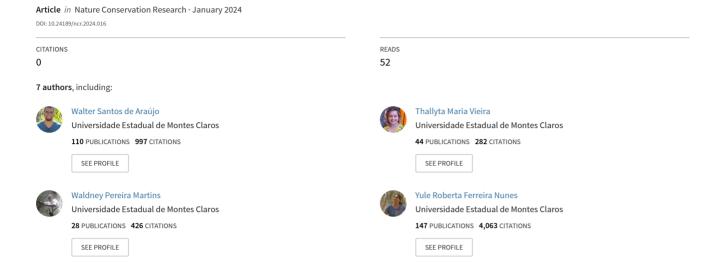
Impact of vereda dryness on the insect herbivore diversity in adjacent cerrado areas in Brazilian Protected Areas



IMPACT OF VEREDA DRYNESS ON THE INSECT HERBIVORE DIVERSITY IN ADJACENT CERRADO AREAS IN BRAZILIAN PROTECTED AREAS

Walter S. de Araújo^{1,*}, Luana T. Silveira¹, Luiz A. D. Falcão¹, Thallyta M. Vieira¹, Waldney P. Martins¹, Yule R. F. Nunes¹, Julio M. Grandez-Rios^{2,3}

¹Universidade Estadual de Montes Claros, Brazil ²Universidade Federal do Rio de Janeiro, Brazil ³Instituto de Investigaciones de la Amazonía Peruana, Peru *e-mail: walterbioaraujo@gmail.com

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Unravelling the factors that influence plant-insect interactions remains a fundamental concern in terrestrial ecology. In the present study, we evaluated the impact of varying degrees of drying on cerrado areas adjacent to veredas on the species richness, abundance and composition of the insect herbivore fauna. Additionally, we examined differences in these impacts between various guilds (chewing and sucker insects) and developmental stages (adult and immature insects). The research has been performed in study areas located in three Protected Areas in Brazil. In total, we recorded 106 species of herbivorous insects across five orders (Coleoptera, Hemiptera, Hymenoptera, Lepidoptera, and Orthoptera). Hemiptera and Coleoptera stood out as the orders with the highest species diversity and individual numbers. Among the families, Cicadellidae and Curculionidae exhibited the highest richness in species and abundance of individuals. We found that richness of herbivorous insects was higher in wet zones (20.2 \pm 6.5) of the veredas compared to dry zones (12.3 \pm 7.5), as well as the abundance of herbivorous insects was higher in wet zones (49.4 \pm 25.5) than in the dry zones (15.8 \pm 7.9). Whithin insect guilds, the abundance of chewing insects was higher in wet zones (34.0 \pm 13.6) than in dry zones (16.3 \pm 14.8), but this difference was not observed for the diversity of sucking insects. Regarding developmental stage, immature insects exhibited higher species richness in wet zones (10.4 \pm 5.0) compared to dry zones (5.3 \pm 2.1), while adult insect diversity did not show differences between the studied zones. Furthermore, the species composition of herbivorous insects, various trophic guilds (chewers and suckers) and developmental stages (adults and immature insect) did not significantly differ among the zones studied within the veredas. According to our findings, herbivorous insects exhibit a preference for wet environments, which provide better conditions and higher-quality food resources for development and reproduction.

Key words: feeding guilds, habitat modification, herbivorous insects, palm swamps, savannas

Introduction

The diversity of herbivorous insects is remarkably high in tropical ecosystems (Stork, 2018; Slade & Ong, 2023). However, most of the studies are focused on humid tropical forests (Godfray et al., 1999; Novotny & Miller, 2014), whereas comprehensive understanding of this diversity in the tropical savannas is notably scarce (Del-Claro & Torezan-Silingardi, 2009). For instance, the Brazilian Cerrado is a savannic biome, recognised for its ecological richness, and harbours a high number of plant species, thus providing a vast niche for a wide range of herbivorous insects (Araújo et al., 2014; Cintra et al., 2020). While studies on biodiversity in the Cerrado region have increased (Borges et al., 2015), there are still gaps in the understanding of herbivorous insects and their impact on savanna ecosystems (Del-Claro & Torezan-Silingardi, 2009). The

complex interactions among insects, host plants, and other organisms in the Cerrado offer valuable insights into tropical ecological dynamics, emphasising the pressing need for further in-depth research to fill this knowledge gap.

