

Diversity of gall-inducing insect associated with a superhost plant species: Plant architecture, resource availability and interspecific interactions

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Manuscript received: 24 November 2019. Revision accepted: 23 February 2020.

Abstract. *Fagundes M, Santos EML, Duarte KLR, Santos LM, Vieira JS, Oliveira CHD, Silva PS. 2020. Diversity of gall-inducing insect associated with a superhost plant species: Plant architecture, resource availability and interspecific interactions. Biodiversitas 21: 1182-1189.* The role of interspecific competition in the organization of herbivorous insect communities may vary depending on resource availability. Trees are structurally more complex and have greater resource availability for herbivorous insects than shrubs. In this study, we evaluated the roles of plant architecture and interspecific interactions on community organization of the gall-inducing insect associated with trees (adult plants) and shrubs (young plants) of *Copaifera langsdorffii*. Our results showed that the species composition of gall-inducing insect communities associated with *C. langsdorffii* differed statistically between trees and shrubs. In addition, the trees presented greater diversity of gall-inducing insects than the shrubs, corroborating the hypothesis of plant architecture. The results of the analysis of null models showed that the co-occurrence of gall-inducing insect species associated with trees not differ from the co-occurrence predicted by chance. Thus, interspecific interactions cannot be used to explain the community organization of the gall-inducing insects on *C. langsdorffii* trees. On the other hand, the co-occurrence of gall-inducing insect species differed from the co-occurrence predicted by chance when shrubs plants were analyzed, indicating that biotic interactions can shape the structure of the gall-inducing insect community on shrubs. The lower availability of oviposition sites probably generates a dispute for these resources among females of different species of gall-inducing insects only in the shrubs. Therefore, the role of competition in the organization of herbivore insect communities on their host plant may vary depending on the ontogenetic stage of the host plant.

Keywords: *Copaifera langsdorffii*, herbivorous insects, interspecific competition, null models, ontogenetic development

INTRODUCTION

Studies from a variety of taxonomic groups have shown evidences both favoring and denying the potential role of competition on species distribution (Kaplan and Denno 2007; Cornelissen et al. 2013). Especially for herbivore insects, the importance of interspecific competition on community organization is one of the most debated topics in ecology (Reitz and Trumble 2002; Kaplan and Denno 2007). In fact, the ecologists' view on the role of the interspecific competition in the organization of the herbivore community has changed over time (Kaplan and Denno 2007). During the 1980s competition was not seen as a force able to shape the herbivore community, as the feed resource was not considered a limiting factor (Lawton and Strong 1981). Besides, the assumption that plants have physical and chemical defenses and especially induced defenses has helped to challenge that idea (Reitz and Trumble 2002). Recently, several studies have shown that competition can be a driving force herbivore insect community structure, but variation in resource availability and feeding habit of herbivores (i.e. chewing, suckers,

miners or gall-inducing insects) can affect the results of interspecific competition on community organization (Cornelissen and Stiling 2008; Ramos et al. 2019). For example, although the resource (number of meristems for oviposition) may be abundant for gall-inducing insects, the short time window that surrounds the phenology of the species (i.e. period of plant leaf-budding and adult emergence of gall-inducing insects) may limit temporally the number of meristems available for female oviposition, generating a dispute for sites more suitable for oviposition between different species (Cornelissen et al. 2013; Fagundes et al. 2018).

