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Spatial distribution of phytophagous insects, natural enemies, and pollinators on *Leucaena leucocephala* (Fabaceae) trees in the Cerrado

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Abstract

Leucaena leucocephala (Lam.) de Wit (Fabaceae) is widely used to regenerate degraded landscapes in tropical and subtropical regions and serves as a protein source for animals in agrosilvopastoral systems. Thus, our objective was to assess the spatial distribution of insects on the tree crown (vertical: upper, middle, and basal canopy; horizontal: north, south, east, and west) and leaf surfaces (adaxial and abaxial) of *L. leucocephala*. Phytophagous insects, natural enemies, and pollinators were quantified fortnightly in 20 trees for 2 yr. North-facing tree branches had the greatest numbers of phytophagous insects, natural enemies, and pollinators. Branches facing west had the most species-rich and biodiverse phytophagous and pollinator assemblages, whereas for natural enemies, species richness and biodiversity were greatest on branches facing north or south. The greatest numbers of individuals and highest levels of species richness of phytophagous insects, natural enemies, and pollinators were observed in the upper and middle parts of the *L. leucocephala* canopy. The most individuals and highest levels of species richness and biodiversity for phytophagous insects, natural enemies, and pollinators were observed on the abaxial face of *L. leucocephala* leaves. The species with the highest abundance and k-dominance (common or constant species) on *L. leucocephala* trees were the phytophagous insects *Trigona spinipes* F. (Hymenoptera: Apidae: Meliponinae) and *Tropidacris collaris* Stoll (Orthoptera: Romaleidae) and the natural enemies *Camponotus* sp.2 (Hymenoptera: Formicidae) and *Brachymyrmex* sp. (Hymenoptera: Formicidae). These results can inform strategies related to pest control and maintenance of natural enemies and pollinators in *L. leucocephala* plantations. Biopesticide application, for example, may be more effective at eliminating target organisms if directly applied on their preferred sites, and a targeted application can minimize negative effects for non-target organisms.

Key Words: abundance; biodiversity; natural enemies; savannah

Resumen

Leucaena leucocephala (Lam.) Wit (Fabaceae) es ampliamente usada en el proceso de recuperación de suelos degrados en regiones tropicales y subtropicales así como fuente de proteínas para animales en sistemas agroforestales. Nuestro objetivo fue evaluar la distribución espacial de los insectos en las copas de las árboles (vertical- parte mas alta, parte media e parte baja de la copa del arbol; y en la horizontal- norte, sur, este y oeste) y en las susperficies de hojas (adaxial y abaxial) de árboles de *L. leucocephala*. Los insectos fitófagos, enemigos naturales y polinizadores fueron cuantificados dos veces por mes en 20 árboles durante dos años. El número, mas grande, de fitófagos, enemigos naturales y polinizadores individuales fueron observados en las ramas orientadas al norte. La mayor riqueza de especies y biodiversidad de fitófagos se observaron en las ramas orientadas al oeste y para los enemigos naturales y polinizadores en las ramas orientadas al norte/sur y oeste, respectivamente. Los mayores valores de individuos, riqueza de especies, biodiversidad de fitófagos, enemigos naturales y polinizadores fueron observados en la parte mas alta y media de la copa del arbol de *L. leucocephala*. Los fitófagos y enemigos naturales mas abundantes y con la mas grande k-dominancia observados en las muestras (común/especie constante) fueron *L. leucocephala* y *Trigona spinipes* F. (Hymenoptera: Apidae, Meliponinae), *Tropidacris collaris* Stoll (Orthoptera: Romaleidae), *Camponotus* sp.2 (Hymenoptera: Formicidae) y *Brachymyrmex* sp. (Hymenoptera: Formicidae), respectivamente. Estos resultados pueden ser un soporte para programas de reducción del uso de pesticidas y conservacion de enemigos naturales y polinizadores en plantaciones de *L. leucocephala*. Por ejemplo, aplicaciones de biopesticidas pueden alcanzar mejores resultados si esta dirigido a organismos de destino, mas allá de minimizar los efectos negativos en aquellos que no son de destino.

