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Galling inducing insects associated with a tropical shrub: The role of resource concentration and species interactions

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Abstract. Gall-forming insects are sophisticated sedentary herbivores that present high level of specificity with host plant, but their performance can be affected by biotic and abiotic factors. In this study we have tested two predictions: a) plants that have a greater number of conspecific neighbors have greater richness and abundance of gall-forming insects, and b) interspecific competition is a force capable of shaping the organization of gall-forming insect communities in super-host plants. We used the *Copaifera oblongifolia* (Fabaceae)/galling insects' system to test these predictions. Fieldwork was carried out in areas of Cerrado (Brazilian Savanna) in northern Minas Gerais, Brazil. To test the first hypothesis, we evaluated with generalized linear mixed models, the effects of the number of conspecific neighbors on the richness and abundance of galls associated with 67 *C. oblongifolia* individual plants belonging to two populations. To test the second hypothesis, we used null models to evaluate whether a plant of *C. oblongifolia* colonized by a species of gall is preferred or avoided by another species of gall. A total of 2901 gall-forming insects belonging to 15 species were collected from the host plant *C. oblongifolia*. We observed negative relationships between the number of conspecific neighbors and the abundance and richness of gall-forming insects associated *C. oblongifolia*. Thus, our data did not support the resource concentration hypothesis. Instead, we used the resource dilution theory to explain the negative relation between resource concentration and frequency of attack by galling insects. Our results also showed that the co-occurrence pattern of gall-forming insects in the host plant did not differ from those expected by chance. Therefore, the structure of the gall-forming insect community associated to single *C. oblongifolia* plants cannot be attributed to deterministic factors such as interspecific competition.

[Keywords: community structure, gall-forming insect diversity, insect competition, null models, resources dilution]

Resumo. Diversidade de insetos galhadores associados com um arbusto tropical: efeitos da concentração do recurso e das interações interespecíficas. Os insetos galhadores são herbívoros sedentários sofisticados que apresentam alto nível de especialização com sua planta hospedeira, mas sua performance pode ser afetada por fatores bióticos e abióticos. Neste estudo nós testamos duas hipóteses: a) plantas que possuem maior número de vizinhos coespecíficos apresentam maior riqueza e abundância de insetos galhadores, e b) a competição interespecífica é uma força capaz de molda a organização das comunidades de insetos herbívoros associados com uma planta super-hospedeira. O sistema *Copaifera oblongifolia* (Fabaceae)/ insetos galhadores associados foi usado para testar estas hipóteses. Os trabalhos de campo foram desenvolvidos em áreas de Cerrado do norte de Minas Gerais, Brasil. Para testar a primeira hipótese, nós avaliamos, com modelos lineares generalizados de efeitos mistos, os efeitos do número de vizinhos coespecíficos na riqueza e abundância de galhas associadas com 67 arbustos de *C. oblongifolia* pertencentes a duas populações. Para testar a segunda hipótese, nós usamos modelos nulos para avaliar se um arbusto de *C. oblongifolia* colonizado por uma espécie de inseto galhador é preferido ou evitado por uma outra espécie de inseto galhador. Um total de 2901 insetos galhadores pertencentes a 15 diferentes espécies foi coletado nos 67 arbustos de *C. oblongifolia*. Nós observamos uma relação negativa entre o número de vizinhos coespecíficos e a riqueza e a abundância de insetos galhadores associados com *C. oblongifolia*. Assim, nossos resultados não corroboraram a hipótese da concentração do recuro e nós usamos a teoria da diluição do recurso para explicar este resultado. Nossos resultados também mostraram que o padrão de co-ocorrência dos insetos galhadores na planta hospedeira não diferiu daquele esperado pelo acaso. Portanto, a estrutura da comunidade de insetos galhadores associada com *C. oblongifolia* não pode ser atribuída a eventos determinísticos com a competição interespecífica.

[Palavras chave: competição entre insetos herbívoros, diversidade de insetos galhadores, estrutura de comunidade, modelos nulos, diluição do recurso]