Variation in resource availability between individuals within a host plant species affect the distribution and abundance of insect herbivores and many trends have been reported worldwide (see Lara et al. 2008; Kuchenbecker and Fagundes 2018). Specifically, the plant architecture hypothesis (Lawton 1983) predicts that structurally more complex plants can sustain greater diversity of herbivorous insects because they are more apparent (*sensu* Feeny 1976), have a higher number of oviposition sites (i.e. number of meristems), and more microhabitats for colonization and

escape from natural enemies (Jeffries and Lawton 1984; Kuchenbecker and Fagundes 2018). At the species level, some studies have shown that plant architecture positively influenced richness and abundance of herbivore insects (e.g. Araújo et al. 2006; Lara et al. 2008; Costa et al. 2011; Kuchenbecker and Fagundes 2018). In this scenario, it would be reasonable to think that mature tree plants should have greater diversity of gall-inducing insects than their young shrub co-specific relative. Various attributes of host plant such as height (Lawton 1983; Lara et al. 2008), canopy volume (Price et al. 1998), number of meristems (Larson and Whitham 1997), branching patterns (Marquis et al. 2002; Espírito-Santo et al. 2007) have been used as architectural measures and related to herbivore diversity in a plant species.

Gall-inducing insects are sophisticated herbivores whose immature stages develop within host plant tissues and the adult stage is ephemeral and free-living (Fagundes et al. 2019). Females of gall-inducing insects show high oviposition specificity with the taxa and the organ/tissue of the host plant (Carneiro et al. 2009). The females generally oviposit in meristematic tissues that have restricted temporal distribution, especially in seasonal environments (Egan and Ott 2007; Fagundes et al. 2018). Chemical and structural changes occur in tissues near the oviposition site, resulting in the formation of structures known as galls or cecidia that house the immature insect within it (Ozaki et al. 2014). Although gall-inducing insects develop protected inside galls, their performance may be affected by environmental conditions (Horner and Abrahamson 1992; Coutinho et al. 2019), top-down (Fagundes et al. 2005; Hood and Ott 2010) and bottom-up forces (Richards et al. 2015), and interspecific interactions such as competition (Kaplan and Denno 2007; Cornelissen et al. 2013; Johansson et al. 2015).

Superhost plants (i.e. plants that host high diversity of gall-inducing insects, sensu Veldtman and MacGeogh 2003) are excellent models for evaluating the role of different abiotic and biotic factors on the organization of gall-inducing insect communities (Fagundes et al. 2018, Coutinho et al. 2019). For example, in addition to the direct action of environmental factors (see Coutinho et al. 2019, Fagundes et al. 2019), several host plant characteristics such as architecture (Lawton 1983; Costa et al. 2010), tissue quality (Lawton and Strong 1981; Cuevas-Reyes et al. 2004; Costa et al. 2016), phenology (Fagundes et al. 2018), ontogenetic stage (Queiroz et al. 2013) and plant sex (Cornelissen et al. 2013) have been used as descriptors of the structure of the gall-inducing insect community associated with its superhost plant.

Copaifera langsdorffii (Fabaceae) is a tropical tree species of wide geographical distribution. This species presents complete deciduousness during the dry season of the year and a diverse fauna of gall-inducing insects (Fagundes 2014; Souza et al. 2018). By using this system, we evaluated the role of plant architecture and interspecific competition in the organization of gall-inducing insect communities associated with adult (tree) and young (shrub) of *C. langsdorffii* individuals. We specifically tested two predictions: (i) trees have greater diversity of galling

insects than their relate shrub and (ii) interspecific competition is a force capable of shaping the structure of gall-inducing insect communities in superhost plants.

MATERIALS AND METHODS

Study area

The study was done in a private reserve (16° 40'03.2" S, 43° 48'35.6" W), located in the municipality of Montes Claros, Minas Gerais, Brazil. The reserve has an area of about 20 ha and soil is characterized as nutrient-poor dystrophic red-yellow latosol (Souza et al. 2018). The climate is semi-arid, with well-defined dry and rainy seasons: the dry season occurs from March to October, and the rainy season occurs from November to February. The average annual temperature is 23 °C, with annual precipitation of approximately 1000 mm (Costa et al. 2016). The vegetation is characterized as Cerrado Stricto Sensu with medium-sized trees (about 8m high), which have twisted branches and thick bark. The tree stratum is spaced, allowing the undergrowth development of young trees, shrubs and grasses.

