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Individual-based plant-visitor networks in Brazilian palm swamps under different dryness levels

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Abstract
Interactions between plants and floral visitors have a significant influence on the structure and function of ecosystems. The study of these interactions can be performed through the analysis of ecological networks, allowing an understanding of the complexity of ecosystem functioning. The objective of the present study was to verify whether the characteristics of individuals of *Byrsonima intermedia* (Malpighiaceae) affects its role in the network of interactions with floral visitors in Brazilian palm swamps (*veredas*). *Veredas* with different levels of dryness were studied, including one degraded *vereda* (advanced stage of drying), one intermediate *vereda* (low drying), and one preserved *vereda* (no drying). For sampling, we selected 45 individuals of the *Byrsonima intermedia* plant, 15 in each area, where they were monitored to observe the behavior of floral visitor insects and to measure the characteristics of the plant individuals. As a result, the networks of all sampled area were significantly modular and specialized, with the preserved *vereda* showing greater specialization. In this study, we observed that the networks of individuals of *Byrsonima intermedia* and their floral visitors were mainly composed of non-oil-collecting bees. The results show that the abundance of resources offered by each individual in the network, the size of the flower and the plant height are some factors that can determine its role in the network of interactions in the studied *veredas*. Finally, it is concluded that individual plant interactions can be affected both by environmental characteristics and by plant morphological attributes.

Keywords Cerrado · Ecological networks · Morphological traits · Plant-pollinator interactions

Introduction

Interactions between flowering plants and visiting floral insects have a significant influence on the structure and function of ecosystems (Memmott et al. 2007). Pollinators play an essential ecological role, as pollination ensures sexual reproduction, promoting greater genetic variability among plants, and conserving species diversity (Kearns et al. 1998). Understanding insect-plant interactions contributes to our comprehension of the plant reproductive system, and how the animals rely on their flowers, fruits, and other resources (Memmott et al. 2007). These interactions can be studied through the analysis of complex interaction networks (Vizentin-Bugoni et al. 2018), which allows the representation, characterization, and comparison of the complexity of ecological communities (Jordán 2009). This approach promotes a more complete understanding of ecosystem functions (Ings et al. 2009).

Individuals of a particular plant species represent the fundamental units of interaction within the ecological systems they inhabit, and their interactions affect demography and population evolution (Benkman 2013) in various contexts. These ecological interactions among individuals connect populations of different species, influencing community stability and organization (Pascual and Dunne 2006). They control the flow of energy in ecosystems and shape the evolution of community-level traits. Consequently, ecological interactions affect individual fitness, demography, and evolution of population characteristic

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composition (Guimarães 2020). In the simplest scenario, characterized by a homogeneous environment with no individual variation in attributes or preferences, plant-pollinator networks should exhibit a homogeneous structure, resulting in randomness of interactions or fully connected interaction networks (Vizentin-Bugoni et al. 2018; Guimarães 2020; Arroyo-Correa et al. 2021). Networks of individual resources and/or plant-pollinator networks are expected to be structured by differences in resource abundance (resource availability—the quantity of flowers on individual plants for floral visitors) (Guimarães 2020; Arroyo-Correa et al. 2021). However, if there is variation in interactions and the importance of individual plants in sustaining floral visitors within this network, there tends to be a significant role played by variability in space, time, and, most importantly, the attributes of these individuals. For example, variations in size and morphological attributes among individuals of a plant species are expected to represent different quantities and qualities of resources for floral visitors, influencing the structure of their interactions and, consequently, their reproductive success (Araújo et al. 2008; Guimarães 2020; Arroyo-Correa et al. 2021).