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INTRODUCTION

Galls or cecydias are tumors resulting from hypertrophy and hyperplasia of plant cells in response to the action of cecidogenic agents such as insects, fungi, bacteria and viruses (Fernandes and Martins 1985; Bergamini et al. 2017). The formation of insect galls promotes morphological and physiological changes in plants that begin soon after the female galling insect lays her eggs in the plant tissue (Arduim and Kraus 2001; Höglund 2014). The gall-forming insects can be found in different organs of the plant, such as leaves, stems and roots (Stone and Schönrogge 2003; Carneiro et al. 2009). The gall-forming insects present high specificity with the host plant and the organ of the plant (Price et al. 1987; Araújo et al. 2017). In general, each species of insect induces galls with their own characteristics (i.e., shape, size, color and hairiness), that can be used as a way of identifying the gall-forming species (Maia et al. 2008; Stone and Schonrogge 2003; Coelho et al. 2017). Although the larvae of the gall-forming insects grow protected within plant tissues, their performance can be affected by local microclimatic variations (Fernandes and Price 1985; Coelho et al. 2017), natural enemies (Fagundes et al. 2005; Maia and Azevedo 2009), architecture (Espirito-Santo et al. 2007; Costa et al. 2010) and host plant density (Araújo and Guilherme 2012), as well as by interactions occurring within the same trophic level (Kaplan and Denno 2007; Cornelissen et al. 2013; Fagundes et al. 2018).

Specifically, the hypothesis of resource concentration (Root 1973) suggests that more concentrated resource patches present greater diversity of herbivorous insects. This relationship occurs because herbivores locate more concentrated patches of resources more easily and take longer to feed and reproduce in these patches (Tahvanainen and Root 1972; Root 1973; Ralph 1977). The hypothesis of resource concentration has implications for applied entomology as well as community ecology (Rhainds and English-Loeb 2003; Otway et al. 2005; Souza and Fagundes 2017). Studies on tropical and temperate habitats tend to corroborate the hypothesis of resource concentration (Rhainds and English-Loeb 2003; Cuevas-Reyes et al. 2004; Fleck et al. 2007). However, herbivore responses to resource concentration may be affected by the degree of herbivore-host specialization, herbivore dispersal ability and interspecific interactions occurring within and between trophic levels (Joshi et al. 2004; Otway et al. 2005). Thus, lack of correlation (Grez and Gonzales 1995; Kuchenbecker and Fagundes 2018), or even negative relationships (Marques et al. 2000; Yamamura 2002; Souza and Fagundes 2017) between resource concentration and herbivore diversity have also been documented.

The role of competition in the organization of herbivorous insect communities is one of the topics most discussed by ecologists (Reitz and Trumble 2002; Kaplan and Denno 2007). Recently, some studies have shown that competition may affect the community organization of sedentary herbivores such as leaf-mining and gall-forming insects (Kaplan and Denno 2007; Tack et al. 2009; Santos and Fernandes 2010; Cornelissen et al. 2013). When experimental manipulations are not possible, comparing observed patterns of co-occurrence with patterns that may occur at random is a conventional technique for interspecific competition studies (Cornelissen and Stiling 2008; Morin et al. 2011). Many authors have used co-occurrence analyzes to test the role of competition in organizing herbivore insect communities in their host plants (e.g., Tak et al. 2010; Jennings et al. 2010; Cornelissen et al. 2013). In these cases, although the resource seems not to be limiting, the short temporal window that involves the phenology of the species (leaf-flushing of the host plant and adult hatching) has a strong role in the interactions between gall-forming species and are able to shape the organization of gall-forming insect communities (Cooley et al. 2003; Fagundes et al. 2018).

Characterizing the insect community structure and discussing the mechanisms that determine the organization of insect communities associated with super-host plants (sensu Veldtman and McGeoch 2003) produce important insights for both applied entomology and community ecology (Yamamura 2002; Cornelissen and Stiling 2008; Costa et al. 2016). *Copaifera oblongifolia* (Fabaceae) is a shrub that can be classified as a super-host for galling insects. We used this system to test two predictions regarding the hypothesis of resource concentration and interspecific competition among herbivorous insects, respectively: a) plants that have a greater number of conspecific neighbors present greater richness and abundance of gall forming insects that plants in less dense patches, and b) interspecific competition among gall-forming insects is a force capable of shaping the organization of the gall-forming insect communities into super-host plants, leading to assumption that gall forming insects on host plants is different from expected by chance.

MATERIALS AND METHODS

Study area

The study was conducted in a rural area of the municipality of Jequitaí (17°13′56′′ S - 44°26′9′′ W), North of Minas Gerais, Brazil. The region is located in the transition between the Cerrado and Caatinga biomes. The climate of the region is classified as Tropical Savanna Climate (Aw), with dry winters and wet summers. The average annual temperature is 23.2 °C and the average precipitation is approximately 1000 mm/year, mainly from November to February (Alvares et al. 2014; Kuchenbecker and Fagundes 2018). In this region, two populations of *Copaifera oblongifolia* were selected for data collection. The first population occurred in an abandoned pasture and the second occurred in an area of deforested Cerrado in the early stage of regeneration. These populations were approximately 8 km apart. The soil where the two populations occurred was classified as dystrophic (dystrophic red-yellow latosol with sandy texture). The two populations showed the same plant density (deviance=0.048, P=0.2568) and were similar in phenology and plant size.

