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ARTICLE

Galls of *Palaeomystella oligophaga* (Lepidoptera, Agonoxenidae) associated with *Macairea radula* (Melastomataceae) in Neotropical *veredas:* effects of environment type, resource concentration, and plant architecture

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Abstract. The diversity of galling insects may be associated with abiotic factors, such as hygrothermal stress, and biotic factors of the host plants, such as structural complexity and resource concentration. In the present study, we aimed evaluate the occurrence of galling insects *Palaeomystella oligophaga* (Lepidoptera, Agonoxenidae) associated with *Macairea radula* (Melastomataceae) in *veredas* of northern of Minas Gerais, testing the effect of environmental stress, resource concentration and plant architecture. The study was carried out in three *veredas* with distinct levels of soil drying and conservation (preserved, intermediate and degraded). In each *vereda,* were selected 20 individuals of the *Macairea radula* for galling sampling. For each focal plants were sampled the abundance of galls, plant height (m), number of branches and number of individuals close to the focal plant within a radius of 5 m. In total, were sampled 2,030 galls of *Palaeomystella oligophaga* on *Macairea radula.* The abundance of galls differed significantly between the plants of the different *veredas,* being higher in the plants of the Vereda da Almescla (intermediate conservation level). In addition, the abundance of galls was positively correlated with plant height, and the number of nearby individuals (considering all plant species). Our results demonstrate that both anthropic alterations that lead to the dryness of the *veredas,* and structural characteristics of the host plants, can affect the occurrence of galls of *Palaeomystella oligophaga.*

Keywords. Cerrado; Environmental stress; Habitat preference; Insect occurrence; Palm Swamp Forest.

INTRODUCTION

Gall-inducing insects are endophagous herbivores with high specialization (Stone & Schönrogge, 2003), as they engage in intimate interactions with plant tissues and can be extremely specific in their choice of hosts (Fernandes & Price, 1992; Price *et al.,* 1998). Gall-inducers are capable of inducing morphophysiological modifications in plants, known as galls, which they use for feeding, development, and protection against natural enemies (Carvalho-Fernandes *et al.,* 2012). Galls are structures developed as a result of tissue modifications in the plant (Ribeiro & Fernandes, 2000), through hypertrophy and hyperplasia of plant cells (Stone & Schönrogge, 2003). Most species of gall-inducing insects are specialists on their host plants, but the choice of host plant by female gall-inducing insects for oviposition can depend on various environmental factors and plant

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characteristics (Fleck & Fonseca, 2007). The diversity of gall-inducing insects may be associated with abiotic factors, such as hygrothermal stress, and factors related to the host plant, such as structural complexity and resource concentration (Gonçalves-Alvim & Fernandes, 2001). However, studies testing the simultaneous effects of these factors on the distribution of gall-inducing insects in plants occurring in Neotropical environments are still scarce.

It is known that environments with different levels of hygrothermal stress may differ in species number and interactions (Araújo *et al.,* 2024). In the case of gall-inducing insects, xeric environments (*e.g.,* savannas), characterized by scleromorphic and xeromorphic plants, tend to have a higher occurrence of gall-inducing insects compared to mesic environments (*e.g.,* forests) (Neves *et al.,* 2010; Leal *et al.,* 2015; Bergamini *et al.,* 2017; Araújo *et al.,* 2024), as predicted by the environmental hygrothermal stress hypothesis (Fernandes & Price, 1992). This occurs because gall-inducing insects have a greater preference for plants found in environments with lower water and nutritional availability (Bergamini *et al.,* 2017), as these tend to have higher concentrations of defense compounds such as tannins and other phenolic compounds (Silva *et al.,* 2017), which are used by gall-inducers for gall construction (Hartley, 1998). Some studies indicate that gall-inducing insects may also be positively affected by stress gradients caused by anthropogenic disturbances (Fagundes *et al.,* 2020; Araújo *et al.,* 2024).