Understanding how interactions between plants and floral visitors are affected by disturbances is crucial for predicting the ecological and evolutionary processes in the face of ongoing changes (Tylianakis et al. 2008). For instance, the intensification of habitat modification due to human activities tends to reduce biodiversity, in both plants and insects, which can disrupt ecological interactions (Tylianakis et al. 2010). Studies have indicated that interactions between flowers and floral visitors are highly sensitive to habitat disturbance (Spiesman and Inouye 2013; Stout 2014; Valiente-Banuet et al. 2015). Habitat loss can alter species composition, negatively affect species richness and abundance, and consequently affect interspecific interaction networks within a community (Spiesman and Inouye 2013). Due to human activities, natural ecosystems have been extensively altered, leading to a decline in both plant and insect biodiversity and their ability to provide essential services for our survival, as well as for their conservation and maintenance (Memmott et al. 2007; Tylianakis et al. 2010).

Some pollinators require undisturbed areas for nesting, pollination, and foraging, which makes them vulnerable to habitat degradation (Kearns et al. 1998; Senapathi et al. 2015). These disturbances often lead to a reduction in the abundance and diversity of floral resources (such as pollen and nectar) and the destruction or degradation of natural habitat refuges (Ollerton et al. 2011). Therefore, understanding how networks of individuals are structured and which processes are essential for the dynamics of these interactions represents a crucial step in understanding how anthropogenic disturbances can affect interactions within individual-based networks.

Palm swamp forests, also called *veredas*, are important floodable communities found in wetlands of the Brazilian Cerrado. The main disturbances in these ecosystems are agricultural and livestock activities, cattle trampling, clay and peat exploitation, urbanization encroachment, road construction, and drainage channel development (Nunes et al. 2022). These disturbances lead to soil desiccation, sedimentation, erosion, a decline in the water table level, and consequently, alterations in the plant composition of these environments (Ávilla et al. 2021; Nunes et al. 2022). This can result in the loss of floral-visiting insects that are more sensitive and dependent on humid environments, whereas those that are more tolerant to drier conditions, such as insects found in the Cerrado, are likely to be more common in *veredas* undergoing advanced drying processes (Tylianakis et al. 2010; Senapathi et al. 2015). *Veredas* with a higher degree of conservation technically maintain normal conditions that are favorable for plants to provide floral resources, thus sustaining more specialist floral visitors (Souza et al. 2016). The floristic composition of *veredas* can vary according to their zones: the edge zone, closest to the Cerrado with well-drained soil; the middle zone, with soil saturated with water for a significant part of the year; and the fund zone, where the soil remains permanently waterlogged (Araújo et al. 2009). Palms of the species *Mauritia flexuosa* L.f., commonly known as *buriti*, are found in the wettest zones of *veredas* (Araújo et al. 2009).

The present study aimed to investigate whether the individuals' characteristics of *Byrsonima intermedia* A. Juss. (Malpighiaceae) affect their role in the interaction network with floral visitors in *vereda* areas at different conservation states (degree of drying). Specifically, we addressed the following questions: (1) Who are the plant's floral visitors? What is the structure of the networks accounting for these individuals and their floral visitors? And which individuals play crucial roles in the interaction network, thus probably contribute ensuring reproductive success at the species level? (2) What is the primary ecological driver of individual roles in the network, considering predictors based on niche (individual size, morphological differences, and distribution in the community) and neutrality (abundance of floral resources)? (3) Do these patterns vary between *vereda* areas at different conservation stages (level of drying)?

Materials and methods

Study area

The study was conducted in three *veredas* located in Northern Minas Gerais, Brazil (Fig. 1). These are: 1) Vereda das Pedras (14°53′18″ S and 45°20′31″ W), located within the Private Natural Heritage Reserve Porto Cajueiro (RPPN