The studied system

Copaifera oblongifolia Mart. (Fabaceae), popularly known as Pau d'ólinho, is a shrub that reaches up to 2.5 m in height. This shrub produces new leaves between July and September, flowering occurs from February to May and fruits mature from August to October (Veloso et al. 2017). In areas of the Cerrado, in central Brazil, *C. oblongifolia* occurs in open areas such as abandoned pastures, borders of Cerrado fragments and cultivated areas. In these areas, the shrub occurs in patches, reaching high densities and often inhibits the development of other plants (Veloso et al. 2017). This species supports a high richness of gall-forming insects that can be found in the leaves and branches of the host plant (MF, personal observations).

Fieldwork

Fieldwork was carried out during the summer of 2018 (January to February). This study period was selected because leaves of host plant are mature and galls were fully developed. A total of 67 plots of 25 m² (5 x 5 m) were demarcated in the two populations of *C. oblongifolia* selected for the study (36 in the deforested Cerrado area and 31 in the abandoned pasture area also within the Cerrado biome). These plots were at least 30 m apart from each other. The center of each plot was represented by the target plant (*C. oblongifolia* specimen used for sampling richness and abundance of galls). As a measurement of the resource concentration, we counted the number of individuals of *C. oblongifolia* present in each plot to determine the density of *C. oblongifolia* plants per plot (number of individuals/m²). Finally, the target plant of each plot was cut at ground level, individually placed inside a plastic bag and taken to the Conservation Biology Laboratory of the Montes Claros State University (UNIMONTES) where the whole plants were examined and gall-forming species richness and abundance were determined for each individual plant. Galling insect species were identified according to the external morphology of galls (see Costa et al. 2016).

Statistical analyses

In order to test the first hypothesis (plants with the highest number of conspecific neighbors present greater gall-forming insect richness and abundance), Generalized Linear Mixed Models (GLMM's) were constructed where the richness or abundance of gall-forming insects was used as response variable and the density of plants per plot was used as explanatory variable, assuming a Poisson distribution and populations sites (abandoned pasture and deforested Cerrado habitats) as a random effects. These models were tested with Analysis of Variance (ANOVA) comparing the original models with the null models through the chi-square test. These analyzes were performed using the lmer package in the R software.

The second hypothesis (interspecific competition among gall species is a force capable of shaping the organization of gall-forming insect communities in super-host plants) was tested through the analysis of null models. In this case, the null models were used to compare observed and expected co-occurrence patterns of galls in the target plants of each *C. oblongifolia* population. The C-scores index (Stone and Roberts 1990), calculated on the basis of the presence/absence of galls matrix by target plant, was used to quantify the co-occurrence of gall-forming insects. The null hypothesis is that the presence of a species of gall-forming in the plant does not influence the occurrence of other species of gall-forming in the same plant. When the calculated co-occurrence index values for the original data matrix (observed C-score) fall out of 95% of the C-scores found in the randomized matrices (calculated C-score) the null hypothesis should be rejected. Thus, we assume that the distribution of gall in plants is different from chance and must be determined by biological interactions (Ribas and Schoereder 2002; Cornelissen et al. 2013). These analyzes were performed using the Ecosim software.

Results

A total of 2901 galls belonging to 15 gall-forming species were collected from the 67 *C. oblongifolia* target plants. The most abundant gall-forming insects were G13, G1 and G2, respectively representing 45%, 14% and 11% of the total abundance of galls sampled. The most frequent gall-forming insects were G13, G2 and G1, occurring, respectively, in 89%, 80% and 72% of the plants sampled. Most of