Brazilian Cerrado encompasses a range of ecosystems from open grasslands to savannas and forested areas (Ratter et al., 1997). Among these physiognomies, the cerrado *sensu stricto* stands out as the most widely distributed savanna physiognomy, constituting 70% of the Cerrado area (Ribeiro & Walter, 2008). This vegetation consists of spaced trees within an herbaceous-shrub matrix dominated by grasses. Another vegetation typical in the Cerrado are the veredas. This is a very typical landscape in the Cerrado formed by hygrophilous forests, characterised by the dominance of the palm tree *Mauritia flexuosa* L.f. and wetland conditions, surrounded by grasslands and Neotropical

savannas (Ávila et al., 2021; Nunes et al., 2022). These veredas play a pivotal role in maintaining regional hydrological balance, acting as natural filters and regulating water flow, and they function as indicators of water availability for the surrounding vegetation (Nunes et al., 2022).

In recent years, the Brazilian Cerrado biome has faced pressing environmental challenges due to habitat degradation and fragmentation (Colli et al., 2020). These impacts, primarily driven by human activities in agriculture and livestock, have been increased by climate changes (Diniz-Filho et al., 2020). The accumulation of these impacts has led to changes in water availability, resulting in the drying out of the veredas, which affects all the surrounding ecosystems (Nunes et al., 2022). Recent studies have reported that veredas of southeastern Brazil are currently undergoing a drying trend, largely attributed to significant historical anthropogenic impacts (Ávila et al., 2021; Nunes et al., 2022). These human-induced pressures on the landscape primarily entail the removal of natural vegetation and the establishment of monocultures and pastures (Nunes et al., 2022). Consequently, the veredas have suffered from a reduction in the water table level, decreased water flow in the vereda channel, soil moisture reduction, and high mortality of wetland species (Nunes et al., 2022). The drying process of the veredas initially occurs in the highlands near the springs (upstream zone) and extends towards the lowlands (downstream zone); therefore, the zones that were previously humid in the paths are now dry. The drying out of vegetation, such as the veredas in the Cerrado, can have pronounced impacts on the occurrence and diversity of insect species. Although this is an urgent matter, there are few studies evaluating the impacts of the drying out of the veredas on biodiversity, particularly herbivorous insects (Nunes et al., 2022; Araújo et al., 2024).

The reduction in water availability directly affects the abundance and distribution of plant species (Nunes et al., 2022), which serve as potential resources for herbivorous insects. As these insects rely on specific plant hosts for food and habitat, the diminishing availability of these plants can significantly impact their populations. Additionally, water deficit in the vegetation can increase plant stress (Osakabe et al., 2014), which may impact the occurrence of insects on plants (Huberty & Denno, 2004). Moreover, the alterations in the surrounding landscape prompt shifts under microclimatic conditions, affecting

the suitability of the environment for different insect species. For instance, recent studies have discussed that free-living herbivorous insects of various trophic guilds (e.g. chewers and suckers) and at various ontogenetic stages (e.g. immatures and adults) may exhibit distinct responses to anthropogenic environmental changes (Oliveira et al., 2020; Silveira & Araújo, 2021). The alteration of plant characteristics due to drying not only directly impacts the herbivorous insect populations but also disrupts the intricate ecological balance, potentially leading to cascading effects on other trophic levels and the overall biodiversity of the region.

The increasing impacts on the Cerrado vegetation offers a unique opportunity to explore how these species respond to the changing state of vegetation. Thus, our aim was investigating the diversity of insect herbivores in cerrado areas located adjacent to wet and dry zones in Brazilian veredas. For this purpose, we tested the following hypotheses: 1) the species richness and abundance of herbivorous insects are higher in cerrado areas adjacent to vereda wet zones than in cerrado areas adjacent to vereda dry zones; 2) the species composition of herbivorous insects differs between cerrado areas in the dry and wet zones of the veredas; 3) herbivorous insects from various trophic guilds and developmental stages exhibit distinct response patterns to environmental drying.