Study system

Copaifera langsdorffii (Fabaceae), popularly known as "Pau d'óleo" or "Copaíba", is a tropical tree that reaches up to 20 m in the Brazilian Cerrado (Fagundes et al. 2018). The plant is deciduous, with leaf fall occurring between July and September and the emission of young leaves occurs shortly after the fall of old leaves produced in the previous growing season (Souza et al. 2018). The species presents supra-annual fruiting, altering years of low and high reproductive investment (Souza and Fagundes 2017). *C. langsdorffii* presents the most diverse neotropical fauna of gall-inducing insect (Costa et al. 2011; Fagundes 2014). These galls have specific external morphology (color, shape, hairiness, ornamentation) that allows the identification of each gall-inducing insect species (Fagundes 2014; Costa et al. 2016).

Fieldwork

During the early winter of 2019, prior to the fall of the host plant leaves, 40 individuals of *C. langsdorffii* (20 adult/tree and 20 young/shrub plants) were selected and marked in the study area. The categorization of plants as shrub or tree was based on their biometric characters (i.e. height, diameter at breast height, and canopy volume). Canopy volume was determined using the formula for volume of a cone [$V = (\pi \cdot r^2 \cdot l) / 3$], where 'r' is canopy mean radius and 'l' is canopy height. Tree individuals were over 5 m tall (average = 7.44, pattern error = 0.42), DBH greater than 0.3 m (average = 0.76, pattern error = 0.09) and canopy volume greater than 16.95 m³ (average = 57.83, pattern error = 14.91). Shrub were less than 3 m tall (average = 2.43, pattern error = 0.13), DBH less than 0.14 m (average = 0.08, pattern error = 0.006) and canopy volume less than 5.12 m³ (average = 1.67, pattern error = 0.31). The plants selected for the study had a minimum distance of 30 m from each other. Moreover, these plants

had no conspecific neighbors within a 10m radius. In this year of study the population of *C. langsdorffii* did not enter the reproductive stage.

The richness and abundance of galls per plant was estimated by counting the number of galls present in 10 terminal branches of the canopy of each plant selected for the study. These branches were collected at different points around entire canopy of the plants looking to get representative samples of the entire host plant and to avoid possible effects of micro-habitat on branch development and colonization of gall-inducing insects (Costa et al. 2010; Souza and Fagundes 2017). The branches were between 25 and 35 cm in length and the diameter ranged from 30 and 40 cm. After collection, these branches were placed in plastic bags and taken for screening and identification of gall-inducing insects at the Conservation Biology Laboratory of Montes Claros State University. External gall morphology was used to characterize each gall-inducing insect species (see Costa et al. 2010; Fagundes 2014).

Statistical analyzes

To assess whether the diversity of galling insects varied between tree and shrub plants of *C. langsdorffii*, we first compared the composition of the gall-inducing insect community between adult and young individuals using multivariate analysis. Thus, we ordered the tree and shrub plants, based on the abundance matrix of gall-inducing insects present in each plant, using the non-Metric Multidimensional Scaling (nMDS) technique. This analysis was based on the species abundance and the Chord index was used as a dissimilarity measure. Subsequently, we performed a nonparametric permutation test (ANOSIM) with 5000 permutations to test the significance of the groups formed in nMDS. The Chord distance was used as a measure of dissimilarity. These procedures were performed in the software PAST (Hammer et al. 2001).

Next, we compared the richness and abundance of gall-inducing species between trees and shrub plants. In this case, we built two Generalized Linear Models (GLM), where the response variables were the richness or abundance of gall-inducing species and the explanatory variable the ontogenetic stage of plants (i.e. tree and shrub) of the *C. langsdorffii*. In the construction of models where richness or abundance was the explanatory variables, we used the Poisson (corrected for Quasipoisson) and Gaussian error distribution, respectively. These models were later tested with Analysis of Variance (ANOVA) based on F test. These analyzes were performed using the R software (R Core Team 2015).