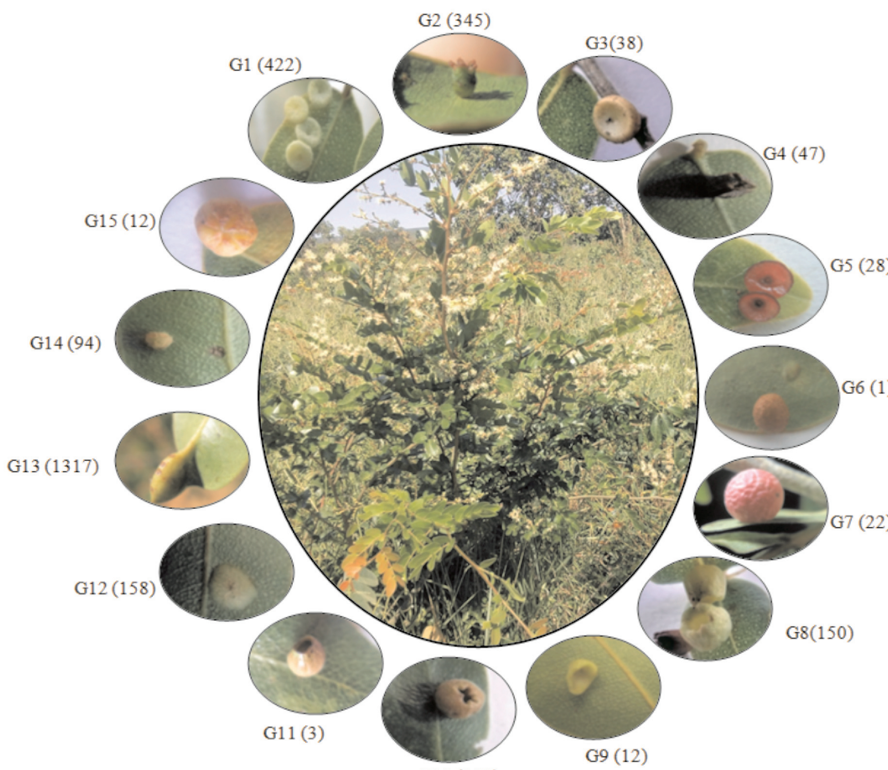

Figure 1. Morphological characterization of host plant and galls associated with *Copaifera oblongifolia* (Fabaceae). The numbers in parenthesis show the abundance of each gall collected from 67 plants.

Figura 1. Caracterização morfológica da planta hospedeira e das galhas associadas com *Copaifera oblongifolia* (Fabaceae). Os números entre parêntesis indicam a abundância de cada galha coletadas nas 67 plantas.

Table 1. C-score indices of the randomized and observed matrices for galling insects associated with 67 plants of two populations of *Copaifera oblongifolia* located at abandoned pasture and deforested Cerrado. The minimum and maximum values of the indices calculated for 5000 randomized matrices are showing together with the observed index and *P*-values in two-tailed tests (obs=observed values, exp=expected values).

Tabela 1. Índices de C-score das matrizes randomizadas e observada de insetos galhadores associados com 67 arbustos de duas populações de *Copaifera oblongifolia* localizadas em pastagem abandonada e Cerrado em regeneração. Os valores mínimos e máximos dos índices calculados para 5000 matrizes randomizadas são mostrados juntos com o índice observado e os valores de *P* de um teste bicaudal.

Populations	C-scores of randomized matrices		Observed C-scores	*P*-values	
	minimum	maximum		obs<exp	obs>exp
Abandoned pasture	18.011	21.583	19.628	0.475	0.541
Deforested Cerrado	24.272	27.477	26.218	0.710	0.296

the gall-forming insects occurred in the leaves (94% of the species) and only one gall-forming insect, G3, was observed in the stems of the host plant (Figure 1).

The richness (deviance=245.16, chi-sq=4.315, P=0.037) (Figure 2A) and abundance (deviance=2521.1, chi-sq=68.041, P<0.001) (Figure 2B) of gall-forming species per plant showed negative relationships with the density of plants per plot. Therefore, plants located in patches with more concentrated resources presented lower richness and abundance of gall-forming species than plants located in less dense plots.

The observed values of the co-occurrence index (C-score index) did not differ from the co-occurrence index values of the simulated matrices in the two studied populations (Table 1, Figure 3). Hence, these results corroborate the null hypothesis and indicate that interspecific interactions cannot be used to explain the organization of the gall-forming insect communities associated with *C. oblongifolia* in these populations.

DISCUSSION

Recent surveys indicate that several species of the *Copaifera* genus are colonized by a

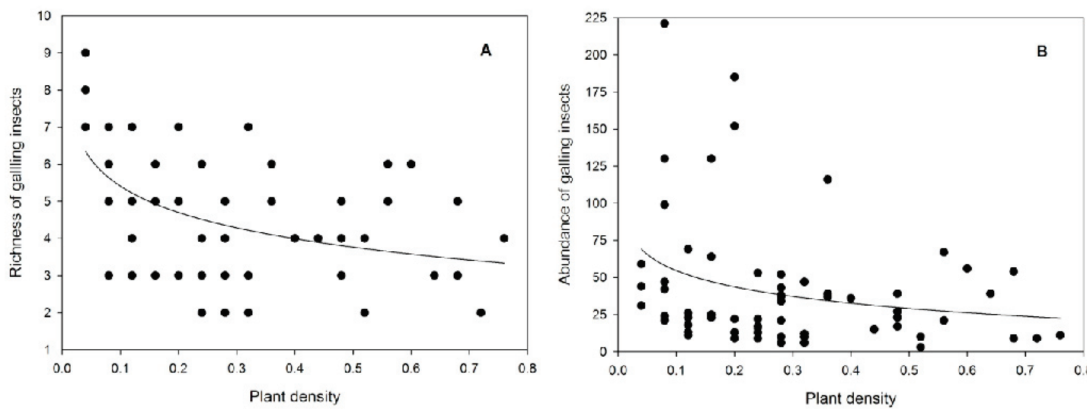

Figure 2. The effects of resource concentration (number of conspecific plants per square meter) on richness (A) and abundance (B) of galling insects associated with *Copaifera oblongifolia*.