In tropical environments, *veredas* are vegetation that are experiencing drastic effects due to anthropogenic impacts (Nunes *et al.,* 2022). *Veredas* are hydrophilic forests, also known as palm swamp forests, typical of the moist environments of the Brazilian Cerrado (Almeida *et al.,* 2016). Because they are vegetation associated with hydromorphic soils and shallow groundwater tables, *veredas* are highly sensitive to anthropogenic disturbances (Bahia *et al.,* 2009). Anthropogenic activities such as deforestation, wildfires, and alterations in land use, which reduce groundwater recharge and promote the drying of hydromorphic soils, negatively influence typical *vereda* plants (Nunes *et al.,* 2022). In this sense, it is expected that the intensification of anthropogenic disturbances will increase the drying level of *veredas,* and consequently, their level of environmental stress, which may positively affect the distribution of gall-inducing insects in these environments (Araújo *et al.,* 2024).

Plant characteristics can also be affected by environmental factors. Water availability can significantly influence plant characteristics, with well-watered plants typically growing larger, having more extensive canopies and branching, while drought conditions result in reduced growth and smaller canopies (Lawton & Schröder, 1977). These structural changes affect the suitability of plants as hosts for gall-inducing insects, as larger, more complex plants provide more resources and oviposition sites (Araújo & Santos, 2009; Fleck & Fonseca, 2007). For instance, studies show that more complex plants (*i.e.,* larger with a greater canopy volume) exhibit a higher occurrence of gall-inducing insects compared to structurally simpler plants (Fagundes *et al.,* 2019; Cuevas-Reyes *et al.,* 2004), as expected according to the plant structural complexity hypothesis (Lawton & Schröder, 1977). In this regard, several parameters of plant architecture, such as height and canopy size, have been positively correlated with gall abundance (Collevatti & Sperber, 1997; Araújo *et al.,* 2006; Araújo & Santos, 2009).

Another factor that can affect the occurrence of insect galls is the density of plants in the vegetation, as postulated by the resource concentration hypothesis (Fleck & Fonseca, 2007). Thus, some studies show that areas with higher vegetation density exhibit a greater occurrence of gall-inducing insects compared to areas with sparse vegetation (Gonçalves-Alvim & Fernandes, 2001; Cuevas-Reyes *et al.,* 2004). The higher occurrence of gall-inducing insects in plants within denser vegetation is attributed to the greater availability of resources, specifically the increased presence of plants in these environments (Fleck & Fonseca, 2007). At the community level, a greater increase in plant abundance in the vegetation may positively affect the richness of gall-inducing insects (Gonçalves-Alvim & Fernandes, 2001). However, considering that each gall-inducing insect tends to be specific to its host plant, at the population level, each species of gall-inducing insect tends to respond only to the increase in abundance of its specific host species (Fleck & Fonseca, 2007).

In this sense, the objective of the present study is to evaluate the occurrence of gall-inducing insects associated with host plants in Neotropical *veredas.* For this purpose, the following hypotheses will be tested: (i) the hygrothermal stress hypothesis, which predicts a higher occurrence of gall-inducing insects in stressed environments (*i.e.,* xeric) compared to less stressed environments (*i.e.,* mesic); (ii) the architectural complexity hypothesis, which suggests that structurally more complex plants host a greater number of insect galls than structurally simpler plants, and (iii) the resource concentration hypothesis, which predicts that plant density positively affects the occurrence of gall-inducing insects. Our expectations are that the occurrence of gall-inducing insects will be higher in *veredas* with high hygrothermal stress (*i.e.,* advanced drying level), and that gall abundance will be positively related to architectural complexity and plant density.