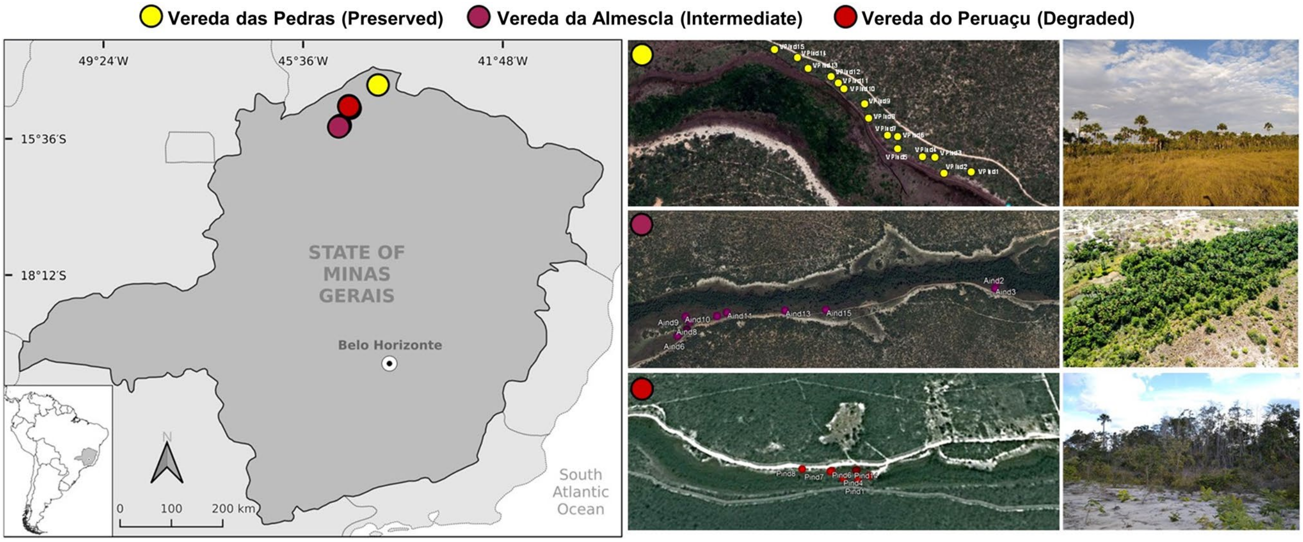


Fig. 1 Location of the sampled *veredas* (Vereda das Pedras—preserved *vereda*, Vereda da Almescla—intermediate *vereda*, and Vereda do Peruaçu—degraded *vereda*) in Minas Gerais State (Brazil) and the distribution of *Byrsonima intermedia* individuals sampled in each of them

Porto Cajueiro), in the municipality of Januária; 2) Vereda da Almescla (15°21′37.2″ S and 44°54′45.9″ W) located within the Environmental Protection Area of Rio Pandeiros (EPA Rio Pandeiros), in the municipality of Bonito de Minas; 3) Vereda do Peruaçu, within the Veredas do Peruaçu State Park (PEVP) (14°56′13″ S and 44°37′44″ W), situated in the municipality of Cônego Marinho. The climate in the region where these *veredas* are located falls under the *Aw* category according to Köppen classification, with an average temperature of 22 °C and an annual average precipitation around 1000 mm (Alvares et al. 2014). This climate is characterized by a distinct dry season, particularly pronounced during the winter (Alvares et al. 2014).

The three studied *veredas* exhibit different conservation states as follows: Vereda das Pedras is a no signs of anthropogenic activities area unlike what is observed in the other studied *veredas* (Ávila et al. 2021; Nunes et al. 2022). Therefore, this area was taken as the preserved *vereda*. The Vereda da Almescla is undergoing a drying process, where anthropogenic activities such as livestock farming, agriculture, grazing, timber extraction, and wildfires are noticeable (Ávila et al. 2021; Nunes et al. 2022). However, it is still possible to observe water-saturated soil due to high water table levels and the presence of typical vegetation of hydrophilic environments. Therefore, this area was taken as the intermediate disturbance *vereda*. The Vereda do Peruaçu shows an advanced state of degradation and drying (Nunes et al. 2022). As a result, soil drying has occurred, leading to the death of a significant portion of *Mauritia flexuosa* L.f. (buriti) individuals and the encroachment of cerrado *sensu stricto* plants into the *vereda*. Therefore, this area was taken as the degraded *vereda*.

