáñez et al., 2013) suggests that the specialized species were interacting with the generalists (and these among themselves) contributing to increase the strength of the generalists in the network.

Of all of the species of bees captured during this study, including solitary and social bees, *Apis mellifera* was the most abundant in the two species of *Ludwigia*. This species was also very frequent in flowers of *L. elegans* (Gimenes, 1997, 2002, 2003) in São Paulo state and in the flowers of *Ludwigia tomentosa* (Cambess.) (Carvalho et al., 2012) in Mato Grosso do Sul state. Although it is a visiting generalist, *A. mellifera* is considered an efficient pollinator in flowers of *Ludwigia* due to its size and behavior, which facilitate contact with the reproductive structures during the collection of nectar and pollen (Gimenes, 1997). *Apis mellifera* also has its foraging activity synchronized with the flowering peak of *Ludwigia* (Gimenes, 1997, 2003) and its abundance in these flowers is associated with its being a highly eusocial species, with a very efficient communication system between the individuals of the colony (Seeley, 1985).

Table 2. Pollen types (plant species) and bee species belonging the interaction networks of floral visitors of *Ludwigia sericea* and *Ludwigia peruviana*, with their respective abbreviations.

Botanical family	Pollen type	Abbreviation	Subfamily of bees	Bee species	Abbreviation
Arecaceae	*Arecaceae sp*	Aresp	Andrenidae	*Rhophitulus flavitarsis*	Rhofla
Asteraceae	Asteraceae sp1	Astsp1	Apidae	*Apis melífera*	Apimel
	Asteraceae sp2	Astsp2		*Bombus (Fervidobombus) pauloensis*	Bompau
	Asteraceae sp3	Astsp3		*Centris (Centris) varia*	Cenvar
	Asteraceae sp4	Astsp4		*Exomalopsis analis*	Exoana
	Asteraceae sp5	Astsp5		*Melissoptila marinonii*	Melmar
	Asteraceae sp6	Astsp6		*Melissoptila paraguayensis*	Melpar
	Baccharis anomala DC.	Bacano		*Mourella caerulea*	Moucae
	Baccharis microdonta DC.	Bacmic		*Paratetrapedia volatilis*	Parvol
	Baccharis sp L.	Bacsp		*Plebeia emerina*	Pleeme
	Campovassouria cruciata (Vell.) R.M.King & H.Rob.	Camcru		*Tetrapedia diversipes*	Tetdiv
	Chrysolaena platensis H. Rob.	Chrpla		*Trigona spinipes*	Trispi
	Erechtites valerianifolius (Wolf.) DC.	Eneval	Colletidae	*Tetraglossula anthracina*	Tetant
	Gochnatia polymorpha (Less.) Cabrera	Gocpol	Halictidae	*Augochlora (Augochlora) amphitrite*	Augamp
	Stevia tenus	Steten		*Augochlorella ephyra*	Augeph
	Trixis sp	Trisp		*Dialictus micheneri*	Diamic
	Vernonanthura westiniana (Less) H. Rob.	Verwes		*Pseudagapostemon pruinosus*	Psepru
Begoniaceae	*Begonia cucullata* Willd.	Begcuc	Megachilidae	*Coelioxys* cfr. *chacoensis*	Coecha
Caesalpinaceae	*Senna araucarietorum* H.S. Irwin & Barneby	Senara		*Coelioxys tolteca*	Coetol
Campanulaceae	*Lobelia camporum* Pohl.	Lobcam		*Megachile* aff. *brasiliensis*	Megbra
	Lobelia sp Pohl.	Lobsp		*Megachile (Austromegachile) facialis*	Megfac
Caprifoliaceae	*Lonicera japônica* Thunb.	Lonjap		*Megachile (Austromegachile) fiebrigi*	Megfie
Convolvulaceae	*Ipomoea grandifolia* L.	Ipogra		*Megachile (Moureapis) maculata*	Megmac
	Ipomoea purpurea Roth.	Ipopur		*Megachile (Moureapis) pleuralis*	Megple
Erythroxilaceae	*Erythroxylum deciduum* A.St.-Hil	Erydec			
Fabaceae	*Mimosa flocosa* L.	Mimflo			
Lamiaceae	*Lycopus* sp L.	Lycsp			
	Tectona grandis L.f.	Tecgra			
Lauraceae	*Cinnamomum amoenum* (Nees) Kosterm.	Cinamo			
Lythraceae	*Heimia myrtifolia* Cham. & Schltdl.	Heimyr			
Malpighiaceae	*Janusia guaranítica* (A.St. Hil.) A. Juss.	Jangua			
Melastomataceae	*Leandra* sp	Leasp			
	Tibouchina cerastifolia Cogn.	Tibcer			
Mimosaceae	*Acacia recurva* DC.	Acarec			
Onagraceae	*Ludwigia peruviana* (L.) H. Hara	Ludper			
	Ludwigia sericea (Cambessides) H. Hara	Ludser			
Phytolaccaceae	*Phytolacca dioica* L.	Phydio			