Palabras Clave: abundancia; biodiversidad; enemigos naturales; sabana

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Leucaena leucocephala (Lam.) de Wit (Fabaceae) is a widely cultivated species for the reforestation of degraded areas, such as pastures and eroded landscapes, and as a protein source for animal feed in agrosilvopastoral systems because of its high dry matter production and excellent nutritional value (Atawodi et al. 2008). This plant is resistant to salinity and adapted to different soil types, precipitation, and sunshine levels. *Leucaena leucocephala* can also be used in windbreaks to prevent wind and water erosion and to improve environmental conditions (Hai et al. 2007).

Trees used as windbreaks can influence host location and distribution of pests and natural enemies (Rao et al. 2000; Brandle et al. 2004). Horizontal branch stratification in relation to cardinal points may affect insect abundance and richness. This occurs due to the wind direction and intensity (Leite et al. 2011a,b,c); insolation (Unsicker & Mody 2005), microclimate formed by the plant canopy (Basset 1991; Leite et al. 2011a), and herbivore preference for spaces free of natural enemies (Unsicker & Mody 2005; Leite et al. 2012). Plants offer significant resources for biodiversity, and their branches and leaves may alter the environment by shading, which affects moisture and evapotranspiration, and can serve as a refuge for insect herbivores and natural enemies by creating vertical stratification (Brandle et al. 2004). Moreover, physical and chemical leaf characteristics can influence insect distribution (Peeters 2002). Herbivory rates may differ depending on light intensity and seasonal variation of climate (Guedes et al. 2000; Zanuncio et al. 2001), which are related to aspects such as: (1) age and height of leaf insertion in the plant canopy; (2) leaf thickness and epidermis hardness; and (3) trichome presence (Almeida Cortez 2005). Leaf chemical composition, such as lignin, cellulose, and fiber contents, and the presence of tannins and extrafloral nectaries, may influence the occurrence and distribution of phytophagous insect (Peeters 2002). Insects prefer to eat the abaxial leaf surface with softer tissue, more protruded ribbing, slender cortex, and thinner epidermis as compared with the adaxial leaf surface. The abaxial surface can also serve as a refuge for insects against natural enemies and protect the eggs from rainfall. On the other hand, an epidermis with rigid texture and high silica or lignin content is a mechanical barrier that reduces oviposition by insects (Lara 1991).

The most common insects associated with *L. leucocephala* are *Acanthoscelides macrophthalmus* (Schaeffer) (Coleoptera: Chrysomelidae) (Raghu et al. 2005), *Coccus longulus* (Douglas) (Hemiptera: Coccidae) (Elder et al. 1998), and *Heteropsylla cubana* Crawford (Hemiptera: Psyllidae), the latter responsible for damage in various parts of the world and dispersed by winds (Elder et al. 1998; Ndlovu et al. 2000; Rao et al. 2000). *Heteropsylla cubana* is the main pest that causes *L. leucocephala* total defoliation and plant death (Santana 2008; Drumond & Ribaski 2010). In Brazil, it was 1st reported in 2000 in Espírito Santo state, in 2005 in Minas Gerais and Paraná states, and in 2006 in Bahia State (Santana 2008).

The distribution of phytophagous insects, natural enemies, and pollinators on *L. leucocephala* in Brazil requires further study to establish sampling plans for pest management (Toledo et al. 2006). The objective was to identify phytophagous insects, natural enemies, and pollinators and their distribution throughout *L. leucocephala* tree vertical canopy stratification (upper, middle, basal parts, and trunk), horizontal stratification (branch orientation related to sun exposure: north, south, east, and west faces) and leaf surfaces (adaxial and abaxial parts).

Materials and Methods

STUDY SITES

This study was carried out in a pasture area in the Cerrado Biome of the Instituto de Ciências Agrárias at the Universidade Federal de Minas Gerais (ICA/UFMG), Brazil. Samples were collected from Jan 2014 to Mar 2016 in an area with Aw climate, i.e., tropical savanna with a dry winter and a rainy summer according to the classification of Köppen, and a dystrophic red-yellow latosol (Vianello & Alves 1991).

STUDY DESIGN

One hundred meter long windbreaks (plants used as a barrier to the wind) with 2 *L. leucocephala* rows spaced 3 × 3 m apart were used. Seedlings of this species were prepared in a nursery and planted in Sep 2012 in 30 × 30 × 30 cm holes with 160 g of natural reactive phosphate mixed into the subsoil of a *Brachiaria decumbens* Stapf (Poaceae) pasture.