MATERIAL AND METHODS

Study area

The study was conducted in three *veredas* in the Northern region of Minas Gerais, Brazil (Fig. 1). The first is Vereda das Pedras (14°53′18″S and 45°20′31″W), located in the Private Reserve of Natural Heritage Porto Cajueiro (RPPN Porto Cajueiro), belonging to the municipality of Januária. The second is Vereda da Almescla (15°21′37.2″S and 44°54′45.9″W), located in the Environmental Protection Area – APA of Rio Pandeiros, in the municipality of Bonito de Minas. The third is Vereda do Peruaçu (14°56′13″S

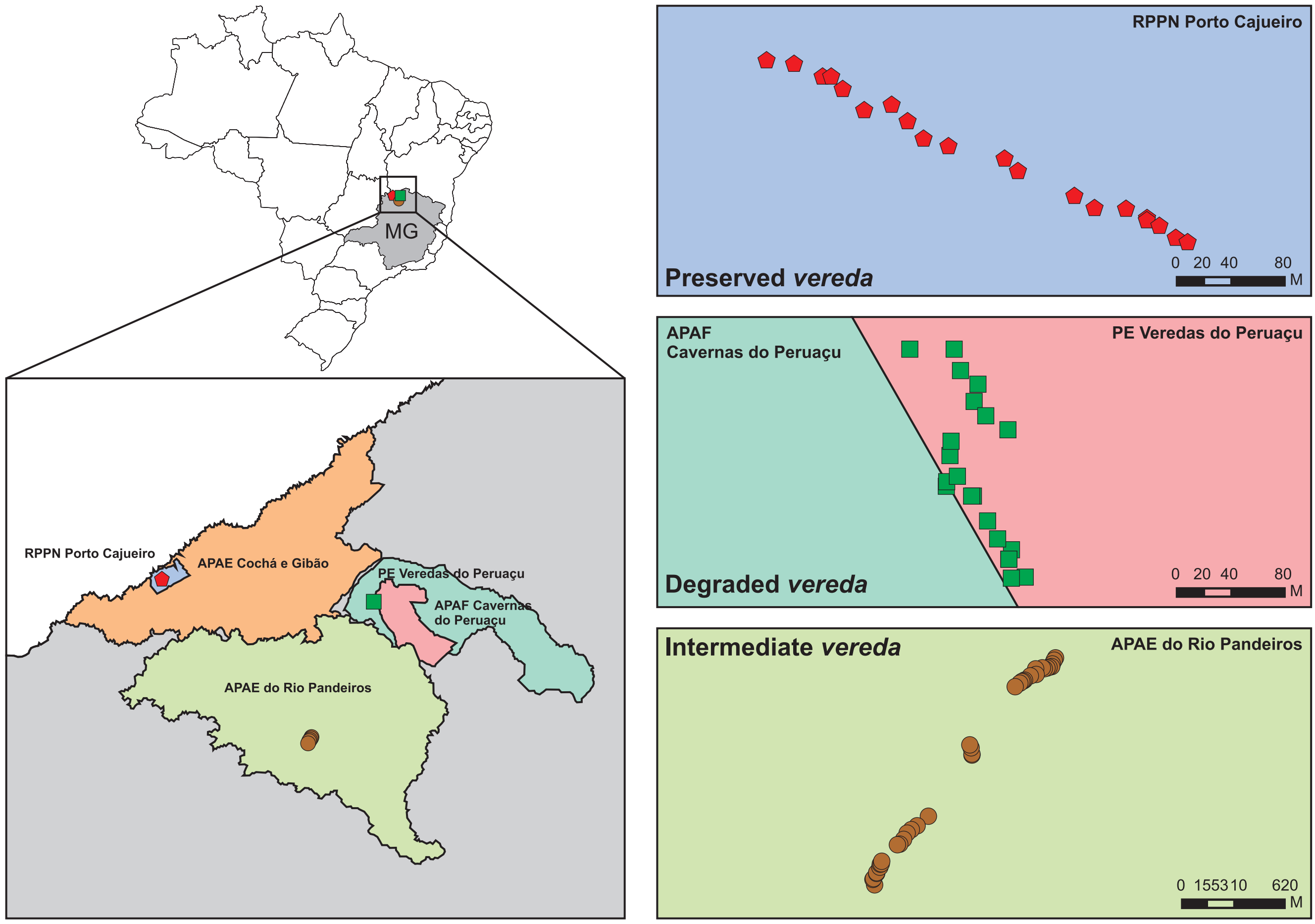

Figure 1. Location of the three *vereda* areas sampled in the Northern region of Minas Gerais, Brazil. Red dots represent sampled plants in Vereda das Pedras (preserved *vereda*), green dots represent plants from Vereda do Peruaçu (degraded *vereda*), and brown dots represent plants from Vereda da Almescla (intermediate *vereda*).

