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# The abundance of specialist and generalist lepidopteran larvae on a single host plant species: Does spatial scale matter?

Laura Braga<sup>1\*</sup> and Ivone Rezende Diniz<sup>2</sup>

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## Abstract

Specialist insects are more sensitive to spatial variations than generalists, which are able to exploit diverse hosts in various habitats. This study investigated whether specialist lepidopteran larvae feeding on a single host, *Roupala montana* Aubl. (Proteales: Proteaceae), maintain consistent abundance rates across spatial scales. We compared the abundance of specialist and generalist larvae at local and regional scales during the same period of collection, with equal sample efforts, and in the same type of vegetation, within a Brazilian savanna biome. Particularly, we focused on the following questions: Does spatial scale matter to the abundance of specialist larvae on a single host plant species? What is the relationship between the abundance of specialists and generalists among spatial scales? As predicted, in general, specialist larvae were present at higher densities on their specific host plants than generalists. However, we sought to learn how this abundance changed or did not change with spatial scale, as well as whether community similarity increased with spatial proximity. In this study, most larvae of specialist species on *R. montana* occurred at both local and regional scales, but they differed in abundance at different spatial scales. Moreover, although specialist larvae exhibited higher densities on *R. montana* than generalists, this pattern was not always consistent. The assemblage of larvae in neighboring areas showed greater mutual similarity, and there was a negative relationship between distance and similarity.

Key Words: diet breadth; Lepidoptera; spatial distribution; *Roupala montana*

## Resumo

Insetos especialistas são mais sensíveis às variações espaciais do que os generalistas, devido à sua habilidade em explorar diversas plantas hospedeiras em vários habitats. Este estudo investigou se lagartas especialistas em uma única planta hospedeira, *Roupala montana* Aubl. (Proteales: Proteaceae), tem abundância consistente através das escalas espaciais. Nós comparamos a abundância das lagartas especialistas e generalistas, em escala local e regional, durante o mesmo período de amostragem, com esforço amostral similar, e mesmo tipo de vegetação no bioma Cerrado (savana brasileira). Particularmente, as seguintes questões foram discutidas: A escala espacial importa para a abundância de lagartas especialistas em uma única planta hospedeira? Qual é a relação entre a abundância de especialistas e generalistas entre escalas geográficas? Como previsto, em geral, lagartas especialistas apresentam maiores densidades em suas plantas hospedeiras do que as generalistas. No entanto, nós queríamos avaliar as mudanças ou não na abundância das lagartas especialistas e generalistas em diferentes escalas espaciais, assim como se a similaridade entre as comunidades aumenta com a proximidade espacial. No presente estudo, a maioria das lagartas especialistas em *R. montana* ocorreu em ambas escalas, local e regional, mas suas abundâncias variaram espacialmente. Embora, em geral, as lagartas especialistas ocorram em maiores densidades em *R. montana* do que as espécies generalistas, este padrão não foi sempre consistente. As comunidades de lagartas de localidades próximas mostraram maior similaridade entre si, e a relação entre a distância e similaridade foi negativa.

Palavras Chaves: amplitude de dieta; Lepidoptera; distribuição espacial; *Roupala montana*

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Herbivorous insects exhibit a wide range of diets, from diets specializing on one plant species, genus, or family to diets that include host plants belonging to several families. However, most herbivorous insect species are specialists, and studies suggest that a high degree of specificity is characteristic of tropical herbivorous insects (Janzen 1988; Marquis 1991; Diniz & Morais 2002; Dyer et al. 2007). Several factors may affect the spatial variation of herbivorous insects (Roslin & Kotze 2005), including differences in landscape, communities of plants, soil types, diet breadth (Ødegaard 2006), variations in the chemical and physical quality of the host plant (Gaston et al. 2004; Murakami et al. 2008), composition and abundance of natural enemies (Denno et al. 2005; Gripenberg & Roslin 2007; Connahs et al. 2009), environmental

structure, and the micro- and macro-climatic conditions of each area (Gripenberg & Roslin 2005).

Insects with specialist diets are more sensitive to spatial variations than generalists because of the ability of the latter to exploit different hosts in different habitats (Gaston & Lawton 1990; Novotny & Basset 2005; Novotny & Weiblen 2005). However, in the context of a single specialist species of a single host plant, they are usually more abundant than generalists (e.g., Bendicho-López et al. 2006). The low abundance of generalist species on host plant species can be explained by the competitive exclusion of the generalists by the specialist species, predicted by the tri-trophic interaction hypothesis (Mooney et al. 2012), or by generalists' behavior of feeding only occasionally on the

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host examined, despite having high overall population levels when all host plant species occupied are considered (Novotny & Basset 2000). Nevertheless, a specialist species may be rare in the case of single host plants, particularly when the species has a genuinely low population density (Novotny & Basset 2000; Diniz et al. 2011).