Phytophagous, natural enemy, and pollinator insects were visually counted fortnightly for 2 yr in twenty 16-mo-old *L. leucocephala* trees. This was done on the adaxial and abaxial leaf surfaces of the upper, middle, and basal parts of the canopy on branches facing north, south, east, and west. A total of 12 leaves per canopy position and 9 per tree branch position were sampled. Insects were collected from the leaves, flowers, and trunks of 20 trees each sample period for a total of 52 sample periods. All collected insects were separated into morphospecies and stored in flasks with 70% ethanol and sent for identification to the following taxonomists: Ayr de Moura Bello (Coleoptera) at the Laboratório de Biodiversidade Entomológica, Instituto Oswaldo Cruz; Ivan Cardoso Nascimento (Formicidae) at the Departamento de Ciências Biológicas, Universidade Estadual do Sudoeste da Bahia; Paulo Sérgio Fiuza Ferreira (Hemiptera) at the Departamento de Entomologia, Universidade Federal de Viçosa; and Luci Boa Nova Coelho (Cicadellidae) at the Instituto de Biologia, Universidade Federal do Rio de Janeiro.

STATISTICAL ANALYSES

The ecological indices (diversity, relative abundance and species richness) were calculated per sample and insect species of each taxon with the BioDiversity Professional, Version 2 (©1997 The Natural History Museum; http://www.sams.ac.uk/dml/projects/benthic/bdpro/index.htm) software. Diversity (D) was calculated using the Hill formula of 1st order: N1 = exp (H'), where H' is the Shannon–Weaver diversity index (Hill 1973), calculating the diversity with the actual species number (Hill 1973; Jost 2006). Relative abundance (rA) was expressed by (rA) = n × 100/P where n is the species numbers and P is the sum of all species numbers. Species richness (S) was calculated by S = richness (number of species present) (Lazo et al. 2007). We calculated the k-dominance by plotting the percentage of cumulative abundance against log species rank (Lambshead et al. 1983). The k-dominance values indicate the dominance and evenness of distribution of individuals among species (Gee et al. 1985). The frequencies of each insect species per sample were classified as: constant (≥50% presence), common (11–49% presence), and rare (≤10% presence) (adapted from Siqueira et al. 2008).

Results

Eighteen rare, 3 common (*Trigona spinipes* F. [Hymenoptera: Apidae], *Brachymyrmex* sp. [Hymenoptera: Formicidae], and *Tropidacris collaris* Stoll [Orthoptera: Romaleidae]), and 1 constant species (*Camponotus* sp.2 [Hymenoptera: Formicidae]) were observed on *L. leucocephala* trees (Table 1). The phytophagous insects of the Hemiptera order (representing sucking insects) had the greatest numbers of species (4) and families (5) represented in the samples collected. The greatest numbers of natural enemies were from the Hymenoptera order, with 1 species, 4 genera, 3 morphospecies, and 3 families being identified (Table 1).

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Table 1. Order, family, feeding behavior (Feeding), and frequency of insects on *Leucaena leucocephala* in Montes Claros, Minas Gerais State, Brazil.

Order	Family	Species	Feeding	Frequency
Coleoptera	Chrysomelidae	NI	Leaf	Rare-L
Diptera	Otitidae	*Euxesta* sp.	Leaf	Rare-Tr
	Dolichopodidae	NI	Predator	Rare-L
	Syrphidae	*Episyrphus balteatus* De Geer	Predator	Rare-L
Hemiptera	NI	NI	Leaf	Rare-L
	Aetalionidae	*Aethalion reticulatum* L.	Leaf	Rare-L
	Cercopidae	*Mahanarva posticata* Stal	Leaf	Rare-L
	Cicadellidae	*Ferrariana trivittata* (Signoret)	Leaf	Rare-L
	Cicadellidae	*Dalbulus maidis* (De Long e Wolcott)	Trunk	Rare-Tr
	Fulgoroidae	NI	Leaf	Rare-L
	Membracidae	NI	Leaf	Rare-L
Hymenoptera	Apidae	*Trigona spinipes* Fabricius	Generalist	Common-L
	Apidae	*Tetragonisca angustula* Latreille	Pollen	Rare-L
	Formicidae	*Camponotus* sp.1	Generalist	Rare-L
	Formicidae	*Camponotus* sp.2	Generalist	Constant-L
	Formicidae	*Camponotus* sp.3	Generalist	Rare-L
	Formicidae	*Brachymyrmex* sp.	Generalist	Common-L
	Vespidae	*Polistes* sp.	Predator	Rare-L
Lepidoptera	Arctiidae	NI	Leaf	Rare-L
Mantodea	Mantidae	*Mantis religiosa* L.	Predator	Rare-L
Odonata	NI	NI	Predator	Rare-L
Orthoptera	Romaleidae	*Tropidacri scollaris* Stoll	Leaf	Common-L