Material and Methods

Study area

The research has been carried out in vereda ecosystems situated in the Northern region of Minas Gerais state, Brazil (Fig. 1). The study area is located within the domain of the Brazilian Cerrado and presents various types of phytophysiognomies, such as riparian forests, hygrophilous forests (veredas), savannas (cerrado sensu stricto), and grasslands (campos) (Ribeiro & Walter, 2008). However, the northern region of Minas Gerais state is close to the transition with the Caatinga, a typically arid Brazilian ecosystem, which influences the vegetation of the study area, with the occurrence of some dry forests (mata seca) (Ávila et al., 2021). The climate in the study area is tropical, designated as Aw in the Köppen classification (Alvares et al., 2013). The climate is characterised by dry winters and an average annual temperature ranging between 22.2°C and 22.7°C. Annually, the study area experiences rainfall ranging at 1008-1073 mm.

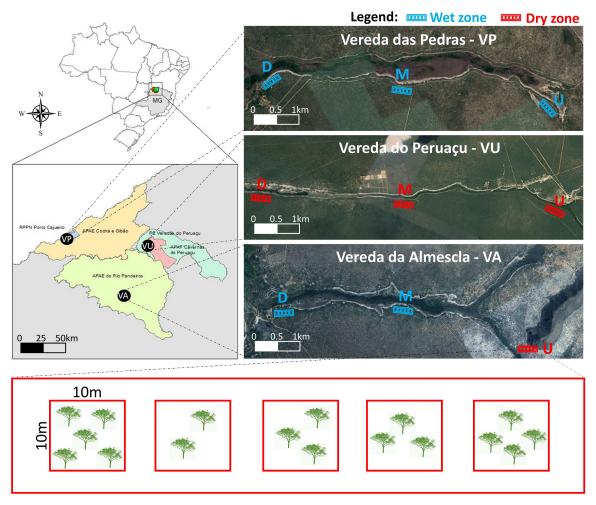


Fig. 1. Location of the three studied veredas in the Northern region of Minas Gerais state, Brazil, namely Vereda das Pedras located in the PNHR Porto Cajueiro in the Cochá e Gibão Environmental Protection Area, Vereda da Almescla situated in the Rio Pandeiros Environmental Protection Area, and Vereda do Peruaçu located in the Veredas do Peruaçu State Park. In each vereda, the study was performed along the upstream (U), midstream (M), and downstream (D) areas, which represent wet vereda zones (blue plots) and dry vereda zones (red plots). Sampling was performed in adjacent cerrado, on woody plants found within five 10×10 -m plots. The plot representations on the veredas are illustrative and not to scale.

Data collection took place in three distinct veredas located in various Protected Areas (Fig. 1), namely 1) Vereda das Pedras (14.8883° S, 45.3419° W), located within the Private Natural Heritage Reserve (PNHR) Porto Cajueiro in the Cochá e Gibão Environmental Protection Area, in the municipality of Januária; 2) Vereda da Almescla (15.3602° S, 44.9125° W) situated in the Rio Pandeiros Environmental Protection Area, in the municipality of Bonito de Minas; 3) Vereda do Peruaçu (14.9369° S, 44.6289° W) located in the Veredas do Peruaçu State Park, spanning the municipalities of Januária and Cônego Marinho. Each studied vereda covers an area of approximately 6 km in length and maintains an altitude varying 800-900 m a.s.l. All studied veredas are characterised by hygrophilous forests dominated by Mauritia flexuosa palms, surrounded by open field areas (grasslands) and cerrado *sensu stricto* (savannas), usually situated in a transitional strip spanning a few meters (less than 100 m).

Recent studies show that the veredas in the northern region of Minas Gerais state are undergoing a drying process (Avila et al., 2021; Nunes et al., 2022). In these veredas, the decline in the water table level first occurs in the highlands near the springs, in the early stages of drying; only the vereda upstream zone is dry, while moisture persists in the lower areas. On the other hand, in veredas in an advanced stage of drying, both the highlands (upstream zone) and the lowlands (downstream zone) are dry. Therefore, the selected veredas in the present study represent various levels of drying, with variations in the quantity of dry and humid zones along its length, ranging from completely dried-up ones (e.g. Vereda do Peruaçu: dry

zones in upstream and downstream regions), partially dried-up veredas (e.g. Vereda da Almescla: dry zones only in upstream region), and veredas still showing no signs of drying (e.g. Vereda das Pedras: no dry zones) (Fig. 1).