Null model analyzes were used to test whether the occurrence of gall-inducing species associated with trees and shrubs plants does not differ from chance. The null hypothesis predicts that the occurrence of one gall-inducing species in one individual plant does not interfere with the occurrence of another species of gall insect in the same plant (Fagundes et al. 2019). In this case, the gall-inducing insect community is randomly structured and interspecific interactions cannot be used to explain the structure of

galling insect communities in their plants (Ribas and Schoederer 2002; Cornelissen et al. 2013). We use the C-score index (Stone and Roberts 1990) as a measure of co-occurrence of gall-inducing insects in the two different ontogenetic stages (i.e. tree and shrub) of *C. langsdorffii*. This index was calculated based on the binary matrix of gall-inducing insects occurrence in tree and shrubs through the formula $C = (r_i - S)(r_j - S) / S^2$, where r_i and r_j are the totals of the rows, and S_{ij} is the number of sites occupied by both species (Cornelissen et al. 2013). When the C-score index value of the original matrix (observed C-score) falls outside the frequency distribution of 95% of the C-score values of the randomized matrices (calculated C-score), the null hypothesis is rejected. Thus, it is assumed that species distribution is different from chance and biological interactions can be used to explain the community structure (Ribas and Schoederer 2002). We used a fixed-fixed model, where the rows and columns of the original matrix were preserved, with 5000 randomizations to generate simulated C-Score index values. These procedures were performed in the software EcoSim (Gotelli and Entsminger 2001).

RESULTS AND DISCUSSION

Historical patterns

A total of 2095 galls belonging to 17 gall-inducing species were collected from the 40 plants of *C. langsdorffii* (Table 1). Galls G3, G6 and G12 were more abundant in both trees and shrubs. In fact, these three gall-inducing species represented 86% and 85% of the total number of gall-inducing insects sampled from tree and shrub, respectively. Recent studies indicate that some species of the genus *Copaifera* harboring a high diversity of gall-inducing insects (Costa et al. 2016; Fagundes et al. 2018; Santos et al. 2018; Coutinho et al. 2019). Historical/evolutionary aspects of the host plant species such as family or genus size (Kuchenbecker and Fagundes 2018), geographic distribution, and center of origin of the species (Fleck and Fonseca 2007; Fagundes and Fernandes 2011) have been used to explain the high diversity of herbivorous insects associated with a host plant species. The genus *Copaifera* belongs to one of the largest botanical families (Souza and Lorenzi 2005) and is composed of 72 species distributed throughout the Americas and West Africa (Dwyer 1951). *C. langsdorffii* is distributed throughout Latin America, occurring in sympatry with other species of the genus *Copaifera* (Santos et al. 2018; Coutinho et al. 2019). Similarities in the chemical constitution of phylogenetically close plants allow host selection failures during oviposition process and gall-inducing insect radiation among different hosts species (Mopper 2005; Johansson et al. 2015). Thus, these historical/ evolutionary aspects of the host plant could help explain the high diversity of gall-inducing insects associated with *C. langsdorffii*.

Table 1. Morphological traits, abundance, and frequency (percentage of occurrence) of all gall-inducing insects collected from trees (n = 20) and shrubs (n = 20) of *Copaifera langsdorffii* (Fabaceae)

Gall	Taxon	Morphology	Trees		Shrubs	
			Abundance	Frequency	Abundance	Frequency
G1			0	0	14	5
G2	Cecidomyiidae		91	85	15	35
G3	Cecidomyiidae		987	100	250	70
G4			6	20	2	5
G5			2	5	0	0
G6	Hymenoptera		219	95	91	70
G7			2	10	0	0
G8			25	35	14	30
G9	Cecidomyiidae		7	20	4	15
G10			1	5	0	0
G11			33	60	7	15
G12	Cecidomyiidae		111	65	140	50
G13			16	5	0	0
G14			7	10	0	0
G15			21	40	25	10
G16			1	5	0	0
G17	Cecidomyiidae		1	5	3	5
Total			1530	16	565	12

Ecological patterns

In general, our results showed that the role of interspecific competition on community organization of gall-inducing insects may vary depending on the ontogenetic stage of the host plant. Indeed, we found no evidence that competition can affect community organization of gall-inducing insects on trees. In contrast, in shrubs, the results of null model analysis suggest that interspecific competition may be a force capable of shaping the gall-inducing insect communities.