NI = not identified, L = leaf, Tr = trunk.

The greatest numbers of phytophagous, natural enemy, and pollinator individuals were observed on branches facing north. However, phytophagous insects and pollinators had the highest levels of species richness and biodiversity on branches facing west, and natural enemies on branches facing north or south. The greatest numbers of individuals and highest levels of species richness and biodiversity for phytophagous insects were observed in the upper canopy of *L. leucocephala* trees, and those for the natural enemies in the upper and middle canopy parts. The greatest numbers of individuals and highest levels of species richness and biodiversity of phytophagous insects and natural enemies were observed on the abaxial face on *L. leucocephala* leaves (Table 2).

In relation to the cardinal directions, chewing phytophagous insects were most abundant (n = 11) on the branches facing north with 3 species present. The greatest abundance (n = 5) of sucking phytophagous insects was observed in the west position with 4 species found. The greatest predatory ant abundance (n = 28) was found on the north-facing branches with 4 species, and the greatest abundance of the pollinator *Tetragonisca angustula* Latreille (Hymenoptera: Apidae) (n = 4) on the west-facing branches on *L. leucocephala* trees (Table 3).

The abundance of chewing (n = 11) and sucking (n = 6) phytophagous insects was highest in the upper part of the *L. leucocephala* canopy with 4 and 6 species, respectively. Predatory ants had the greatest abundance (n = 42) also in the upper part of the canopy with 3 species. The pollinator *T. angustula* was most abundant (n = 6) in the middle part of the *L. leucocephala* canopy (Table 4).

The phytophagous insects *T. spinipes* and *T. collaris* and the natural enemy insects *Camponotus* sp.2 and *Brachymyrmex* sp. had the highest abundance and greatest k-dominance on the abaxial face of *L. leucocephala* leaves (Table 5).

Discussion

Trigona spinipes and *T. collaris* were the phytophagous insects with highest frequencies and were classified as common species. These insects are harmful crop pests. For example, *T. spinipes* damages sprouts to obtain fibers to construct its nests (Silva et al. 1997). *Trigona spinipes* can also negatively influence pollination, thereby reducing or inhibiting fructifications. For example, *Cucurbita moschata* (Duchesne) (Cucur-

Table 2. Number of individuals (NI), species richness (S), and diversity levels (DI) of phytophagous, natural enemy, and pollinator insects on *Leucaena leucocephala* as function of the branch position (cardinal points and canopy parts) and leaf surface per plant over 2 yr in Montes Claros, Minas Gerais State, Brazil.

	Cardinal point				Canopy part				Leaf surface	
Variable by insect guild	North	South	East	West	Upper	Middle	Basal	Trunk	Abaxial	Adaxial
Phytophagous insects										
NI	12	3	3	10	17	11	0	2	19	9
S	4	3	1	6	9	4	0	2	7	5
DI	7.33	7.04	1.44	14.71	21.39	8.64	0	3.92	14.28	11.94
Natural enemies and pollinators										
NI	33	23	25	24	46	35	24	17	70	35
S	7	7	6	3	7	5	4	3	9	3
DI	7.17	7.54	8.10	4.59	6.60	7.20	4.68	5.75	9.68	3.12

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Table 3. K-dominance and abundance (in parentheses) of phytophagous, natural enemy, and pollinator insects on *Leucaena leucocephala* as function of branch position (cardinal points) per plant over 2 yr in Montes Claros, Minas Gerais State, Brazil.