Figura 2. Efeitos da concentração do recurso (número de plantas coespecíficas por metro quadrado) na riqueza (A) e abundância (B) de insetos galhadores associados com *Copaifera oblongifolia.*

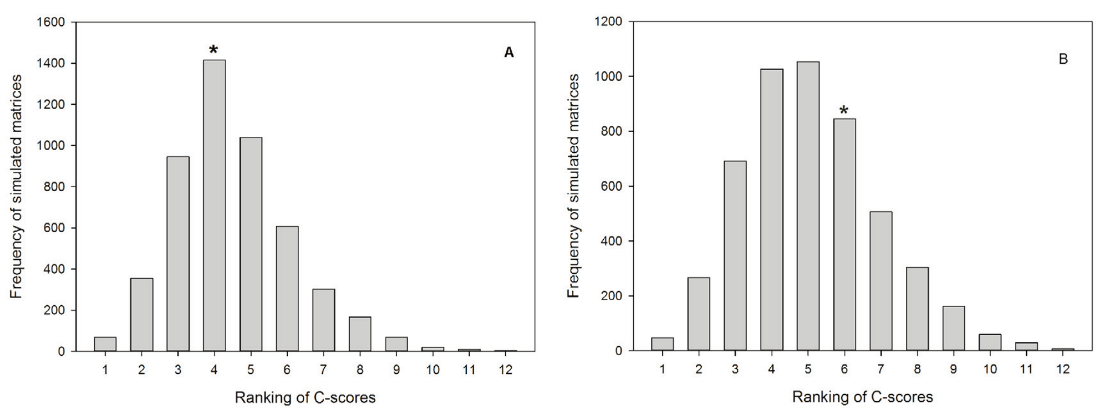

Figure 3. Frequency of simulated matrices, using fixed-fixed models, based on co-occurrence of galling insects associated with *Copaifera oblongifolia* plants in two populations of host plant located in abandoned pasture (a) and deforested Cerrado (b). The asterisk indicates where the observed C-scores coincided with the frequency class of the C-scores of the 5000 simulated matrices. See also table 1 with the observed C-scores and the minimum and maximum values of the simulated C-scores for each plant population.

Figure 3. Frequência das matrizes simuladas, usando modelos fixo-fixo, baseada na co-ocorrência de insetos galhadores associados com *Copaifera oblongifolia* em duas populações da planta hospedeira localizadas em (pastagem abandonada (A) e Cerrado em regeneração (B). Os asteriscos indicam onde o índice de C-score observado coincidiu com a classe de frequência do C-score simulado para 5000 matrizes. Veja também a tabela 1 mostrando os valores mínimos e máximos do valores de C-Score das matrizes simuladas para cada população da planta hospedeira.

diverse fauna of gall-forming species (Costa et al. 2016; Santos et al. 2017; Fagundes et al. 2018). Although host specificity is a striking feature of gall-forming insects (Carrneiro et al. 2009), there is a possibility that the same species of gall-forming insect attacks hosts that are phylogenetically close (Stireman et al. 2005). Failures in oviposition between host phylogenetically close are important mechanism of radiation and speciation of galling insects (Cooley et al. 2003; Stireman et al. 2005; Egan and Ott 2007; Whipple et al. 2009; Johansson et al. 2015). Among the 15 gall-forming insects found on *C. oblongifolia* in this study, 12 had been recorded on *C. langsdorffii* in previous study (see gall associated with *C. langsdorffii* in Costa et al. 2016), a sympatric species in the studied region. Thus, it is likely that the high diversity and similarity of gall-forming insects occurring in these two *Copaifera* species may be associated with irradiation events between the two host plant species.

