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

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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), mantêm uma abundância consistente através das escalas espaciais. Nós comparámos 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

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
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, *Roupaula montana* Aubl. (Proteaeae), 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 *Stenoma 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 specialists and generalists in 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

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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 specialist 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, *Hc* = 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 *r* = 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,
Species richness with 3 species: (1) Erebidae (Arctiinae), with 1 species: *Symma-
chis hippodice* Godman, 1903; and 3) Riodinidae, with 1 species: *Symma-
chis 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 $r = 4.80$, df = 4, $P = 0.008$; *S. cathosiota*: $t = 3.45$, 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 (Limi-
macodidae), which was present in 4 of the areas, and *Episimus* sp. (Tor-
tricidae), *Semyla 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.

The results of the Mantel similarity test showed a negative relationship in the distance between study areas and the similarities in the assem-
blage 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 ($r = -0.08; P = 0.4$).

\begin{table}[h]
\centering
\begin{tabular}{|l|c|c|c|c|c|}
\hline
\textbf{Parameter} & \textbf{PEP} & \textbf{PNCV} & \textbf{FAL} & \textbf{PNB} & \textbf{JBB} \\
\hline
Species richness$^*$ & 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 \\
\hline
\end{tabular}
\caption{Species richness, abundance, and frequency of plant species with
\lepidopteran larvae in the 5 study areas of the Cerrado (GO and DF) from May
\textit{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 Brasilia (DF); and JBB – Jardim Botânico de Brasilia (DF).}}
\end{table}
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                                      | PEP  | PNCV | FAL  | PNB  | JBB  |
|---------------|-------------------------|----------------------------------------------|------|------|------|------|------|
| Specialist    | Erebidae                | *Idalus lineosus* Walker, 1869               | 19   | 13   | 40   | 47   | 35   |
|               | Riodinidae              | *Symmachia hippodice* Godman, 1903           | 01   | 01   | 16   | 08   | 10   |
|               | Depressariidae          | New genus Depressariidae                     | 567  | 23   | 03   | 24   | 06   |
|               |                         | *Stenoma cathosiosa* Meyrick, 1925           | 38   | 01   | 70   | 60   | 52   |
|               |                         | *Chlamydasis platyspora* Meyrick, 1922       | 2    | 0    | 0    | 0    | 0    |
|               |                         | *Eomichla* sp.                              | 2    | 0    | 1    | 0    | 0    |
| Generalist    | Psychidae               | *Oikiticus kirbyi* Guilding, 1827            | 0    | 0    | 0    | 0    | 1    |
|               | Oecophoridae            | *Inga encamina* Meyrick, 1912                | 0    | 0    | 3    | 0    | 1    |
|               | Depressariidae          | *Antaeotricha* sp.                           | 0    | 0    | 0    | 0    | 1    |
|               |                         | *Antaeotricha* sp12.                         | 0    | 0    | 6    | 2    | 0    |
|               |                         | *Depressariidae* 1                          | 1    | 0    | 0    | 0    | 0    |
|               | Gelechiidae             | *Rhosologia* sp.                            | 1    | 0    | 0    | 0    | 0    |
|               | Zyggaenidae             | *Picnotena* sp.                             | 3    | 0    | 2    | 0    | 7    |
|               | Megalopygidae           | *Megalopyge albicollis* (Walker, 1855)       | 0    | 0    | 1    | 3    | 0    |
|               |                         | *Pterocladia roseata* (Hopp, 1922)          | 2    | 0    | 0    | 0    | 0    |
|               |                         | *Podalia* sp.                               | 2    | 0    | 0    | 0    | 0    |
|               | Limacodidae             | *Phobetron hipparchia* Cramer, 1777          | 3    | 2    | 1    | 0    | 1    |
|               |                         | *Semyra incisa* Walker, 1855                | 1    | 0    | 1    | 1    | 0    |
|               |                         | *Limacodidae* 1                             | 0    | 1    | 0    | 0    | 0    |
|               | Tortricidae             | *Episimus* sp.                              | 11   | 25   | 0    | 0    | 1    |
|               |                         | *Platynota rostrana* (Walker, 1863)         | 0    | 0    | 1    | 0    | 1    |
|               | Saturniidae             | *Automeris illustris* (Walker, 1855)        | 1    | 0    | 0    | 0    | 0    |
|               |                         | *Hylesia ebalus* Cramer, 1775               | 1    | 0    | 0    | 0    | 0    |
|               |                         | *Saturniidae* 1                             | 1    | 0    | 0    | 0    | 0    |
|               | Hesperiidae             | *Chioides catillus* (Cramer, 1780)          | 0    | 0    | 0    | 1    | 0    |
|               |                         | *Hesperidae* 1                              | 2    | 0    | 0    | 0    | 0    |
|               |                         | *Hesperidae* 2                              | 0    | 0    | 0    | 1    | 0    |
|               |                         | *Hesperidae* 3                              | 0    | 0    | 1    | 0    | 0    |
|               | Riodinidae              | *Halonympha pucipuncta* (Spitz, 1930)        | 8    | 0    | 0    | 0    | 0    |
|               |                         | *Riodinidae* 1                              | 0    | 0    | 0    | 1    | 0    |
|               | Noctuidae               | *Tautobriga glaucops* Hampson, 1926          | 0    | 5    | 1    | 4    | 0    |
|               | Geometridae             | *Stenalcidia* sp3.                          | 0    | 0    | 1    | 0    | 1    |
|               |                         | *Glena* sp1.                                | 0    | 0    | 1    | 0    | 0    |
|               |                         | *Pleuroprucha asthenaria* (Walker, 1861)    | 0    | 0    | 0    | 1    | 0    |
|               | Notodontidae            | *Farigia magniphaga* Schaus, 1928            | 0    | 0    | 3    | 0    | 0    |
|               |                         | *Farigia* sp.                               | 0    | 0    | 1    | 0    | 0    |
|               | Erebididae              | *Lophocampa citrina* (Spp, [1843])          | 0    | 3    | 0    | 1    | 0    |
|               |                         | *Carales astur* (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  |
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. cathosiotata and the new genus of Depressaridae, which were rare in only 1 study area. The species I. lineosus, S. cathosiotata, 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 distributions 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). Rougala 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 higher 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 & Sarmento 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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