	North		South		East		West	
Insect guild	Taxon	K-dominance	Taxon	K-dominance	Taxon	K-dominance	Taxon	K-dominance
Phytophagous insects	*T. spinipes*	50.0 (6)	*T. colaris*	33.3 (1)	*F. trivittata*	100 (3)	*T. colaris*	40 (4)
	T. colaris	83.3 (4)	*T. spinipes*	66.7 (1)	*A. reticulatum*	100 (0)	*M. posticata*	60 (2)
	Arctiidae	91.7 (1)	Membracidae	100 (1)	*T. colaris*	100 (0)	*A. reticulatum*	70 (1)
	Membracidae	100 (1)	*A. reticulatum*	100 (0)	Fulgoroidea	100 (0)	Fulgoroidea	80 (1)
	A. reticulatum	100 (0)	*F. trivittata*	100 (0)	Arctiidae	100 (0)	Chrysomelidae	90 (1)
	F. trivittata	100 (0)	Fulgoroidea	100 (0)	*M. posticata*	100 (0)	Hemiptera	100 (1)
Natural enemies and pollinators	*Camponotus* sp.2	69.7 (23)	*Camponotus* sp.2	69.6 (16)	*Camponotus* sp.2	56.0 (14)	*Camponotus* sp.2	70.8 (17)
	T. angustula	78.8 (3)	*Brachymyrmex* sp.	78.3 (3)	*Brachymyrmex* sp.	84.0 (7)	*T. angustula*	87.5 (4)
	Brachymyrmex sp.	87.9 (3)	*Camponotus* sp.3	82.6 (1)	*Camponotus* sp.3	88.0 (1)	*Brachymyrmex* sp.	100 (3)
	Camponotus sp.3	90.9 (1)	*E. balteatus*	87.0 (1)	Dolichopodidae	92.0 (1)	*Camponotus* sp.3	100 (0)
	M. religiosa	93.9 (1)	Odonata	91.3 (1)	*T. angustula*	96.0 (1)	*M. religiosa*	100 (0)
	Camponotus sp.1	97.0 (1)	*T. angustula*	95.7 (1)	*Polistes* sp.	100 (1)	*Camponotus* sp.1	100 (0)
	Polistes sp.	100 (1)	*Polistes* sp.	100 (1)	*M. religiosa*	100 (0)	*E. balteatus*	100 (0)

Table 4. K-dominance and abundance (in parentheses) of phytophagous, natural enemy, and pollinator insects on *Leucaena leucocephala* as function of the canopy part per plant over 2 yr in Montes Claros, Minas Gerais State, Brazil.

	Upper canopy		Middle canopy		Basal canopy		Trunk	
Insect guild	Taxon	K-dominance	Taxon	K-dominance	Taxon	K-dominance	Taxon	K-dominance
Phytophagous insects	*T. colaris*	41.2 (7)	*T. spinipes*	45.5 (2)	*T. spinipes*	100 (0)	*Euxesta* sp.	50 (1)
	M. posticata	52.9 (2)	*F. trivittata*	72.7 (3)	*F. trivittata*	100 (0)	*D. maidis*	100 (1)
	T. spinipes	64.7 (2)	*T. colaris*	90.9 (2)	*T. colaris*	100 (0)	*A. reticulatum*	100 (0)
	A. reticulatum	70.6 (1)	Membracidae	100 (1)	Membracidae	100 (0)	*T. colaris*	100 (0)
	Fulgoroidea	76.5 (1)	*A. reticulatum*	100 (0)	*A. reticulatum*	100 (0)	*F. trivittata*	100 (0)
	Arctiidae	82.4 (1)	Fulgoroidea	100 (0)	Fulgoroidea	100 (0)	Fulgoroidea	100 (0)
	Chrysomelidae	88.2 (1)	Arctiidae	100 (0)	Arctiidae	100 (0)	Arctiidae	100 (0)
	Hemiptera	94.1 (1)	*M. posticata*	100 (0)	*M. posticata*	100 (0)	*M. posticata*	100 (0)
	Membracidae	100 (1)	Chrysomelidae	100 (0)	Chrysomelidae	100 (0)	Chrysomelidae	100 (0)
Natural enemies and pollinators	*Camponotus* sp. 2	67.4 (31)	*Camponotus* sp. 2	60.0 (21)	*Camponotus* sp. 2	75 (18)	*Camponotus* sp. 2	58.8 (10)
	Brachymyrmex sp.	87.0 (9)	*T. angustula*	77.1 (6)	*Polistes* sp.	87.5 (3)	*Brachymyrmex* sp.	82.4 (4)
	Camponotus sp. 3	91.3 (2)	*Brachymyrmex* sp.	94.3 (6)	*T. angustula*	95.8 (2)	*Camponotus* sp. 3	100 (3)
	M. religiosa	93.5 (1)	*Camponotus* sp. 3	97.1 (1)	*E. balteatus*	100 (1)	*M. religiosa*	100 (0)
	Dolichopodidae	95.7 (1)	*Camponotus* sp. 1	100 (1)	*Camponotus* sp. 3	100 (0)	*Camponotus* sp. 1	100 (0)
	Odonata	97.8 (1)	*M. religiosa*	100 (0)	*M. religiosa*	100 (0)	*E. balteatus*	100 (0)
	T. angustula	100 (1)	*E. balteatus*	100 (0)	*Camponotus* sp. 1	100 (0)	Dolichopodidae	100 (0)