Several studies show that ecological interactions that occur between and within trophic levels can shape the structure of gall-inducing insect communities associated with a host plant (Fagundes et al. 2005; Costa et al. 2016; Ramos et al. 2019). Larger plants can be more easily located, provide more oviposition sites for females and shelter from natural enemies (Lawton 1983; Jeffries and Lawton 1984; Araújo et al. 2006). Therefore, plant architecture represents an important factor that can

positively affect the diversity of gall-inducing insects (Araújo et al. 2006; Espírito-Santo et al. 2007). Our results corroborate this general assumption that more complex plants should harbor greater herbivorous diversity. In fact, the composition of the gall-inducing species varied between trees and shrubs of *Copaifera langsdorffii* (Anosim: $R = 0.0826$, $P = 0.0117$, Figure 1). The most frequent gall-inducing species sampled from trees were G3, G6 and G2, while the most frequent species on shrub were G3, G6 and G12. The gall-inducing species G5, G7, G10, G13, G14 and G16 were not found on shrubs, while only G1 was not found on tree (Table 1). In addition, we observed that the richness (Deviance = 7.6515, $F = 12.1813$, $P = 0.0012$) and abundance (Deviance = 8925.6, $F = 10.9467$, $P = 0.0022$) of gall-inducing species also varied between tree and shrub of *C. langsdorffii*. In fact, gall-inducing species richness and abundance were, respectively, 75% and 130% higher in tree compared to shrub (Figure 2.A-B).

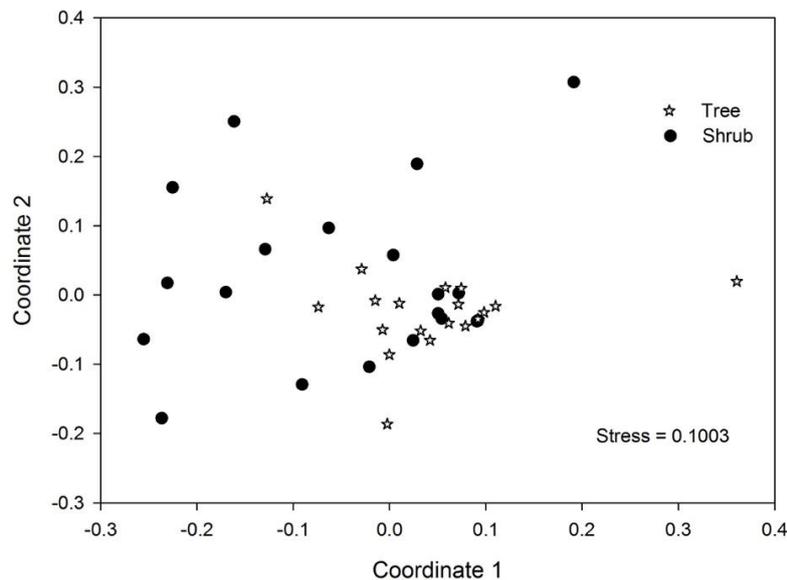


Figure 1. Non-metric Multidimensional Scaling (nMDS) showing the ordination of gall-inducing insect herbivores collected from trees ($n = 20$) and shrubs ($n = 20$) of *Copaifera langsdorffii*