and 44°37′44″W), situated in the Veredas do Peruaçu State Park, located in the municipalities of Januária and Cônego Marinho. These three *veredas* are part of the sampling sites of the Long-Term Ecological Project PELD-VERE, composed of different researchers and institutions, which study the effect of *veredas* drying in the northern region of Minas Gerais on biodiversity. The climate of the area is tropical, with well-defined seasons of dry winters and rainy summers. The annual average temperature and rainfall are 26.8°C and 920 mm, with rainfall ranging from 900 to 1,200 mm (Alvares *et al.,* 2013).

The three studied *veredas* present different levels of preservation (Araújo *et al.,* 2024). The selected *veredas* are part of the sampling sites of the Long-Term Ecological Research Project – PELD-Veredas. Vereda das Pedras is the most preserved, with a watercourse with a large water volume and no evidence of drying, exhibiting a vegetation structure and floristic composition characteristic of *veredas* (Araújo *et al.,* 2024). This *vereda* shows no signs of drying or recent anthropogenic impacts. On the other hand, Vereda da Almescla has an intermediate level of conservation, with a relatively well-preserved structure but already showing signs of groundwater reduction and drying, presenting a watercourse with a reduced but constant water volume (Almeida *et al.,* 2016). This *vereda* suffers anthropogenic impacts due to pasture and agricultural activities in its surroundings. Meanwhile, Vereda do Peruaçu is in an advanced stage of degradation due to the reduction of the water table, with a high level of soil drying, absence of water in the *vereda*'s watercourse, and alterations in vegetation structure, such as high mortality of *Mauritia flexuosa* individuals and advancement of cerrado *sensu stricto* plants into the *vereda*'s interior (Nunes *et al.,* 2022). As the species *Mauritia flexuosa* is typical of the moist soils of *veredas,* its mortality is used as an indicator of the drying of these ecosystems (Nunes *et al.,* 2022). Impacts on the Vereda do Peruaçu result from changes around the park, with the conversion of natural vegetation into agriculture and pasture, as well as from recurring anthropogenic fires that spread from neighboring properties into the park.

Study system

The target plant of the present study is *Macairea radula,* belonging to the family Melastomataceae, commonly known as *capuchinha* (Araújo *et al.,* 2013). In the study area, this species is found in high abundance in the middle zone of the *vereda* (Grandez-Rios *et al.,* 2024). This species is associated with galls induced by the moth *Palaeomystella oligophaga* (Lepidoptera, Agnoxenidae) that develop in the axillary buds of the leaves, presenting a yellow-orange color and being covered by long trichomes that envelop the host (Lara *et al.,* 2008; Silva & Romero, 2008; Albuquerque *et al.,* 2013). Galls of

Palaeomystella oligophaga on *Macairea radula* plants are very common and abundant in the *veredas* of the Northern region of Minas Gerais (Grandez-Rios *et al.,* 2024). The species *Macairea radula* is the only one of its genus present in the state of Minas Gerais (Lara *et al.,* 2008). It is a shrub species, up to 2 m tall, branched, evergreen, perennial, found associated or not with watercourses (Gonçalves-Alvim *et al.,* 1999). Its inflorescence is a panicle type, with campanulate flowers of lilac color; corolla with 4 lilac petals, with a cream-colored base and yellow stamens, and the inflorescence is of the compound panicle type (Rocha *et al.,* 2020).

Data sampling

Insect gall sampling was conducted in May and June 2022, at the beginning of the dry season, where 20 individuals of the plant *Macairea radula* were selected in each of the *veredas* (preserved, intermediate, and degraded). Plant individuals were randomly selected, and no minimum distance between them was adopted. The abundance of galls was counted on each sampled plant through direct observations on focal plants. Additionally, other 40 individuals were selected in the Vereda da Almescla area, where the height (m) and number of branches were measured to assess plant structural complexity. This criterion was adopted because this *vereda* had a larger number of plant individuals, which allowed for the analysis of structural parameters. The number of individuals near the focal plant within a radius of 5 m, of the same species and different species, was also recorded to evaluate resource concentration.