Table 5. K-dominance and abundance (in parentheses) of phytophagous, natural enemy, and pollinator insects on *Leucaena leucocephala* as function of leaf surface per plant over 2 yr in Montes Claros, Minas Gerais State, Brazil.

	Abaxial face		Adaxial face	
Insect guild	Taxon	K-dominance	Taxon	K-dominance
Phytophagous insects	*T. spinipes*	36.8 (7)	*T. collaris*	33.3 (3)
	T. collaris	68.4 (6)	*F. trivittata*	66.7 (3)
	Membracidae	79.0 (2)	Fulgoroidea	77.8 (1)
	A. reticulatum	84.2 (1)	Arctiidae	88.9 (1)
	M. posticata	89.5 (1)	*M. posticata*	100 (1)
	Chrysomelidae	94.7 (1)	*A. reticulatum*	100 (0)
	Hemiptera	100 (1)	Chrysomelidae	100 (0)
Natural enemies and pollinators	*Camponotus* sp.2	58.6 (41)	*Camponotus* sp.2	82.9 (2)
	Brachymyrmex sp.	80 (15)	*T. angustula*	97.1 (5)
	T. angustula	85.7 (4)	*E. balteatus*	100 (1)
	Camponotus sp.3	90 (3)	*Camponotus* sp.3	100 (0)
	Polistes sp.	94.3 (3)	*M. religiosa*	100 (0)
	M. religiosa	95.7 (1)	*Camponotus* sp.1	100 (0)
	Camponotus sp.1	97.1 (1)	Dolichopodidae	100 (0)
	Dolichopodidae	98.6 (1)	Odonata	100 (0)
	Odonata	100 (1)	*Polistes* sp.	100 (0)

bitaceae) flowers only visited once by *T. spinipes* produced no fruit, which may be due to insufficient amounts of pollen carried by workers of this bee species (Serra & Campos 2010). Their small body size is also important, because these bees only occasionally touch the stamens and stigmas, thereby reducing the chance of successful pollination. In addition, these bees visit the flower individually, without group behavior, a foraging pattern characteristic of this species on other plants (Serra & Campos 2010). Thus, as pollinator, *T. spinipes* contributes little to fruit production (Serra & Campos 2010). In addition, the phytophagous species *T. collaris* can damage wild plant species, including palm, fruit, grain, and *Casuarina glauca* Sieber ex Spreng (Casuarinaceae) trees (Costa et al. 2003).

The greatest abundance of Hemiptera and Hymenoptera orders on *L. leucocephala* trees differs from findings of others studies in the Cerrado. Coleoptera, Lepidoptera, and Hymenoptera were described as the most abundant orders of insects in the Brazilian Cerrado (Pinheiro et al. 2002; Zanuncio et al. 2002; Zanetti et al. 2003). The small number of insects on *L. leucocephala* trees we found in this study may be explained by 3 hypotheses. Firstly, it is an exotic species and thus has an expected low abundance of native insect species as predicted by the natural enemy hypothesis. The natural enemy hypothesis suggests that a plant species outside its geographic distribution leaves behind specialized pests and thus will have a competitive advantage over native plants in their new habitat (Keane & Crawley 2002).