Several knowledge gaps in the literature on specialized vs. generalist insects have been identified, and studies involving even simple comparisons of the communities of herbivores that feed on the same plant species at large scales are rare (Lewinsohn et al. 2005; Novotny et al. 2007). Furthermore, little is known about the identities of such species and their abundances. It is well known that the abundance of a species depends primarily on local factors (Müller et al. 2011), such that one can expect to find larger spatial variations as scales increase. However, when considering only the community of herbivores whose diet is restricted to a single host plant species in similar habitats, one may expect a more consistent pattern.

Our system of study includes the externally folivorous lepidopteran larvae that occur on a single host plant, *Roupala montana* Aubl. (Proteales: Proteaceae), in the Cerrado Biome (savanna-like vegetation). This host plant supports a rich and diverse fauna of lepidopteran species within this biome, comprising 62 species in 22 families (Bendicho-López et al. 2006). These species are well known, including their degrees of specialization (Diniz & Morais 1995, 1997; Diniz et al. 2001; Bendicho-López et al. 2003, 2006; Bendicho-López & Diniz 2004). The specialization of these larvae is not a local event; for example, there are some species, like *Stenomoma cathosiota* Meyrick (Depressariidae), that are specialists on *R. montana* in the Cerrado of Brazil (Diniz & Morais 1995, 1997; Diniz et al. 2001; Bendicho-López et al. 2006), as well as in the dry forests, rainforests, and cloud forests of Costa Rica (Janzen & Hallwachs 2004).

Many authors have suggested that the generalist habit may be more common in herbivores that have low dispersal ability, due to their difficulty in finding suitable host plants and the unpredictability of these host plants as resources (Coley & Barone 1996). In contrast, specialized species generally use abundant and easily found host plants (Jaenike 1990). Therefore, the objective of this study was to determine, for the first time, changes in the abundance of specialist larvae on *R. montana* and changes in the proportion of specialist and generalist insects at different spatial scales. The diets of both types of insects were studied during the same period of time, with equal sampling efforts, and in similar biotopes. Complementarily, we analyzed the turnover of species and the similarities of larval communities on *R. montana* between the areas, and their relationships with geographical distances.

Specifically, we addressed the following questions: Does spatial scale matter to the abundance of specialist larvae on a single host plant species? What is the relationship between the abundance of specialists and generalists among spatial scales?

Our hypothesis was that specialist larvae on *R. montana* (a group of species feeding restrictively on this host plant species) will occur consistently across spatial scales because *R. montana* is distributed widely and has a high density in the Cerrado Biome, making it an apparent and predictable resource. Thus, we expected that specialist larvae will follow the spatial distribution of the host plant with relatively high abundance.

## Materials and Methods

### STUDY AREA

The study was conducted in 5 areas of the Cerrado sensu stricto in Central Brazil, located in the states of Goiás (GO) and Distrito Federal (DF) (Fig. 1). These areas have similar vegetation types over both

oxysoils and rocky outcroppings, with altitudes ranging from 1,034 m to 1,289 m. The climate of the areas is characterized by dry winters (Apr through Sep) and wet summers (Oct through Mar), and all areas are located within protected zones. The 5 areas are as follows: 1 – Parque Estadual dos Pireneus (PEP) (Pireneus State Park), Pirenópolis, GO (15°48.033'S, 48°50.058'W); 2 – Parque Nacional Chapada dos Veadeiros (PNCV) ("Chapada dos Veadeiros" National Park), Alto Paraíso, GO (14°09.636'S, 47°47.480'W); 3 – Fazenda Água Limpa (FAL) (Experimental Farm of the Brasília University), Brasília, DF (15°57.265'S, 47°55.752'W); 4 – Parque Nacional de Brasília (PNB) (Brasília National Park), Brasília, DF (15°52.512'S, 47°49.843'W); and 5 – Jardim Botânico de Brasília (JBB) (Brasília Botanical Garden), Brasília, DF (15°54.481'S, 47°51.075'W).

Three areas were used in each comparison: PEP, PNCV, and FAL were used on a regional scale (more than 100 km away from one another), and FAL, PNB, and JBB were used on a local scale (less than 15 km away from one another) (Table 1). The distances between the areas were calculated using their geographic coordinates provided by the Sulcom Ltda Program ([http://www.sulcom.com.br/c/calculo\\_de\\_distancia.shtml](http://www.sulcom.com.br/c/calculo_de_distancia.shtml)).