Data collection

The sampling of herbivorous insects was conducted on trees located in the cerrado sensu stricto areas adjacent to wet and dry zones in each vereda (Fig. 1). At each sampling location, five plots of 100 m² were established, where all plants with a circumference equal to or higher than 15 cm were selected for insect sampling. Herbivorous insect collection was conducted on each plant by selecting three branches, where the procedure of beating with an entomological umbrella was carried out (10 beats per branch). Gathered specimens were stored in appropriately labelled containers with 70% alcohol. The insects were identified to the most precise taxonomic level possible and classified into morphospecies based on their external morphological features. Only insect taxa recognised as phytophagous were chosen, in line with information found in the literature (e.g. Carrano-Moreira, 2014). The herbivorous insects were differentiated into suckers and chewers based on their mouthpart type and were also separated into immature (larvae and nymphs) and adults.

Data analyses

We tested if the species richness and abundance of insect herbivores differed between dry and wet zones using generalised linear mixedeffects models (GLMMs) with error distribution of Poisson. In each model, the vereda zones (dry vs. wet) were used as a fixed effect variable and the veredas (Vereda do Peruaçu, Vereda da Almescla, and Vereda das Pedras) as a random effect variable. This criterion was adopted to control possible intrinsic differences between various veredas that may affect the diversity of insects. The models were built considering all herbivorous insects together and also separately for suckers, chewers, adults, and immatures. We also performed the same analysis to compare if the plant species richness differs between dry and wet zones. GLMMs were tested using Chisquare tests and analyses were performed using the lme4 package (Bates et al., 2015).

To test differences in the insect composition between the dry and wet zones, we have carried out an analysis of non-metric multidimensional scaling (NMDS) using abundance data and Bray-Curtis index. In sequence, we performed a nonparametric permutation procedure (ANO-SIM) using the Bray-Curtis index with 999 permutations to test the significance of groups formed by NMDS (Hammer et al., 2001). Values of P and R were obtained to show patterns of similarity among the insect composition of dry and wet zones. These analyses were realised using the metaMDS function in the vegan package. All statistical analyses were conducted in R software ver. 4.2.3 (R Core Team, 2023).

Results

In total, 106 species and 458 individuals of herbivorous insects were sampled, distributed across the orders Coleoptera, Hemiptera, Hymenoptera, Lepidoptera, and Orthoptera (Electronic Supplement 1). The order Hemiptera was the richest with 44 species and the most abundant with 222 individuals. At second rank, was the order Coleoptera with 36 species and 190 individuals. The insects were distributed among 34 families, with special mention to Cicadellidae (Hemiptera) with 123 individuals and 17 species, and Curculionidae (Coleoptera) with 96 individuals and 16 species.

The plant species richness did not differ between the dry (39.0 ± 21.1) and wet (38.6 ± 24.9) zones of the studied veredas (Table 1). On the other hand, the species richness of herbivorous insects was higher in the wet zones (20.2 ± 6.5) compared to the dry zones (12.3 ± 7.5) (Fig. 2a). Furthermore, the abundance of sampled insects was three times higher in the wet zones (49.4 ± 25.5) than in the dry zones of the veredas (15.8 ± 7.9) (Fig. 2b). However, the species composition of herbivorous insects did not differ between the studied dry and wet areas (Stress = 0.063, r = -0.084, p = 0.600).

The guild of chewers was represented by 59 species and 235 individuals, while the suckers had 47 species and 223 individuals. For sucking insects, no differences in species richness and abundance were observed between dry and wet zones (Table 1), but chewing insects showed a higher abundance in wet zones (34.0 \pm 13.6) than in dry zones (16.3 \pm 14.8) (Fig. 3a). The species composition did not differ between dry and wet zones, neither for suckers (Stress = 0.000, r = -0.006, p = 0.443) nor for chewers (Stress = 0.054, r = 0.003, p = 0.383).