Secondly, *L. leucocephala* has a relatively high nitrogen content but low lignin and hemicellulose contents (Beltrán & Wunderle Jr 2014) and contains phlabophene tannins (Cavalcante et al. 2006). Tannins are digestive substance reducers and have an effect proportional to their concentration (Strong et al. 1984). Tannins can reduce insect growth and survival by digestive enzyme inactivation and by producing a tannin–protein complex that hampers digestion (Mello & Silva-Filho 2002).

Thirdly, the association between plants and ants generally requires mutuality interactions (Hölldobler & Wilson 1990; Bronstein 1998) with different insect species. Visitor ants reduce herbivory rates on the leaves, flower buds, and flowers by attacking or preying on phytophagous insects (Junqueira et al. 2001). Extrafloral nectar, such as that which *L. leucocephala* presents in an extrafloral nectary on the petiole (Hughes 1998), is responsible for keeping ants constantly foraging on plant leaves (Dáttilo 2009). Most ant visits to extrafloral nectaries may foster flower or fruit production and reduce pest damage to *L. leucocephala* trees. Budding leaves and developing flowers before the rainy season are common in perennial plants in the Cerrado (Almeida et al. 1998; Felfini et al. 1999; Pedroni et al. 2002; Almeida et al. 2006; Leite et al. 2006), allowing these plants to increase their photosynthetic area when phytophagous insect populations are small (Leite et al. 2012).

The great abundance of chewing phytophagous insects and predatory ants on north-facing branches of the *L. leucocephala* canopy may be due to the food quality, foliar nectary, and flowers exposed to wind currents (north- and east-prevailing winds in the region), which may increase evaporation and nectar concentration (Debruijn & Sommeijer 1997). On the other hand, we found the greatest abundance of sucking phytophagous insects on the west side, where wind intensity is lower and hence humidity higher and temperature lower than on the north side, resulting in decreased desiccation and improved living conditions for these insects (Rao et al. 2000).

The high abundance of the pollinator *T. angustula* on the west side does not agree with the abundance pattern reported for bees, which usually prefer visits at high temperature and light periods with low relative humidity and wind speed (Polatto et al. 2012). Possibly the low wind speed is the determining factor for a visit. Besides that, bees visiting branches in the west side, where wind intensity and temperature are lower and humidity higher could be explained by 2 hypotheses. The 1st is that wind direction influences insect dispersal (Feng et al. 2005; Leite et al. 2011a, 2015), migration (Feng et al. 2005; Leite et al. 2009, 2011b), and pollination. This stingless bee is small, usually less than 0.8 cm long and therefore more sensitive to wind than larger insects (Hilário et al. 2007). The preference for branches facing west may be due to the wind protection in that area favoring flight stability of these bees when they are searching for nectar on plants or when they rest on flowers. Body characteristics and bee physiological limitations, especially small body size, can generate visiting patterns that favor flight according to environmental factors (Antonini et al. 2005).

The 2nd hypothesis is that they are avoiding aggressive species. *Tetragonisca angustula* and *T. spinipes* are stingless bees of different genera found in the same canopy region (middle region), but at different cardinal points (*T. angustula* west and *T. spinipes* north). This could be due to *T. spinipes* being extremely aggressive and attacking

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other insects with its mandibles. *Trigona spinipes* workers show highly aggressive behavior similar to *Apis mellifera* L. (Hymenoptera: Apidae) (Brizola-Bonacina 2012). Because of this aggression, *T. angustula* avoids areas with *T. spinipes*. Despite this last species foraging at different times compared with *T. angustula* (Brizola-Bonacina 2012), the genus *Trigona* forages in groups, preventing other species from visiting flowers that they occupy (Serra & Campos 2010).

Chewing and sucking phytophagous insects, as well as predatory ants, were found to have high abundance in the upper part of the plant canopy. This may be due to 3 reasons. Firstly, young leaves, the best food for phytophagous insects, are found in the upper part of the canopy. The herbivory rates on young leaves of tropical species with higher nutritional quality may be 5 to 25 times higher than on mature leaves of lower nutritional value (Coley & Barone 1996). Large numbers of phytophagous insects, in turn, may have attracted predatory ants. Secondly, the canopy growth regions have a great number of young leaves (Hallé 1998; Bell et al. 1999; Barrios 2003) and, consequently, young extrafloral nectaries full of sugary substances that are highly attractive to ants. Thirdly, low parasitism (Ramanand & Olckers 2013) or predation (Elbanna 2011) risks from natural enemies in upper regions of the canopy could result in the preference of phytophagous insects, especially sucking insects, for these areas.