Our results showed that plants with the highest number of neighbors presented lower richness and abundance of gall-forming insects, rejecting the hypothesis of resource concentration (Root 1973). Negative relationships between the concentration of the resource and the attack of insect herbivores are generally observed when the resources occur in high concentration and herbivore insects have low dispersion ability (Marques et al. 2000; Yamamura 2002). Low dispersion ability of insect precludes migration for more distant host, making female insects concentrate egg laying in a single host plant. Alternatively, when the resource is highly concentrated (high number of conspecific neighbors), migration of female insects can occur more frequently among nearby plants, diluting the egg laying effect among these neighboring plants (Rhainds and English-Loeb 2003; Otway et al. 2005). Thus, plants located in plots with high density of the host plant should present lower richness and abundance of galls due to the dilution of the attack of the female gall-forming insects among nearby plants, as observed in this study.

Systems formed by super-host plants and herbivores of sedentary lifestyle are ideal for the study of interspecific competition using null models (Kaplan and Denno 2007; Cornelissen et al. 2013). The competition for the most suitable oviposition sites among female gall-forming insects may be a limiting resource that generates a community pattern shaped by competition (Cornelissen et al. 2013). Dispute for oviposition sites should occur among herbivorous insects when environmental factors allow insect populations to reach high densities in relation to the availability of resources (Cornelissen and Stiling 2008; Kruger et al. 2010). Unlike other recent studies involving super-host plants and gall-forming insects (e.g., Cornelissen et al. 2013; Fagundes et al. 2018), our results did not corroborate the idea that competition is a shaping force for gall-forming insect communities on *C. oblongifolia*. Our study system is characterized by the high density of the host plant and the possibility of the female galling insects to migrate among nearby plants in search of more suitable sites of oviposition. In this case, the competition for oviposition sites would be minimized within each plant justifying the similarity between the observed and expected indexes found in the two populations of *C. oblongifolia* studied.

In summary, this study showed that *C. oblongifolia* is a super-host species of gall-forming insects. The density of the resource (host plant) negatively affected the richness and abundance of gall-forming insects probably due to the resource dilution effect. However, also is possible that more isolated plants are subjected to highest level of sunlight. In this case, the tissues quality of host plants can change in function of differential action of abiotic factors, affecting gall-forming insect diversity on host plant (see also Egan and Ott 2007; Costa et al. 2016). Finally, the analysis of null models showed that gall-forming insect community structure associated with *C. oblongifolia* cannot be attributed to deterministic factors such as interspecific competition. In our system, the host plant occurs at high density, suggesting that sites to oviposition are not a limiting resource to female of gall-forming insects. However, this hypothesis still deserves to be tested experimentally by manipulating the host plant density under field conditions.

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References

Alvares, C. A., J. L. Stape, P. C. Sentelhas, J. L. M. Gonçalves, and G. Sparovek. 2014. Koppen's climate classification map for Brazil. Meteorologische Zeitschrift **22**:711-728.

Araújo, W. S., and F. A. G. Guilherme. 2012. Distribuição de insetos galhadores em diferentes formações vegetais e paisagens do cerrado brasileiro. Bioscience Journal **28**:810-819.

Araújo, W. S., J. M. Grandez-Rios, L. L. Bargamini, and J. Kollár. 2017. Exotic species and the structure of a plant-galling network. Network Biology **7**:21-32.

Arduin, M., and E. J. Kraus. 2001. Anatomia de galhas de ambrosia em folhas de *Baccharis concinna* e *Baccharis dracunculifolia* (Asteraceae). Revista Brasileira de Botância **24**:63-72.

Bergamini, B. A. R., L. L. Bergamini, B. B. Santos, and W. S. Araújo. 2017. Occurrence and characterization of insect galls in the Floresta Nacional de Silvania, Brazil. Papéis Avulsos de Zoologia **57**:413-431.

Carneiro, A. A. M, R. A. X. Borges, A. P. A. Araújo, and G. W. Fernandes. 2009. Insetos indutores de galhas da porção sul da Cadeia do Espinhaço, Minas Gerais, Brasil. Revista Brasileira de Entomologia **53**:570-592.

Coelho, M. S., M. A. A. Carneiro, C. A. Branco, R. A. X. Borges, and G. W. Fernandes. 2017. Galling insects of the brazilian páramos: species richness and composition along high-altitude grasslands. Environmental Entomology **46**:1243-1253.

Cooley, J. R., C. Simon, and D. C. Marshall. 2003. Temporal separation and speciation in periodical cicadas. Bioscience **53**:151-157

Cornelissen, T., and P. Stiling. 2008. Clumped distribution of oak leaf-miners between and within plants. Basic and Applied Ecology **9**:67-77.

Cornelissen, T., C. D. C Guimarães, J. P. R. Viana, and S. Bárbara. 2013. Interspecific competition influences the organization of a diverse sessile insect community. Acta Oecologica **52**:15-18.