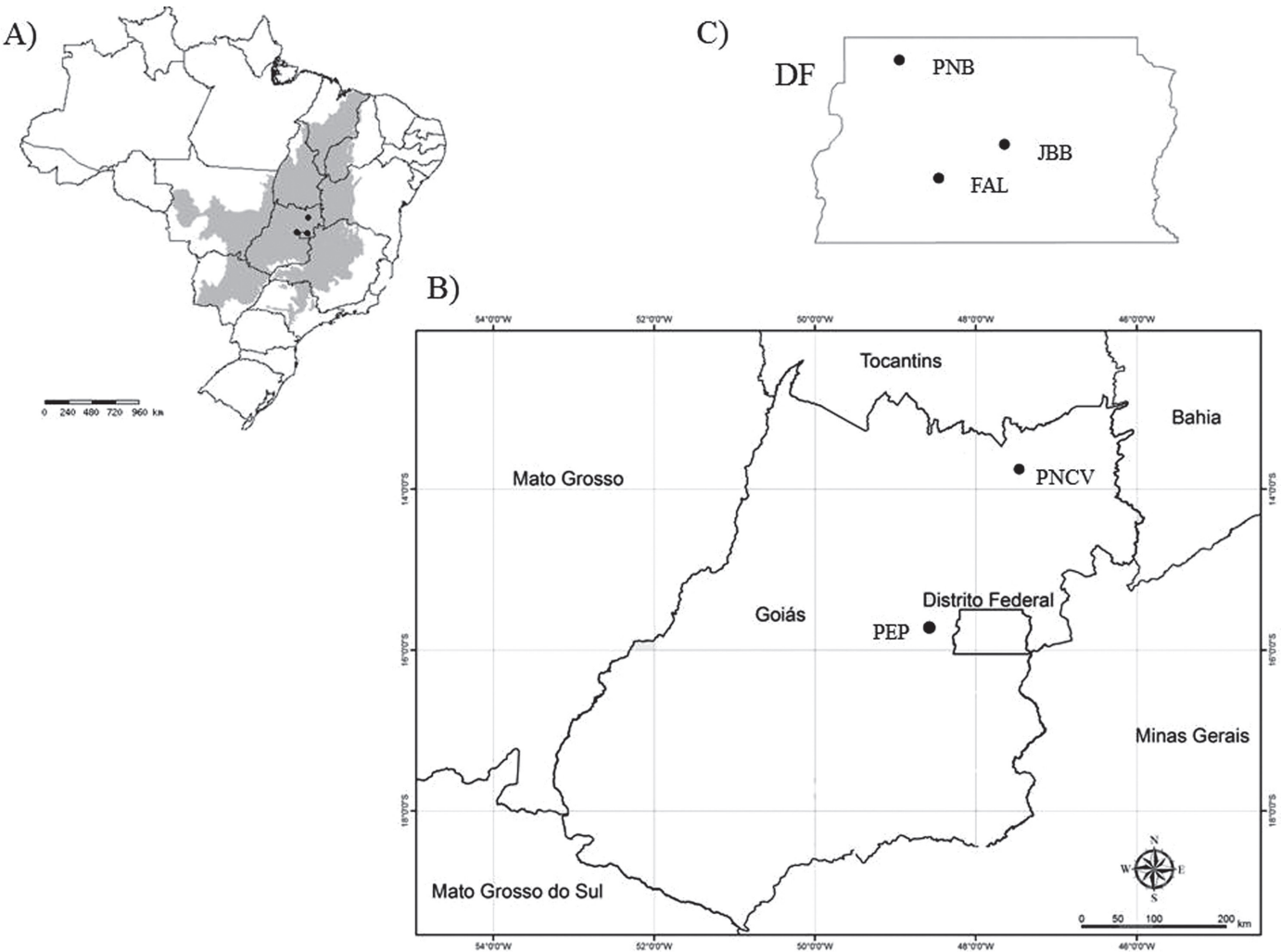
*Roupala montana* is distributed widely in the Brazilian Savanna, especially in the Cerrado sensu stricto (Felfili & Abreu 1999), and it is characterized by a shrubby or arboreal habit and a great plasticity of the leaf morphology — even in the same individual (Carvalho 2003). It is evergreen in that the old foliage persists on the tree until the emergence of new leaves (Franco 1998). As part of the early secondary successional group, it is recommended for restoring degraded ecosystems (Carvalho 2003).

In this work, we considered as specialists those species that are monophagous on *R. montana*. The host plant specialization was inferred based on a previous data set. Over the last 20 yr, surface-feeding larvae found on leaves of Cerrado plants in Brazil were collected and reared in a laboratory, and over 100,000 individuals of 150 plant species of 50 families were surveyed within the study areas. In relation to *R. montana*, over 15,000 individual plants were surveyed for larvae. This database was used to infer which species are specialists and which are generalists.