The nutritious food resource for both insect groups (new leaves for phytophagous insects and new extrafloral nectaries for ants) can explain the high presence of phytophagous insects and ants in the same area (upper part) (Oliveira & Brandão 1991; Ruhren & Handel 1999). The mutualism between ants and plants is a very subtle and complex process (Beattie 1985). There are 4 basic interactions between ants and plants: (1) ants protect plants from herbivores and other enemies, (2) ants feed on essential plant nutrients, (3) ants help with seed dispersion, and (4) ants help with pollination (Beattie 1985). Moreover, ants have a mutualistic relationship with herbivores such as mealybugs. The ants protect mealybugs from natural enemies and feed on their honeydew (Styrsky & Micky 2007).

The finding of *T. spinipes* and *T. angustula* in the middle region of the canopy is similar to reports for *Acacia mangium* Willd. (Fabaceae) (Silva et al. 2014). They likely prefer this region because there is a greater amount of available food resources in this region than in the basal and upper part of the canopy or on the tree trunk (Barrios 2003). In addition, there is lower wind intensity in the middle than in the upper part of the canopy, likely making it a more hospitable area for these insects (Leite et al. 2006). Stingless bees start nectar foraging at 5:20 AM and remain highly active until 10:00 AM (Neves & Viana 2002). This foraging strategy has 3 possible advantages: (1) protecting bees from high temperature and low humidity effects; (2) enabling the collection of non-altered trophic resources, such as nectar, which can increase its sugar concentration due to evaporation during the day (Proctor et al. 1996); and (3) enabling the finding of a greater quantity of food, a limiting factor for bees with heavily populated colonies that are active throughout the year. Acclimatization to high temperatures appears to be essential to insect survival under natural conditions (Romoser & Stoffolano 1994).

The species *T. spinipes* and *T. collaris* (phytophagous) and *Camponotus* sp.2 and *Brachymyrmex* sp. (natural enemies of larvae) were frequently observed on abaxial leaf surface. The greater number of individuals and the higher species richness, diversity, abundance, and k-dominance for phytophagous, natural enemy, and pollinator insects on the abaxial than on the adaxial leaf surface may be because leaf abaxial faces are tender, and phytophagous insects generally prefer young, soft leaves for feeding. Furthermore, the abaxial region has more salient ribbing and a slender cortex, favoring feeding mainly by sucking insects. In addition, this leaf region has better nutritional quality than the adaxial one. and sucking phytophagous insects and mites prefer the abaxial surface of upper leaves (or growth points) (Miranda et al. 1998; Silva et al. 1998; Leite et al. 1999, 2002, 2003). The resistance of the abaxial surface tissue to piercing is lower (due to the presence of lacunary parenchyma) than that of the adaxial side (with palisade parenchyma), which favors greater suction of the phloem sap on the abaxial surface (Chu et al. 1995, 2007). The densities of chewing phytophagous insects are negatively correlated with the effort they need to tear the leaves (Peeters et al. 2007). The abaxial leaf surface, with its thin epidermis, thus favors insect feeding and consequently herbivore activity (Fiene et al. 2013).

The leaf surface can also influence insect oviposition by offering protection from rain, ultra-violet radiation, and natural enemies. This protection is higher when the eggs are laid on the abaxial face and are therefore less exposed to these natural agents (Antônio et al. 2002). Larvae that feed on the abaxial leaf surface can reduce predation risks because the probability of being detected by a predator is lower on the abaxial than the adaxial surface (Krebs & Davies 1993) as reported for sucking insects and ants on *C. brasiliense* (Leite et al. 2006) and for natural enemies, phytophagous insects, and pollinators on *A. mangium* (Silva et al. 2014).

The high frequency and abundance of *T. spinipes* and *T. collaris* indicates that these species have great potential to become *L. leucocephala* tree pests. Moreover, the most frequently found genera *Camponotus* and *Brachymyrmex* are the main natural enemies in *L. leucocephala*. The results from this study can aid pest management programs that aim to utilize natural enemies in the protection of *L. leucocephala*.

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