Data analyses

The abundance of *Palaeomystella oligophaga* galls on *Macairea radula* plants was compared among *veredas* with different preservation levels (preserved, intermediate, and degraded) and also related to plant complexity (plant height and number of branches) and vegetation density (number of nearby plants and number of nearby plants of the same species) using generalized linear models (GLM's). In these models, gall abundance was used as the response variable, while the other variables served as explanatory variables. For testing the hygrothermal stress hypothesis, data collected from all three *veredas* ($N = 60$) were used, but for testing the hypotheses of structural complexity and resource concentration, only data from Vereda da Almescla were used ($N = 40$). All constructed models were checked for residual distribution, and Gaussian error distributions were used. To compare differences between *veredas* (preserved, intermediate, and degraded), post-hoc analysis was performed using the *phia* package (Martinez, 2015). For the presentation of the results, simple linear regressions were used between structural parameters and abundance of galls. All statistical analyses were conducted in R version 4.2.2 (R Development Core Team, 2022).

RESULTS

A total of 2,030 galls of *Palaeomystella oligophaga* associated with *Macairea radula* individuals were sampled. The mean number of *P. oligophaga* galls per plant ranged from 0.3 (± 0.7) to 76.1 (± 33.9) and differed significantly among plants from different *veredas* ($F = 98.797$, $DF = 57$, $p < 0.001$). The mean number of galls was 50 times higher in plants from *vereda* with intermediate level of conservation compared to the others (Fig. 2). Was no difference between the other treatments. Gall abundance was positively correlated with the height of *M. radula* plants ($F = 17.281$, $DF = 39$, $p < 0.001$; Fig. 3), but was not affected by the number of branches per plant ($p = 0.856$). Additionally, we found a positive relationship between gall abundance and the number of nearby individuals (considering all plant species) ($F = 9.213$, $DF = 39$, $p = 0.004$; Fig. 4), but the results did not show a significant effect of the number of nearby individuals of the same species ($p = 0.245$).

DISCUSSION

Our results show that the abundance of insect galls differed among *veredas* with different levels of conservation and was also affected by plant structure and vegetation density. The findings demonstrated that Vereda da Almescla, which has an intermediate level of conservation, exhibited a higher occurrence of galls than the other *veredas.* Additionally, the abundance of *Palaeomystella oligophaga* galls was positively correlated with the height of *M. radula* plants, but the number of branches did not affect gall abundance. On the other hand, gall occurrence was higher in *M. radula* individuals surrounded by other nearby plants, but was not affected by the quantity of neighboring conspecific plants.

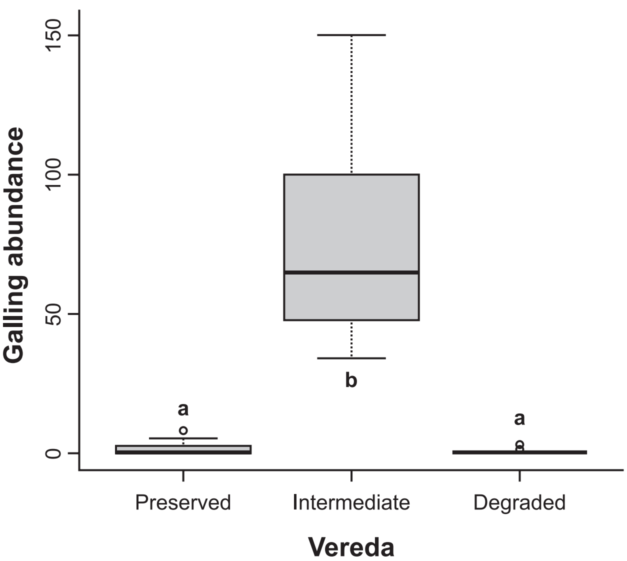

Figure 2. Comparison of the mean abundance of *Palaeomystella oligophaga* galls on *Macairea radula* plants located in *veredas* with different preservation levels (preserved, intermediate and degraded) in the Northern region of Minas Gerais, Brazil.