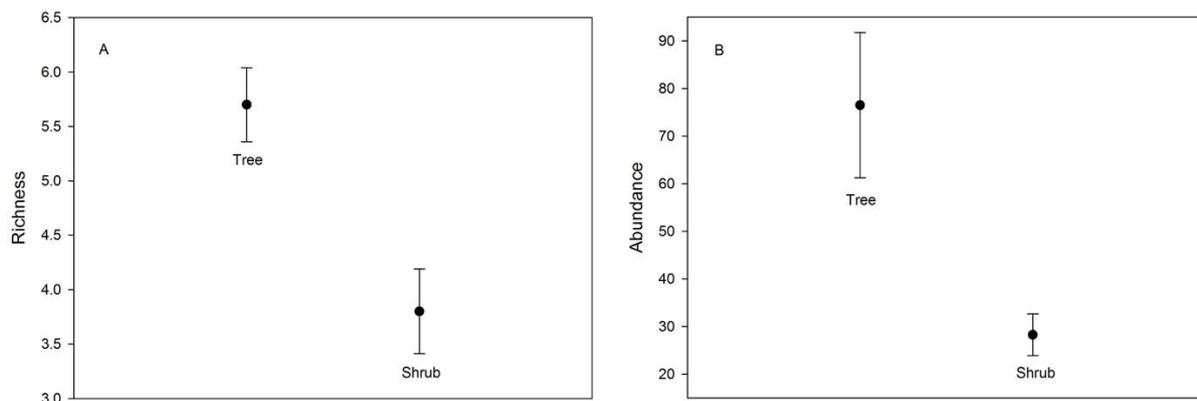


Figure 2. Variation in richness (A) and abundance (B) of gall-inducing insects collected from trees ($n = 20$) and shrubs ($n = 20$) of *Copaifera langsdorffii*. Vertical lines indicate pattern error

Although gall-inducing insects are highly specialized in host organ and species, some studies suggest that local environmental characteristics (Coutinho et al. 2019) and the quality of host plant tissues (Lawton and Strong 1981; Costa et al. 2016) may also affect the organization of gall-inducing insect communities in a host. The young and adults stages of the same species of tree species occupy different strata of a forest. These strata are subject to different environmental conditions such as temperature, humidity and light radiation, which directly affect herbivorous insects (Cuevas-Reyes et al. 2003; Neves et al. 2010). In addition, during ontogenetic development, plants experience changes in their chemical (e.g. concentration of defense compounds and nutrients in tissues), and physical (e.g. size, tissue hardness, leaf shape) attributes that in turn also affect colonization and performance of gall-inducing insects (Queiroz et al. 2013). Thus, the variation observed in the composition of galling insect species among young and adult individuals also may be associated with environmental variations between canopy and understory, as well as variations in plant tissue quality that occur as a result of the ontogenetic development of the host.

Co-occurrence analysis of gall-inducing species on tree showed that the value of the observed C-score index did not differ from the C-scores of the simulated matrices. These results suggest that gall-inducing species occur randomly on trees, corroborating the null hypothesis. On the other hand, when the shrubs were analyzed, the observed C-score index value differed from the C-scores of

simulated matrices. Thus, the occurrence of gall-inducing species on shrubs differed from chance, suggesting that biotic interactions may shape the distribution of gall-inducing insects on young plants (Table 2, Figure 3). In this case, it would be reasonable to think that these results are related to higher resource availability (i.e. oviposition sites) in adult plants (i.e. trees) compared to young plants (i.e. shrubs). Shrubs have lower availability of oviposition sites than their conspecific arboreal partners, generating a dispute for this feature among females of different species of galling insects.

Although resource availability does not seem to be a limiting factor for gall-inducing insects because leaves are very abundant on plants, some characteristics of the plant-galling insect interaction can limit the availability of oviposition sites, generating disputes for more suitable oviposition sites between females of gall-inducing species (Cornelissen et al. 2013). In fact, the high specificity between gall-inducing insects and the host plant (Carneiro et al. 2009), the short temporal window surrounding the phenology of galling insects and the host plant (i.e. budding period of the host plant and emergence of galling insects that have ephemeral life) (Fagundes et al. 2018) and the chemical and physical changes that the plant tissue/organ undergoes soon after the female oviposition (Höglund 2014), make the sites suitable for oviposition scarce, generating a dispute for this resource in plants that harboring large numbers of galling insect species.