Costa, F. V., M. Fagundes, and F. S. Neves. 2010. Arquitetura da planta e diversidade de galhas associadas à *Copaifera langsdorffii* (Fabaceae). Ecología Austral **20**:9-17.

Costa, F. V., R. Reis-Júnior, A. C. M. Queiroz, M. L. B. Maia, and M. Fagundes. 2016. Resource allocation in *Copaifera langsdorffii* (Fabaceae): how supra annual fruiting affect plant characteristics and higher trophic level? Revista de Biología Tropical **64**: 507-520.

Cuevas-Reyes, P., M. Quezada, P. Hanson, D. Rodolfo, and K. Oyama. 2004. Diversity of gall-inducing insects in a Mexican tropical dry forest: the importance of plant species richness, life-forms, host plant age and plant density. Journal of Ecology **92**:707-716.

Espírito-Santo, M. M., F. S. Neves, F. R. Andrade-Neto, and G. W Fernandes. 2007. Plant architecture and meristem dynamics as the mechanisms determining the diversity of gall-inducing insects. Oecologia **153**:353-364.

Egan, S. P., and J. R. Ott. 2007. Host plant quality and local adaptation determine the distribution of a gall-forming herbivore. Ecology **88**:2868-2879.

Fagundes, M., F. V. Costa, S. F. Antunes, M. L. B. Maia, and A. C. M. Queiroz, L. Q. Oliveira, M. L. Faria. 2013a. The role of historical and ecological factors on initial survival of *Copaifera langsdorffii* Desf. (Fabaceae). *Acta Botanica Brasilica* **27**:480-487.

Fagundes, M., M. L. B. Maia, A. C. M. Queiroz, G. W. Fernandes, and F. V. Costa. 2013. Seed predation of *Copaifera langsdorffii* Desf. (Fabaceae) by *Rhinochenus brevicollis* Chevrolat (Coleoptera: Curculionidae) in a Cerrado fragment. Ecologia Austral **23**:218-221.

Fagundes, M., F. S. Neves, and G. W. Fernandes. 2005. Direct and indirect interactions involving ants, insect herbivores, parasitoids, and the host plant *Baccharis dracunculifolia* (Asteraceae). Ecological Entomology **30**:28-35.

Fagundes, M., R. C. F. X., M. L. Faria, L. G. O. Lopes, P. Cuevas-Reyes, and R. Reis- Junior. 2018. Plant phenological asynchrony and community structure of gall-inducing insects associated with a super-host tropical tree species. Ecology and Evolution **8**:10687-10697.

Fernandes, G. W. and R. P. Martins. 1985. As galhas: tumores de plantas. Ciência Hoje **4**:58-64.

Fleck, T., and C. R. Fonseca. 2007. Hipóteses sobre a riqueza de insetos galhadores: uma revisão considerando os níveis intra-específico, interespecífico e de comunidade. Neotropical Biology and Conservation **2**:36-45.

Grez, A. A., and R. H. González. 1995. Resource concentration hypothesis: effect of host plant patch size on density of herbivorous insects. Oecologia **103**:471-474.

Höglund, S. 2014. Timing of growth determines fitness and performance of a galling insect on willow. Ecological Entomology **39**:159-167.

Jennings, D. E., J. J. Krupa, T. Raffel, and J. R. Rohr. 2010. Evidence for competition between carnivorous plants and spiders. Proceedings of the Royal Society **277**:3001-3008.

Johansson J., N. P. Kristensen, J. Nilsson, and N. Jonzén. 2015. The eco-evolutionary consequences of interspecific phenological asynchrony - a theoretical perspective. Oikos **124**:102-112.

Joshi, J., S. J. Otway, J. Koricheva, A. B. Pfisterer, J. Alphei, B. A. Roy, M. Scherer-Lorenzen, B. Schmid, E. M. Spehn, and A. Hector. 2004. Bottom-up effects and feedbacks in simple and diverse experimental plant communities. Insects and Ecosystem Function. W. W. Weisser and E. Seimann (eds.). Springer Verlag, Berlin.

Kaplan, I., and R. F. Denno. 2007. Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory. Ecology Letters **10**:977-994.

Kuchenbecker, J., and M. Fagundes. 2018. Diversity of insects associated with two common plants of the Brazilian Cerrado: responses of two guilds of herbivores to bottom-up and top-down forces. European Journal of Entomology **115**:354-363.

Kruger, R. F., C. J. B. Carvalho, and P. B. Ribeiro. 2010. Assembly rules in muscid fly assemblages in the grassland biome of southern Brazil. Neotropical Entomology **39**:345-353.