Table 2. Pollen types (plant species) and bee species belonging the interaction networks of floral visitors of *Ludwigia sericea* and *Ludwigia peruviana*, with their respective abbreviations (Continuation).

Botanical family	Pollen type	Abbreviation	Subfamily of bees	Bee species	Abbreviation
Polygalaceae	*Polygala* sp L.	Polsp			
Polygonaceae	*Polygonum punctatum* Michx.	Polpun			
Rubiaceae	*Galianthe dichasia* (Sucre & C.G. Costa)	Galdic			
	Rubiaceae sp	Rubsp			
Rutaceae	*Citrus* sp L.	Citsp			
Sapindaceae	*Serjania* sp Radlk.	Sersp			
Solanaceae	*Solanum americanum* Mill.	Solame			
	Solanum variabile Mart.	Solvar			
Styracaceae	*Styrax leprosum* Hook and Am.	Stylep			
Vochysiaceae	*Vochysia ferrugínea* Pohl.	Vocfer			
Unidentified	Indet1	Indet1			
	Indet2	Indet2			

The second most frequent and abundant species in this study was *Augochlora amphitrite*, which was also recorded by Steiner et al. (2010) in flowers of *L. peruviana* in Santa Catarina state and by Gimenes (2002) in flowers of *L. elegans* in the region of state of São Paulo as a frequent species, but without an important role in pollination. *Paratetrapedia volatilis* (rare species in the present study) and *Bombus* spp. were also collected by these researchers in the flowers of *Ludwigia*. The genus *Bombus*, whose behavior is generalist (Alves dos Santos, 1999; Steiner et al., 2010), is considered an important pollinator in elevated altitudes of Brazil (Freitas & Sazima, 2006).

Pollen analysis showed that *Bombus pauloensis* was the most generalist bee species, having interactions with 34 pollen types. *Bombus* was also recorded in other species of *Ludwigia*, being the most frequent visitor and abundant in flowers (Gimenes, 2002; Silveira et al., 1993) and the generalist behavior (Alves dos Santos, 1999; Steiner et al., 2010), probably because it is a social species that during nesting seasons increase its foraging activities and its morphological and behavioral aspects, which facilitate the transportation of a large quantity and variety of pollens. Generalist bee species tend to be more abundant and more resistant to disturbances than the specialist species (Vazquez, 2005; Vazquez & Aizen, 2004).