Table 1. Results of the generalised linear mixed-effects models (GLMM's) evaluating the effects of vereda zone (dry vs. wet) on the plant species richness and insect herbivore diversity variables in adjacent cerrado areas, in the Northern region of Minas Gerais, Brazil

Response variables	Chi-square	p-value
Plant species richness	0.044	0.834
All herbivorous insect richness	3.885	0.049
All herbivorous insect abundance	8.088	0.004
Chewing insect richness	3.636	0.057
Chewing insect abundance	4.505	0.034
Sucking insect richness	2.613	0.106
Sucking insect abundance	0.360	0.549
Adult insect richness	3.403	0.065
Adult insect abundance	2.216	0.137
Immature insect richness	4.655	0.031
Immature insect abundance	0.180	0.672

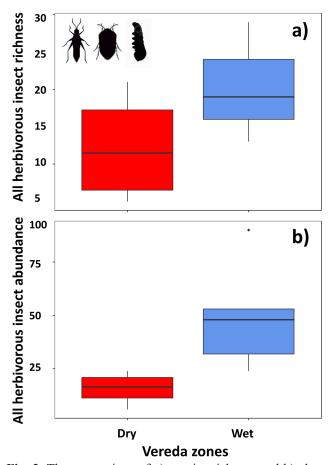
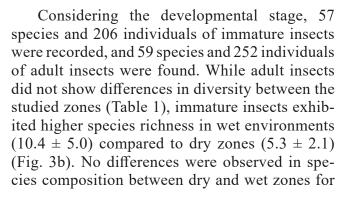


Fig. 2. The comparison of a) species richness and b) abundance of all insect herbivores between vereda zones in the Northern region of Minas Gerais, Brazil.



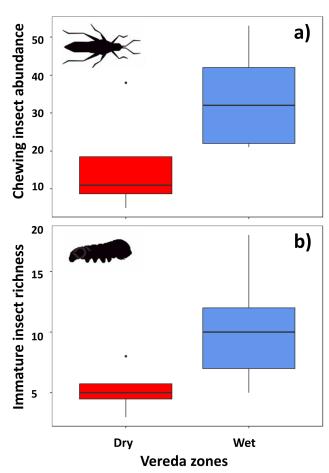


Fig. 3. Comparison of a) chewing abundance and b) immature species richness of insect herbivores between vereda zones in the Northern region of Minas Gerais, Brazil.

adults (Stress = 0.001, r = 0.037, p = 0.322) and immatures (Stress = 0.031, r = 0.046, p = 0.291).

Discussion

The results of our study provide valuable insights into the response of herbivorous insect communities to the drying of veredas and adjacent vegetation. Our key finding is the significant difference in the species richness and abundance of herbivorous insects between wet and

dry zones of the studied veredas. Our results also show that chewer herbivorous insects and immature stages had a higher abundance and species richness in wet environments, respectively. These results align with expectations derived from broader ecological principles and are consistent with studies comparing the distribution of insect herbivores in mesic and xeric habitats (e.g. Silva et al., 2009; Leal et al., 2015). Although there is considerable evidence of a positive correlation between plant and herbivorous insect diversity (Tews et al., 2004; Ricklefs & Marquis, 2012; Araújo, 2013), we believe that this should not be the primary mechanism in our study, as plant species richness did not differ between the dry and wet areas studied. The higher richness and abundance of herbivorous insects in wet zones, as compared to their dry counterparts, can be attributed to the increased availability of food quality and microclimatic characteristics between the studied environments.

Previous studies have reported the preference of herbivorous insects for mesic environments compared to xeric ones (e.g. Fernandes & Price, 1988; Silva et al., 2009; Neves et al., 2010; Leal et al., 2015). Mesic environments, characterised by a higher humidity and water availability, provide favourable conditions for plant development and, consequently, constitute more suitable habitats for free-living herbivorous insects (Fernandes & Price, 1988). The presence of lush vegetation and consistent water availability not only offer abundant food resources but also create more stable microclimates conducive to the life cycle of these insects (Ribeiro & Fernandes, 2000). In contrast, xeric environments, with low humidity and limited water resources, can pose significant challenges for the survival and reproduction of herbivores (Fernandes & Price, 1988). The results of our study corroborate these general patterns observed in previous studies, as comparing dry and wet environments along the veredas represents an ecological contrast between xeric and mesic habitats, respectively.