### FIELD SAMPLING

The data presented here represent a considerable investment of effort, with large numbers of trees surveyed within sites and significant quantities of larvae reared to adulthood in the laboratory for identification. Collections were made between May and Jun 2009, and they included a systematic (1 to 10 min) visual inspection time, scaled to plant size, of the foliage of 1,000 individuals of *R. montana* in each of the 5 Cerrado sensu stricto sites. This collection period coincided with the period of relative peak abundance of larvae in the Cerrado of Central Brazil (Morais et al. 1999). Samplings were made sequentially in time, with about 5 d spent in each area per month. Plant phenologies and climate factors were similar across all study areas.

Five thousand *R. montana* plants, ranging from 0.5 to 2 m in height, were inspected in the 5 study areas, each of which was 4 ha. In total, 1,186 larvae, representing 48 species of 15 families of Lepidoptera, were found on 663 of these plants (13.26%). All larvae were collected, photographed, and reared under laboratory conditions, with a 70% rearing success (although most were identified before adulthood). The larvae were raised in plastic cups and fed fresh leaves from *R. montana* plants as needed until pupation. Voucher specimens of adults were identified from comparisons with specimens in the Entomological Collection of the Department of Zoology at the University of Brasília, Brazil, where they were deposited.



**Fig. 1.** Locations of the 5 study areas, as follows: A) a map of Brazil, with the coverage area of the Cerrado Biome shaded; B) a map of Goiás State, showing the locations of Parque Estadual dos Pireneus (PEP) and Parque Nacional Chapada dos Veadeiros (PNCV); and C) a map of Distrito Federal (DF), showing the locations of Fazenda Água Limpa (FAL), Parque Nacional de Brasília (PNB), and Jardim Botânico de Brasília (JBB).

STATISTICAL ANALYSES

To verify whether there were significant differences in the heights of the *R. montana* plants, the Kruskal-Wallis test was used. Species richness was obtained by counting the number of species found at each site on 1,000 plants of *R. montana*. Pearson's chi-square was applied to compare the proportions of plant frequency with the number of larvae and to compare the abundances of specialist species between study areas. A *t*-test was performed to verify whether each specialist species occurred consistently across spatial scales. The analysis was performed using the abundance of each special-

ist species vs. that of each generalist species. The percentage of the abundance of each specialist species in relation to all individuals at a site was calculated.

The Bray-Curtis similarity index was calculated for 3 sets of data: 1) the entire assemblage, 2) only the specialist species, and 3) only the generalist species. The Mantel test was performed for the 3 sets of data to assess the significance of the relationship between beta diversity (measured as the distance from Bray-Curtis) and geographical distance (km).

Results

The differences in plant heights from the 5 areas were not significant ( $H = 420.7$ ,  $H_c = 422.8$ ,  $P < 0.05$ ). Moreover, the total abundances, species richness, and frequencies of plants with larvae varied among the different areas (Table 2). The frequencies of plants with larvae were significantly different among the areas (Pearson's  $s = 181.02$ ,  $df = 4$ ,  $P < 0.001$ ).

Six species (12.5% of the species found) were monophagous on *R. montana* in the Cerrado (Diniz et al. 2001; Bendicho-López et al. 2006) (Fig. 2), but only 4 of these species occurred in all areas (Table 3). The specialist species belong to 4 families: 1) Depressariidae,

**Table 1.** Distance in kilometers between study areas: PEP – Parque Estadual dos Pireneus (GO); PNCV – Parque Nacional Chapada dos Veadeiros (GO); FAL – Fazenda Água Limpa (DF); PNB – Parque Nacional de Brasília (DF); and Jardim Botânico de Brasília (DF).

Area	PEP	PNCV	FAL	PNB
PEP				
PNCV	215			
FAL	100	199		
PNB	108	190	14	
JBB	105	194	05	11



**Table 2.** Species richness, abundance, and frequency of plant species with lepidopteran larvae in the 5 study areas of the Cerrado (GO and DF) from May through Jun 2009. PEP – Parque Estadual dos Pireneus (GO); PNCV – Parque Nacional Chapada dos Veadeiros (GO); FAL – Fazenda Água Limpa (DF); PNB – Parque Nacional de Brasília (DF); and JBB – Jardim Botânico de Brasília (DF).

Parameter	Study area				
	PEP	PNCV	FAL	PNB	JBB
Species richness <sup>a</sup>	23	15	19	15	15
Relative abundance	672	82	154	158	120
Frequency of plants with larvae (%)	24.40	5	14.10	13.3	9.4

<sup>a</sup>Species richness was obtained by counting the number of species found at each site on 1,000 plants of *R. montana*.