Maia, V. C., and M. A. P. Azevedo. 2009. Micro-himenópteros associados com galhas de Cecidomyiidae (Diptera) em restingas do estado do Rio de Janeiro (Brasil). Biota Neotropica **9**:151-163.

Maia, V. C., M. A. G. Magenta, and S. E. Martins. 2008. Ocorrência e caracterização de galhas de insetos em áreas de restinga de Bertioga (São Paulo, Brasil). Biota Neotropical **8**:167-197.

Marques, E. S. D. A, P. W. Price, and N. S. Cobb. 2000. Resource abundance and insect herbivore diversity on woody fabaceous desert plants. Environmental Entomology **29**:696-703.

Morin, X., L. Fahse, M. Scherer-Lorenzen, and H. Bugmann. 2011. Tree species richness promotes productivity in temperate forests through strong complementarity between species. Ecology Letters **14**:1211-1219.

Otway S. J., T. A. Hector, and J. H. Lawton. 2005. Resource dilution effects on specialist insect herbivores in a grassland biodiversity experiment. Journal of Animal Ecology **74**:234-240.

Price, P. W., G. W. Fernandes, and G. L. Waring. 1987. Adaptative nature of insect galls. Environmental Entomology **16**:15-24.

Ralph, P. C. 1977. Effect of host plant density on populations of a specialized, seed-sucking bug, *Oncopeltus Fasciatus*. Ecology **58**:799-809.

Rhainds, M., and G. English-Loeb. 2003. Testing the resource concentration hypothesis with tarnished plant bug on strawberry: density of hosts and patch size influence the interaction between abundance of nymphs and incidence of damage. Ecological Entomology **28**: 348-358.

Reitz, S. R., and J. T. *Trumble*. 2002. Intraspecific and interspecific differences in two Liriomyza leafminer species in California. Entomologia Experimentalis et Applicata **102**:101-113.

Ribas, C. R., and J. H. Schoereder. 2002. Are all ant mosaics caused by competition? Oecologia **131**:606-611.

Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica Oleracea*). Ecologial Monographs **43**:95-124.

Santos, I. M., V. P. Lima, E. K. S. Soares, M. Paula, and D. C. Calado. 2017. Insect galls in three species of *Copaifera* L. (Leguminosae, Caesalpinioideae) occurring sympatrically in a Cerrado area (Bahia, Brazil). Biota Neotropica **18**: 1-5.

Santos, J. C., and G. W. Fernandes. 2010. Interactions of gall-forming species at different plant spatial scales. Arthropod-Plant Interactions **4**:247-255.

Souza, M. L., and M. Fagundes. 2017. Seed predation of *Copaifera langsdorffii* (Fabaceae): a tropical tree with supra-annual fruiting. Plant Species Biology **32**:66-73.

Stone, L. R. A. 1990. The checkerboard score and species distributions. Oecologia **85**:74-79.

Stireman, J. O., J. D. Nason, and S. B. Heard. 2005. Host-associated genetic differentiation in phytophagous insects: General phenomenon or isolated exceptions? Evidence from a goldenrod-insect community. Evolution **59**:2573-2587.

Stone, G. N., and K. Schönrogge. 2003. The adaptive significance of insect gall morphology. Trends in Ecology and Evolution **18**:512-522.

Stone, L., and A. Roberts. 1990. The checkerboard score and species distributions. Oecologia **85**:74-79.

Tack, A. J. M., O. Ovaskainen, P. J. Harrison, and T. Roslin. 2009. Competition as a structuring force in leaf miner communities. Oikos **118**:809-818.

Tahvanainen, J. O., and R. B. Root. 1972. The influence of vegetational diversity on the population ecology of a specialized herbivore *Phyllotreta cruciferae* (Coleoptera: Crysomelidae). Oecologia **10**:321-346.

Veldtman, R., and M. A. McGeoch. 2003. Gall-forming insect species richness along a non-scleromorphic vegetation rainfall gradient in South Africa: the importance of plant community composition. Austral Ecology **28**:1-13.

Veloso, A. C., P. S. Silva, W. K. Siqueira, K. L. Duarte, I. L. Gomes, H. T. Santos, and M. Fagundes. 2017. Intraspecific variation in seed size and light intensity affect seed germination and initial seedling growth of a tropical shrub. Acta Botanica Brasilica **31**:736-741.

Whipple, A. V., W. G. Abrahamson, M. A. Khamiss, P. L. Heinrich, A. G. Urian, and E. M. Northridge. 2009. Host-Race Formation: Promoted by Phenology, Constrained by Heritability. Journal of Evolutionary Biology **22**: 793-804.

Yamamura, K. 2002. Biodiversity and stability of herbivore populations: influences of the spatial sparseness of food plants Population Ecology **44**:33-40.