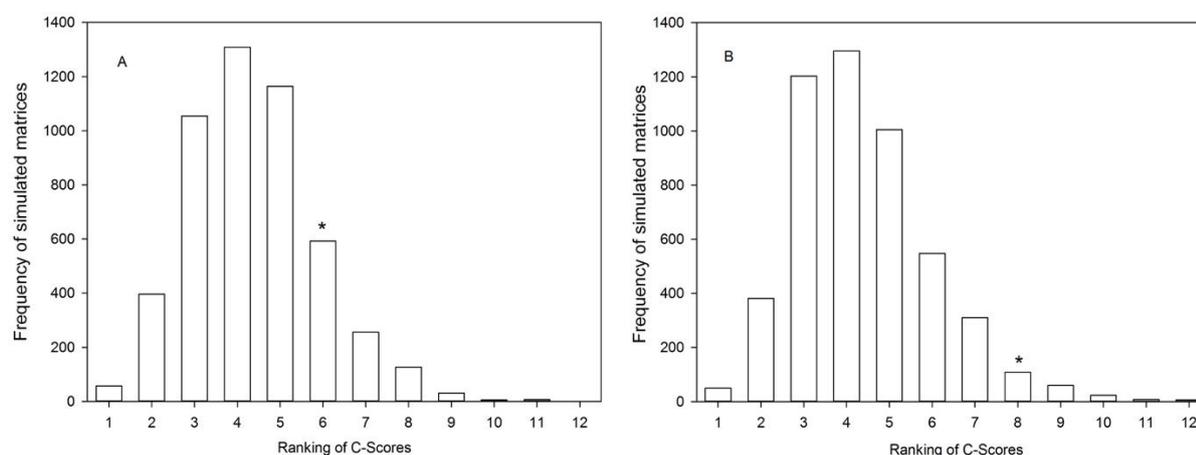


Figure 3. Frequency of simulated matrices, using fixed-fixed models, based on co-occurrence of gall-inducing insects associated with *Copaifera langsdorffii* in two ontogenetic stages (A = trees, B = shrubs) The asterisk indicates where the observed C-scores coincided with the frequency class of the C-scores of the 5000 simulated matrices. See also table 1 with the observed C-scores and the minimum and maximum values of simulated C-scores for each ontogenetic stages of host plant

Table 2. C-score indices of the randomized and observed matrices for galling insects associated with two different ontogenetic stages (trees and shrubs) of *Copaifera langsdorffii*. 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)

Stages of host plant	C-scores of randomized matrices		Observed C-scores	P-value	
	Minimum	Maximum		Obs<exp	Obs>exp
Tree	4.5333	5.8833	5.1000	0.8088	0.2040
Shrub	4.4000	6.5454	5.7272	0.9716	0.0306

In conclusion, this study showed that the community structure of gall-inducing insect species can vary between the ontogenetic stages of the same plant species. In a conservationist view, we might think that maintaining plants at different stages of development in a forest would be important for the conservation of more insect species within a habitat. In addition, we suggest that the role of competition in structuring gall-inducing insect communities may vary depending on the ontogenetic stage of the host plant. Although we have suggested that variation in the availability of oviposition sites may be the generating mechanism of these results, other aspects of the host plant (e.g. tissue nutritional status) and microenvironmental variations should also be considered in future studies as possible variables that may affect the interspecific interactions between herbivores insects (see also Ramos et al. 2019).

ACKNOWLEDGEMENTS

The study was conducted with financial support from Fundação de Amparo a Pesquisa do Estado de Minas Gerais and Pos-Graduate Program of Biodiversity (PPG-BURN)/ Unimontes. The authors also thank gratefully for grants provided by the Fundação de Amparo à Pesquisa de Minas Gerais (FAPEMIG) and Conselho de Aperfeiçoamento de pessoal de Nível Superior (CAPES).

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