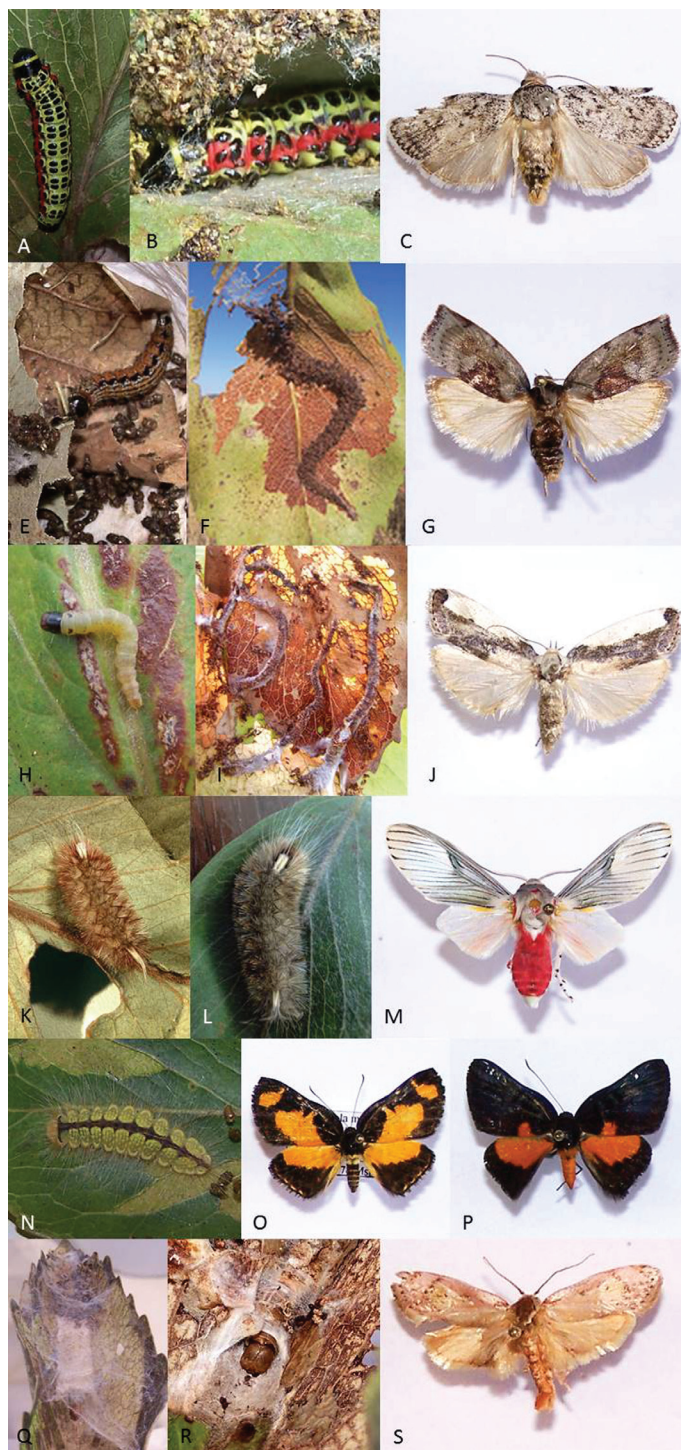
with 3 species: *Stenoma cathosiota* Meyrick, 1925, *Chlamydastis platyspora* Meyrick, 1925, and one species belonging to a new genus (Vitor Becker, pers. comm.); 2) Erebiidae (Arctiinae), with 1 species: *Idalus lineosus* Walker, 1869; 3) Riodinidae, with 1 species: *Symmachia hippodice* Godman, 1903; and 4) Oecophoridae, with 1 species: *Eomichla* sp. (Bendicho-López et al. 2006). The abundance of specialist species varied significantly among the studied areas (Pearson's = 2,364, df = 28,  $P < 0.001$ ) (Table 3). Specifically, among the specialist species that occurred in all areas, only *S. hippodice* did not significantly change in its abundance among the studied areas ( $t = 2.52$ , df = 4,  $P = 0.06$ ). All other species varied significantly in their abundances through the spatial scale (new genus of Depressariidae:  $t = 3.45$ , df = 4,  $P = 0.02$ ; *I. lineosus*:  $t = 4.80$ , df = 4,  $P = 0.008$ ; *S. cathosiota*:  $t = 3.68$ , df = 4,  $P = 0.02$ ).

Some generalist species also occurred on *R. montana* at both the local and regional scales, like *Phobetron hipparchia* Cramer, 1777 (Limacodidae), which was present in 4 of the areas, and *Episimus* sp. (Tortricidae), *Semyra incisa* Walker, 1855 (Limacodidae), and *Tautobriga glaucopis* Hampson, 1926 (Noctuidae), which were present in 3 of the 5 study areas (Table 3).

The specialist species mentioned here as a new genus of Depressariidae showed the highest abundance in PEP, representing 90.7% of the larvae of specialist species and 84% of all larvae in that area. In the PNCV, the same species had the highest abundance but represented only 28% of all larvae. In all 3 study areas at the local scale (FAL, PNB, and JBB), the most abundant species was *S. cathosiota*, representing 45.5%, 61%, and 33% of all larvae, respectively.