The variation in environmental characteristics between dry (i.e. xeric) and humid (i.e. mesic) habitats can play a crucial role in determining the quality of food available to herbivorous insects (Ribeiro & Fernandes, 2000). Humid environments often provide more favourable conditions for the growth and development of plants, resulting in higher plant biomass (Herms & Mattson, 1992). On the other hand, water stress can

induce molecular, physiological, and morphological modifications in plants (e.g. Kar, 2011; Züst & Agrawal, 2017; Sestari & Campos, 2022). In the case of Cerrado plants, water stress, coupled with other stressors such as nutrient-poor and aluminum-rich soils, can intensify sclerophylly in plant tissues, making them less palatable to insect herbivores (Ribeiro & Fernandes, 2000). The nutritional quality of these plants, in turn, can directly influence the richness and abundance of herbivorous insects, as species may respond differently to variations in food resources (Kansman et al., 2022). Furthermore, the specific microclimatic characteristics of each habitat can modulate the availability of resources, influencing trophic interactions between herbivores and plants (Leal et al., 2015). In humid environments, milder climatic conditions may provide a more conducive environment for insect activity and reproduction, contributing to differentiated patterns of species richness and abundance compared to dry environments.

The impact of environmental stress on herbivorous insects extends beyond plant responses, encompassing distinct reactions in immature and adult stages (Silveira & Araújo, 2021). Water stress can impose selective pressures on insect populations, being expected more drastic effects on the immature stages. In the face of limited water availability, immature insects may exhibit altered growth patterns and development rates, potentially impacting their overall fitness (Keosentse et al., 2022). Additionally, water stress can influence the nutritional content of plant tissues, affecting the quality of food resources available to immature insects. In contrast, adult insects may demonstrate behavioural adaptations (Yang, 2001), such as modified foraging patterns or altered reproductive strategies, in response to water stress. The intricate interplay between water stress and the life stages of herbivorous insects is a subject that still needs to be further investigated.

The distribution of sucking and chewing herbivorous insects across diverse environments may reflect specific responses of these groups to varied environmental conditions (Rossetti et al., 2014; Araújo & Oliveira, 2021; Kuchenbecker et al., 2021). Both groups, employing distinct feeding strategies, may demonstrate different levels of ecological specialisation in response to the specific characteristics of each environment (Novotny et al., 2010). For instance, sucking insects,

adapted to extracting nutrients directly from plant tissues, may exhibit a more homogeneous distribution, regardless of variations in environments (Araújo & Oliveira, 2021). In contrast, chewing insects, which consume more external parts of plants, may show a distribution more sensitive to local conditions in savannas (Araújo & Oliveira, 2021), especially if the availability and quality of host plants are affected by factors such as water stress. Understanding these differences in the distribution of sucking and chewing insects is crucial for a comprehensive understanding of the ecology of these insects in diverse ecosystems.

It is noteworthy that the observed differences in herbivorous insect richness and abundance did not correspond to differences in the species composition between wet and dry areas. This result challenges the expectation that assemblages of herbivorous insects might be distinct in response to varying environmental conditions (Leal et al., 2015). While the composition remained relatively consistent, this suggests that certain species of herbivorous insects are adapted to a range of environmental conditions and can persist in both wet and dry areas (Yang, 2001). This stability in species composition could be attributed to factors such as the presence of generalist herbivores or the ability of certain insect species to exhibit phenotypic plasticity in response to changing environmental conditions (Araújo & Oliveira, 2021). Additionally, the lack of significant compositional differences may reflect the spatial and temporal scale of our study, which might not capture more nuanced variations occurring over longer periods.

The study has delved into the intricate dynamics of plant-insect interactions within the unique ecological contexts of neotropical savannas in an ecotonal region between Cerrado and Caatinga ecosystems (Ávila et al., 2021). The results underscored the significance of wet environments in fostering higher species richness, abundance, and diversity of herbivorous insects, with wet zones exhibiting notably higher values compared to dry zones. Notably, within the studied areas located in conservation units across Brazil, the observed preference of herbivorous insects for wetter environments suggests the necessity of preserving these habitats to maintain biodiversity effectively. Conservation managers need to recognise the specific habitat preferences of these insects, particularly their preference for wetter environments, and prioritise the protection and restoration of such habitats within the conservation units. Furthermore, the findings accentuate the role of climate change as a selective pressure, as shifts in precipitation patterns influence habitat suitability for insect populations. Understanding these dynamics is vital for informed conservation strategies aimed at mitigating the impacts of environmental changes on insect communities and, consequently, broader ecosystem health within these ecologically significant regions.