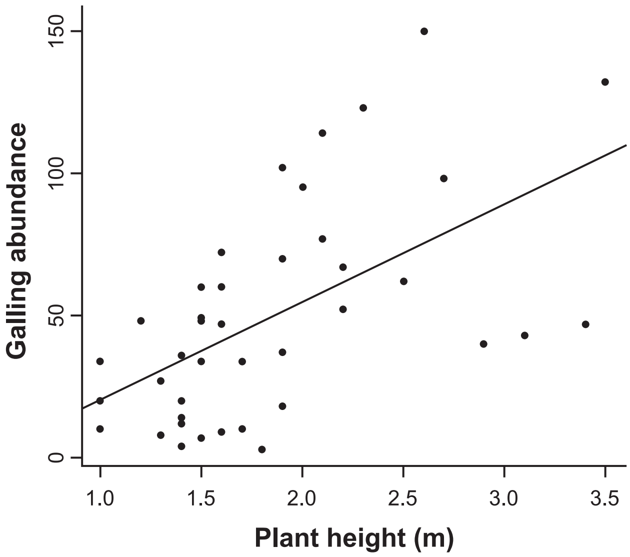

Figure 3. Effect of *Macairea radula* plant height on the mean abundance of *Palaeomystella oligophaga* galls in the Vereda da Almescla, in the Northern region of Minas Gerais, Brazil.

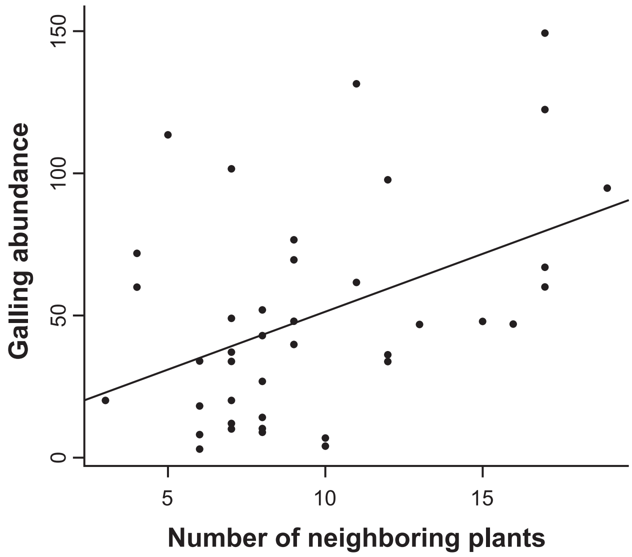

Figure 4. Effect of the number of nearby individuals on the mean abundance of *Palaeomystella oligophaga* galls on *Macairea radula* plants in the Vereda da Almescla, in the Northern region of Minas Gerais, Brazil.

The hygrothermal stress hypothesis (Fernandes & Price, 1988) predicts that plants in environments with hygrothermal stress conditions (xeric environments) tend to accumulate concentrations of secondary metabolites (Fleck & Fonseca, 2007; Araújo *et al.,* 2014), becoming more nutritious for gall-inducing insects, which exhibit greater diversity in these environments (Fernandes & Price, 1988; Araújo *et al.,* 2014). Our results partially supported this hypothesis, as the Vereda da Almescla, which had a higher occurrence of galls, exhibits an intermediate degree of degradation, making it comparatively more xeric than Vereda das Pedras, which shows no evidence of drying (mesic environment). The Vereda da Almescla also exhibits high heterogeneity, with very dry areas upstream of the *vereda* and moist areas downstream, which may affect the occurrence of host plants and gall-inducing insects (Araújo *et al.,* 2024). It was also observed in the field that the plant *Macairea radula* had a larger population size in the Vereda da Almescla, which could affect the incidence of galls. On the other hand, Vereda do Peruaçu, which has an advanced level of drying and therefore the highest level of environmental stress, showed a low abundance of insect galls. One possible explanation for this is that this *vereda* is undergoing intense changes in vegetation structure and composition with the colonization of species of cerrado *sensu stricto* (Nunes *et al.,* 2022). In this sense, many of the typical plants of humid environments, including *M. radula,* are experiencing high mortality, which may negatively affect gall occurrence.