The ratio of the total abundance of specialist species to the total abundance of generalist species for each area varied widely. It was highest in the PEP area (14.2 individuals of specialist species for each individual of the generalist species) and was lowest in PNCV, with 1 or fewer individuals of specialist species (0.86) per 1 individual of generalist species. The local areas had similar proportions of individuals of specialist species per 1 individual of generalist species: FAL with 5.34, PNB with 7.30, and JBB with 6.87. The percentage of abundance of specialist species in relation to generalist species was high in 4 of the studied areas, with 93% in PEP, 84% in FAL, 88% in PNB, and 87% in JBB, whereas it was 46% in PNCV.

Considering the entire assemblage of larvae, the areas with the most similar faunas were FAL and JBB (Bray-Curtis = 0.77) (Table 4). The areas with the least faunal similarity were PEP and PNCV (Bray-Curtis = 0.13). The results were similar for the specialist species, with the greatest similarity between FAL and JBB (Bray-Curtis = 0.85) and the least between PEP and PNCV (Bray-Curtis = 0.11) (Table 4). However, when considering only the generalist species, the results differed in that the most similar areas were PEP and PNCV (Bray-Curtis = 0.29) (Table 4), whereas PNB and JBB (Bray-Curtis = 0) (Table 4) were entirely dissimilar.



**Fig. 2.** Specialist lepidopteran species on *Roupala montana*. (A–C) *Chlamydastis platyspora*: (A) larva, (B) larva inside the shelter, (C) adult; (E–G) *Stenoma cathosiota*: (E) larva, (F) shelter, (G) adult; (H–J) species of new genus of Depressariidae: (H) larva, (I) shelter, (J) adult; (K–M) *Idalus lineosus*: (K–L) 6th instar showing variation in color, (M) adult; (N–O) *Symmachia hippodice*: (N) larva, (O) adult female, (P) adult male; (Q–S) *Eomichla* sp.: (Q–R) larva inside the shelter, (S) adult.

The results of the Mantel similarity test showed a negative relationship in the distance between study areas and the similarities in the assemblage of larvae ( $r = -0.81$ ;  $P = 0.05$ ), and between the study areas and the specialist species on *R. montana* ( $r = -0.58$ ;  $P = 0.05$ ); however, there was no significant relationship between distance and similarity in the assemblage of generalist species ( $r = -0.08$ ;  $P = 0.4$ ).

**Table 3.** Lepidopteran species found in the study areas of the Cerrado (GO and DF), and the abundance and total number of specialist and generalist lepidopteran larvae in each area from May through Jun 2009. PEP – Parque Estadual dos Pireneus (GO); PNCV – Parque Nacional Chapada dos Veadeiros (GO); FAL – Fazenda Água Limpa (DF); PNB – Parque Nacional de Brasília (DF); and JBB – Jardim Botânico de Brasília (DF).