Conclusions

Our study contributes to the literature on how insect communities respond to changing environmental conditions, specifically the drying out of natural vegetation. The conservation of veredas and adjacent vegetation plays a crucial role in maintaining the biodiversity of herbivorous insects, particularly emphasising the importance for chewing and immature insects, which exhibits higher sensitivity to drying effects. Our findings indicates that the wet environments provide better conditions for the development and reproduction of free-living insects, offering higher-quality food resources and more favourable microclimates, mitigating the potential impacts of water stress. Future studies may explore additional responses of herbivorous insects to the drying of veredas, such as variations in the fitness of herbivorous insects along these environments and also the configuration of interaction networks between these insects and their host plants.

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Supporting Information

Additional data to the paper of Araújo et al. (2024) can be found in the **Supporting Information**.

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ВЛИЯНИЕ ЗАСУХИ НА РАЗНООБРАЗИЕ НАСЕКОМЫХ-ФИТОФАГОВ В ЗАБОЛОЧЕННЫХ ПАЛЬМОВЫХ РЕДКОЛЕСЬЯХ НА ТЕРРИТОРИЯХ СЕРРАДО, ПРИЛЕГАЮЩИХ К ООПТ БРАЗИЛИИ

В. С. Араужо^{1,*}, Л. Т. Сильвейра¹, Л. А. Д. Фалькао¹, Т. М. Виейра¹, У. П. Мартинс¹, Ю. Р. Ф. Нуньес¹, Х. М. Грандес-Риос^{2,3}

¹Государственный университет Монтес-Кларос, Бразилия ²Федеральный университет Рио-де-Жанейро, Бразилия ³Перуанский исследовательский институт Амазонки, Перу *e-mail: walterbioaraujo@gmail.com

Выяснение факторов, влияющих на взаимодействие растений и насекомых, остается фундаментальной проблемой экологии. В настоящем исследовании проведена оценка влияния различной степени засухи территорий серрадо, прилегающих к пальмовым болотам, на видовое богатство, численность и состав фауны насекомых-фитофагов. Также были изучены различия в этих воздействиях между различными группами способа питания (грызущих и сосущих насекомых) и стадиями развития (взрослые и молодые насекомые). Исследование проводилось на участках трех особо охраняемых природных территорий Бразилии. Всего было зарегистрировано 106 видов насекомых-фитофагов из пяти отрядов (Coleoptera, Hemiptera, Hymenoptera, Lepidoptera и Orthoptera). Отряды Hemiptera и Coleoptera характеризовались наибольшим видовым разнообразием и числом особей. Среди семейств наибольшим видовым богатством и обилием особей отличались Cicadellidae и Curculionidae. Установлено, что видовое богатство насекомыхфитофагов было выше во влажных зонах (20.2 ± 6.5) пальмовых болот по сравнению с сухими зонами (12.3 ± 7.5) . Численность особей насекомых-фитофагов во влажных зонах (49.4 ± 25.5) была также выше по сравнению с сухими зонами (15.8 ± 7.9). Численность грызущих насекомых во влажных зонах была выше (34.0 ± 13.6) , чем в сухих зонах (16.3 ± 14.8) , но для группы сосущих насекомых-фитофагов различий между зонами увлажнения не было отмечено. Сравнение насекомых разных стадий развития показал, что для группы молодых насекомых отмечено более высокое видовое богатство во влажных зонах (10.4 ± 5.0) по сравнению с сухими зонами (5.3 ± 2.1) , тогда как разнообразие взрослых насекомых не имело значимых различий между изученными зонами. При этом не было обнаружено значимых различий между зонами увлажнения (влажные - сухие) по видовому составу насекомых-фитофагов, их группам по типу питания (грызущие и сосущие насекомые) и стадиям развития (взрослые и молодые насекомые) в пределах каждого изученного пальмового болота. По полученным данным, насекомые-фитофаги отдают предпочтение влажным местообитаниям, которые обеспечивают лучшие условия и более качественные пищевые ресурсы для их развития и размножения.

Ключевые слова: группы способа питания, модификация местообитания, пальмовые болота, травоядные насекомые, саванны