Bees of the genus *Tetrapedia* were considered effective pollinators of *L. sericea* in São Paulo state based on records of pollen collection behavior, frequency and time spent in the flowers (Sazima & Santos, 1982). In the present study, *Tetrapedia diversipes* was classified as an intermediate species and possible pollinator of flowers of *Ludwigia*, due to the presence of a structure (scopa) that facilitates the transport of pollen. Silveira et al. (1993), Alves dos Santos (1999), Steiner et al. (2010), Ruim et al. (2011) and Menezes et al. (2012) verified the interaction of *Tetrapedia diversipes* with flowers of *Ludwigia* in Mata Atlântica areas in the states of Minas Gerais, Rio Grande do Sul, Santa Catarina, Paraná and Rio de Janeiro, respectively.

In this study, *Pseudagapostemon puinosus*, *Rhophitulus fiavitarsis* and the species of *Megachile* can be considered accidental pollinators in the flowers of *Ludwigia*. According to Gimenes (1997, 2002), the first two species cited also presented this type of behavior in flowers of *Ludwigia* during the collection of resources. On the other hand, the genera *Exomalopsis*, *Dialictus* and *Coelioxys* did not behave like pollinators when they visited the flowers.

Although *L. sericea, L. peruviana* and the other plants species sampled in this study are presented as generalist in the interactions with the bee species, and the same occurs for most of the bee species in relation to these plants, the network showed that Megachilidae species largely depend on the *Ludwigia* pollen grains. *Megachile aff. brasiliensis,* collected only from the *L. peruviana, Megachile (Moureapis) pleuralis* and *Rhophitulus flavitarsis* collected only from the *L. sericea,* had oligoletic habits. These habits are generally associated to plants which occur in open areas (Schlindwein 2000). Many plant species that occur in these environments have large pollen grains such as those of the *Ludwigia*, which requires from the bees of the Megachilidae family a scopa (ventral) with long and unbranched hairs enabling them to adequately handle the pollen (Schlindwein, 2004). These results confirmed what Buschini et al. (2009) had observed when analyzing the pollen grains found in *Megachile (Moureapis)* sp. nests. According to these authors, *L. peruviana* and *L. sericea* are the main pollen sources for the offspring of these bees, considered specialists at collecting *Ludwigia* pollen.

Tetraglossula anthracina and *Pseudagapostemon pruinosus* also largely depend on the *L. sericea* pollen. These species were recorded as the main visitors to the *Ludwigia* flowers in other regions in Brazil (Gimenes, 1997; Gimenes et al., 1993, 1996; Schlindwein, 2004; Steiner et al., 2010) and are specialists at collecting pollen and nectar from the flowers of this genus. Moreover, *T. anthracina* is still considered an efficient pollinator due to the morphological and behavioral adaptations (size and quick abdominal movements while collecting), which favored collecting the resources (Gimenes, 1997, 2003; Gimenes et al., 1993, 1996).

The presence of *Plebeia emerina*, *Centris varia*, *Mourella caerulea* and *Augochlorella ephyra* on the *L. sericea* and *L. peruviana* flowers is an unprecedented result of this study, i.e. it was the first time that these species were recorded on the *Ludwigia* flowers in Brazil. This can be attributed to the distribution of these species, which, apart from of *C. varia*, occur preferentially in Southern Brazil (Moure et al., 2007).

Based on the results presented here, it can be concluded that the diversity of bees is high on the *Ludwigia* flowers in this region of Brazil, especially the solitary species. These plants are important for maintaining rare species like those from the family Megachilidae. Furthermore, *L. sericea* and *L. peruviana* are part of a more complex system interacting directly with 24 species of bees and, indirectly, with 49 species of plants. Thus, they connect various solitary bee species to other plants that are part of this important Brazilian biome, which is severely under threat.

Acknowledgments

We thank the Graduate Program in Evolutionary Biology (UNICENTRO) and CAPES for financial support. We also thank Prof. Dr. Gabriel Augusto R. Melo – UFPR (Curitiba, Paraná state) for identification of the bees, Prof. Dr. Juliano Cordeiro – UFPR (Palotina, Paraná state) for identification of the plants and Cláudia I. Silva – UFC (Fortaleza, Ceará state), for the help with palynological study and all support.

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