Type	Family	Species	Study area				
			PEP	PNCV	FAL	PNB	JBB
Specialist	Erebidae	<i>Idalus lineosus</i> Walker, 1869	19	13	40	47	35
	Riodinidae	<i>Symmachia hippodice</i> Godman, 1903	01	01	16	08	10
	Depressariidae	New genus Depressariidae	567	23	03	24	06
		<i>Stenoma cathosiota</i> Meyrick, 1925	38	01	70	60	52
		<i>Chlamydastis platyspora</i> Meyrick, 1922	2	0	0	0	0
Generalist	Oecophoridae	<i>Eomichla</i> sp.	2	0	1	0	0
	Psychidae	<i>Oiketicus kirbyi</i> Guilding, 1827	0	0	0	0	1
	Oecophoridae	<i>Inga encamina</i> (Meyrick, 1912)	0	0	3	0	1
	Depressariidae	<i>Antaeotricha</i> sp.	0	0	0	0	1
		<i>Antaeotricha</i> sp12.	0	0	6	2	0
		Depressariidae 1	1	0	0	0	0
	Gelechiidae	<i>Rhosologia</i> sp.	1	0	0	0	0
	Zygaenidae	<i>Picnotena</i> sp.	3	0	2	0	7
	Megalopygidae	<i>Megalopyge albicollis</i> (Walker, 1855)	0	0	1	3	0
		<i>Pterocladia roseata</i> (Hopp, 1922)	2	0	0	0	0
		<i>Podalia</i> sp.	2	0	0	0	0
		<i>Pterocladia</i> sp.	0	1	0	0	0
	Limacodidae	<i>Phobetron hipparchia</i> Cramer, 1777	3	2	1	0	1
		<i>Semyra incisa</i> Walker, 1855	1	0	1	1	0
		Limacodidae 1	0	1	0	0	0
	Tortricidae	<i>Episimus</i> sp.	11	25	0	0	1
		<i>Platynota rostrana</i> (Walker, 1863)	0	0	1	0	1
	Saturniidae	<i>Automeris illustris</i> (Walker, 1855)	1	0	0	0	0
		<i>Hylesia ebalus</i> Cramer, 1775	1	0	0	0	0
		Saturniidae 1	1	0	0	0	0
	Hesperiidae	<i>Chioides catillus</i> (Cramer, 1780)	0	0	0	1	0
		Hesperiidae 1	2	0	0	0	0
		Hesperiidae 2	0	0	0	1	0
		Hesperiidae 3	0	0	1	0	0
	Riodinidae	<i>Hallonympha pucipuncta</i> (Spitz, 1930)	8	0	0	0	0
		Riodinidae 1	0	0	0	1	0
	Noctuidae	<i>Tautobriga glaucopsis</i> Hampson, 1926	0	5	1	4	0
	Geometridae	<i>Stenalcidia</i> sp3.	0	0	1	0	1
		<i>Glena</i> sp1.	0	0	1	0	0
		<i>Pleuroprucha asthenaria</i> (Walker, 1861)	0	0	0	1	0
	Notodontidae	<i>Farigia magniphaga</i> (Schaus, 1928)	0	0	3	0	0
		<i>Farigia</i> sp.	0	0	1	0	0
	Erebidae	<i>Lophocampa citrina</i> (Sepp, [1843])	0	3	0	1	0
		<i>Carales astur</i> (Cramer, 1777)	0	2	0	0	0
		Erebidae: Arctiinae 1	0	0	0	0	1
		Erebidae: Arctiinae 2	0	1	0	0	0
		Erebidae: Arctiinae 3	0	0	0	1	0
	Unidentified Family	Unidentified species 1	0	0	1	0	0
		Unidentified species 2	0	2	0	0	0
		Unidentified species 3	0	1	0	0	0
		Unidentified species 4	0	0	0	0	1
		Unidentified species 5	1	0	0	0	0
		Unidentified species 6	1	0	0	0	0
		Unidentified species 7	3	0	0	0	0
		Unidentified species 8	1	0	0	0	0
		Total number of specialist larvae	625	38	129	139	103
		Total number of generalist larvae	47	44	25	19	17
		Total number of larvae (specialist + generalist)	672	82	154	158	120

**Table 4.** Bray-Curtis similarity indices between the 5 study areas of the Cerrado (GO and DF). The abundance was transformed using a square root. PEP – Parque Estadual dos Pireneus (GO); PNCV – Parque Nacional Chapada dos Veadeiros (GO); FAL – Fazenda Água Limpa (DF); PNB – Parque Nacional de Brasília (DF); and JBB – Jardim Botânico de Brasília (DF).

Comparison	Area	PEP	PNCV	FAL	PNB
Total fauna	PNCV	0.135			
	FAL	0.160	0.169		
	PNB	0.200	0.358	0.744	
	JBB	0.174	0.228	0.774	0.727
Specialist species	PNCV	0.114			
	FAL	0.163	0.214		
	PNB	0.213	0.422	0.816	
	JBB	0.175	0.298	0.858	0.824
Generalist species	PNCV	0.299			
	FAL	0.119	0.059		
	PNB	0.034	0.167	0.250	
	JBB	0.167	0.066	0.293	0.000

# Discussion

Abundant species at a small spatial scale are expected to repeat similar patterns at larger scales (Collins & Glenn 1990). However, it is known that relative species abundance presents spatial variation, such that a species can be rare in some places and frequent in others (Gaston 1994). Most specialist species on *R. montana* occurred at both local and regional scales, but with spatial variation in abundance; thus, our expectations were not confirmed, because the abundance of specialists was unstable and unpredictable. These results show that some specialist species can be sparse or rare locally as seen in *S. cathosiota* and the new genus of Depressariidae, which were rare in only 1 study area. The species *I. lineosus*, *S. cathosita*, and *S. hippodice* had abundances that were most similar between the closest study areas (FAL, JBB, and PNB), which shows that spatial scale mattered for variations in the abundance of the specialist lepidopteran species. However, the pattern of abundance of the generalist species was consistent, such that the 4 species of generalists present at most scales occurred with consistently sparse abundance on *R. montana*.

The relative role of the quality, among other characteristics, of the host species in generating patterns of specialist insect distribution can be explained when considering only a single plant species at one particular spatial scale (Gripenberg & Roslin 2005). This was done in this study by reducing the focus to a single host plant species in the same type of biotope. Plant chemistry also plays an important role in determining the range of plants that can be exploited by an insect species (Jaenike 1990). *Roupala montana* is known to contain several secondary compounds, such as glycosylated flavonoids (Cunha et al. 2011); thus, even if a host plant is abundant and apparent, it is unknown whether there is variation in the concentrations of certain secondary compounds among the studied areas. Another important issue concerns tri-trophic interactions, i.e., the trophic interactions between plants, herbivores, and predators or parasitoids. Specifically, we do not know whether the pressures of natural enemies vary across spatial scales. Thus, a multitude of factors may be related to the variation in the distribution of specialist species among the studied areas, potentially including, for example, dispersal ability of species, spatial variation in host-plant quality, types and relative abundances of natural enemies, and local environmental factors (Novotny & Weiblen 2005). These factors need to be better explored to achieve a better understanding of the pattern of spatial distribution of these specialist lepidopteran species on *R. montana*.