We found that the height of *M. radula* positively influenced gall abundance, but it was not affected by the number of branches. These results are in accordance with the structural complexity hypothesis (Lawton & Schröder, 1977), which predicts a higher occurrence of gall-inducing insects in plants with greater structural complexity (Fleck & Fonseca, 2007). In the literature, various parameters have been used to assess plant structural complexity, such as the number of branches, number of leaves, crown volume, crown diameter, among others, although plant height (size) is the most commonly used parameter (Collevatti & Sperber, 1997; Fleck & Fonseca, 2007; Araújo & Santos, 2009). Plant size is a direct measure of resource availability for gall-inducing insects, as larger plants offer greater resource availability, oviposition sites, and are more easily spotted by insects (Araújo & Santos, 2009). Contrary to expectations, we found no relationship between abundance of galls and number of branches per plant. One possible explanation for this is that the plant presents asymmetric growth with many small branches on small plants, which may not be selected by galling insects that tend to select more vigorous branches (Fleck & Fonseca, 2007).

The positive relationship between the number of neighboring plants (plant density) around *M. radula* and gall abundance supports the resource concentration hypothesis (Root, 1973). This hypothesis suggests that patches of concentrated resources exhibit a higher occurrence of herbivorous insects (Fleck & Fonseca, 2007). This relationship occurs because herbivores can more easily locate concentrated patches of resources (Tahvanainen & Root, 1972; Root, 1973; Ralph, 1977). Since gall-inducing insects are specialists in their host species, it is likely that the higher occurrence on plants with more neighbors may be related to escaping natural enemies through a dilution effect (Fagundes *et al.,* 2018). However, we did not find an effect of the density of conspecific plants of *M. radula* on gall abundance. Contrary to expectations, it may be that the higher the concentration of co-specific host plants, the lower the number of galls on each individual plant.

CONCLUSION

The study provides evidence of variation in the abundance of galls of *Palaeomystella oligophaga* galls on

M. radula among different *veredas,* but the ability to attribute these findings to the tested hypotheses is limited. While the results support a positive relationship between plant height (architectural complexity) and abundance of galls, as well as a positive effect of overall plant density (resource concentration hypothesis), the findings do not fully align with the hygrothermal stress hypothesis, since no clear pattern of higher gall occurrence in more xeric environments was observed. Additionally, the lack of a significant effect of the number of nearby individuals of the same species further complicates the interpretation of the resource concentration hypothesis. To strengthen these conclusions, incorporating local climatic variables, such as temperature, humidity, and soil moisture, would be valuable in future studies. However, to the best of our knowledge, this is the first study evaluating the populational distribution of gall-inducing insects on plants associated with Brazilian *vereda* environments, which are highly threatened ecosystems and still poorly studied (but see Araújo *et al.,* 2024; Grandez-Rios *et al.,* 2024). Additionally, this is the first study to investigate the occurrence of *Palaeomystella oligophaga* galls on *M. radula* in the context of anthropogenic alterations of natural habitats. Our results demonstrate that both anthropogenic alterations leading to *vereda* drying and structural characteristics of host plants can affect the occurrence of *Palaeomystella oligophaga* galls.

AUTHORS' CONTRIBUTIONS: MICR, WSA: Conceptualization; MICR, PIAB, SCOS, MSD, JMGR: Methodology, Software, Data curation, Formal analysis, Writing – original draft, Visualization, Investigation; JMGR, WSA: Writing – review & editing; WSA: Funding acquisition, Supervision. All authors actively participated in the discussion of the results, they reviewed and approved the final version of the paper.

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