As predicted, at all scales, specialist species occurred in greater densities on *R. montana* than generalist species. Previous local datasets on lepidopteran species in the Cerrado showed that generalists occurred at sparse densities on various host plants and that identified “specialists” were never found to feed occasionally on other hosts (25 yr Cerrado dataset). In the present study, with the exception of PNCV, the abundance of specialist species represented most of the total abundance of species in all study areas. One interesting issue that should be taken into consideration is the choice of host plants for oviposition by female generalists. Some studies have shown that the female generalists of Lepidoptera may not select the most favorable host for the growth and development of their offspring (Bernays 2001). This suboptimal behavior compromises the competitive ability and abundance of the generalist species. Thus, specialists have an advantage of accuracy in relation to the choice of host plants and the development of the offspring, which favors a high abundance on their host plants. Furthermore, some generalist larvae can specifically mix foods on some occasions and can change host plants during development (Gaston et al. 1991), making the abundance of these species on a given plant unstable.

Cerrado vegetation has great heterogeneity (Ribeiro & Walter 1998) and beta diversity, due to the differences in the composition and density of plant species between sites, even in proximate regions that are considered to be homogeneous (Lindoso & Felfili 2007; Silva Júnior & Sarmiento 2009). Consequently, the Cerrado Biome has great diversity of insect herbivores, because the beta diversity among these insect species is obviously related to turnover among host plants (Ødegaard 2006). In this study, most of the generalist species were rare on the *R. montana* host plant, and many occurred in only 1 area, which contributed to little similarity between areas. Consequently, there was no relationship between distance and similarity when only these species were considered. This result likely reflects the heterogeneity and the “turnover” of plant species between areas, because the generalist species also have affinities to host plant species of families other than Proteaceae, which includes *R. montana*.

Some studies have indicated that similarities between communities often decrease with increasing geographic distance (Camargo 1999; Nekola & White 1999; Ferro & Diniz 2007; Novotny et al. 2007), whereas other studies have not found a strong relationship between community similarity and geographic distance (Harrison et al. 1992; Beck & Khen 2007). The negative relationship between distance and similarity is implicit in several ecological and evolutionary phenomena (Nekola & White 1999), such as the dispersal capacity of a species (Singer & Wee 2005), isolation and habitat size, and a species’ history



of colonization and extinction (Nekola & White 1999). Local environmental variables, such as climate, soil, elevation, and topography (Müller et al. 2011), are also likely to be significant; however, these were not objects of this study. Our results suggest a negative relationship between the similarities of species assemblages and geographical distances between areas, both when considering the full community of larvae and when considering only specialist species. This trend is reinforced by the high Bray-Curtis similarity index values between neighboring areas. The floristic and faunal similarities are greater between closer than more distant fragments (Colli et al. 2003). Likewise, the ratio of colonization decreases with the distance between conspecific populations (Tscharntke & Brandl 2004). Thus, the connectivity between the areas of FAL and JBB may also explain the high similarity of the communities of lepidopteran species associated with *R. montana* plants in these areas.

Our study is unique in that it is based on a large assemblage of lepidopteran species that feed on the same plant species across a broad geographic scale. The key issue is: Does spatial scale matter to the abundance of specialist species on a single host plant species? The answer is yes, because we found that the abundance of specialist species was inconsistent across spatial scales. Even the proportion between specialist and generalist species was not as expected, because it was not always consistent with a variation between 46 and 93%; these findings indicate that local mechanisms had strong effects on the lepidopteran species abundance. Aspects of community structure, such as species composition and abundance, were variable and local. Our study also raised questions regarding why some aspects of community structure are more spatially robust than others. The study results seem consistent with findings at broader scales, such as tropical/temperate comparisons of larval diet breadth (e.g., Dyer et al. 2007), which showed that tropical communities have greater representation of specialists than temperate communities. Yet, there is much species turnover among various tropical communities as well as among various temperate communities. Our findings support the hypothesis that specialist lepidopteran species on *R. montana* are maintained across a regional scale but that the abundance of these species varies greatly across geographical spatial scales (Connahs et al. 2009). They also reiterated — even when considering a single host plant — that the abundance of species depends primarily on local phenomena (Müller et al. 2011). Therefore, the presence of a host plant alone is not a good predictor for spatial distribution patterns of specialist lepidopteran species.

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