Study system

The target plant of this study is *Byrsonima intermedia* A. Juss., commonly known as *murici-pequeno*. It is native to the Cerrado biome and occurs in both xeric and wetland environments (Sannomia et al. 2007; Magalhães et al. 2013; Balestra et al. 2014). Its distribution extends widely throughout Brazil, particularly in the North, Northeast, and Central-West regions of the country (Guimarães et al. 2021). It has a shrubby habit, reaching heights of approximately 0.5 to 2.5 m (Sannomia et al. 2007; Balestra et al. 2014). The plant produces showy, yellow-colored, hermaphroditic, zygomorphic flowers arranged in terminal racemes. Its anthesis is diurnal, and the flowers last an average of 48 h (Filho and Lomônaco 2006). The corolla consists of five petals alternating with sepals, with the upper petal (standard) differing from the others. Each of its sepals contains a pair of oil-producing glands (elaiophores) (Oliveira et al. 2007). This plant is self-incompatible and primarily pollinated by bees, offering oil and pollen as floral resources (Boas et al. 2013; Balestra et al. 2014).

Sampling of plant-visitor interactions

The sampling was conducted on three campaigns, being October 2021, May/June 2022, and November 2022, with two consecutive days of sampling employed per area in each campaign. A total of 45 individuals of *Byrsonima intermedia* were selected for the study, with 15 individuals in each *vereda*. The individuals of *B. intermedia* sampled in the three *veredas* were selected to cover the entire study area and were separated at least 5 m from each other, in order to promote a spatially balanced sampling—GRTS (Generalized Random Tessellation Stratified Sampling) where sample effort is spread evenly over the target region (Brown et al. 2015; Fig. 1). Field observations of floral visitors' behavior (defined by the bee's contact with the flower structure) were recorded through direct observations on focal plants during 40 min per plant (two observers on the field), being 20 min in the morning (7 a.m. to 10 a.m.) and 20 min in the afternoon periods (2 p.m. to 5 p.m.). In total our sampling resulted in 5,400 min of sampling in all study (approximately 120 min per individual).

After observation, all floral visitors were collected using an entomological net and subsequently preserved in 70% alcohol for later identification based on morphological characteristics. All collected floral visitors were identified using taxonomic keys at the family and genus levels (Silveira et al. 2002; Oliveira et al. 2013), followed by specific keys for each genus. All collected floral-visiting insects were deposited in the Laboratory of Ecological Interactions and Biodiversity of the Universidade Estadual de Montes Claros.

Measuring the attributes of plant individuals

To assess the potential factors determining the structure of the individual network, we quantified the number of flowers on each individual (floral resource availability on each individual). This quantification was performed by selecting a branch, where we counted the number of inflorescences, multiplied this value by the number of flowers and buds on an inflorescence, and extrapolated this value to the entire individual. Additionally, we recorded the floral and vegetative attributes of each of these individuals to assess morphological variation. The characteristics evaluated included plant height (in meter) and floral size (width and length in millimeter), using five flowers per individual (following Machado and Lopes 2004; Carvalheiro et al. 2014; Souza et al. 2018; Arroyo-Correa et al. 2021).

Statistical analyses

The interaction networks were constructed using a quantitative matrix, with individuals of sampled *Byrsonima intermedia* in the rows, and the observed floral visitors in the columns. A matrix was created for each study area, aggregating all the data sampled in each *vereda*. Sampling effort was assessed considering each combination of an individual plant and a species of floral visitor as a "species", and the frequency of each interaction between pairs in the network as "abundance" (Vizentin-Bugoni et al. 2016). Interaction diversity was estimated using the Chao1 species richness estimator, and the sampling effort was calculated as the ratio between the observed and estimated richness of interactions (Chacoff et al. 2012). The Chao 1 estimator was calculated using the INEXT package (Hsieh et al. 2014) in the R program (R Development Core Team 2022).

For the analysis at network level, specialization and modularity network-level metrics were calculated. Specialization for each network was calculated using the H2 index, which describes how individuals of *Byrsonima intermedia* distribute their interactions based on partner availability throughout the community (Blüthgen et al. 2006). The modularity index was used to quantify the prevalence of interactions within subsets of individuals in the network. This indicates whether there are modules in the network formed by groups of individuals of *Byrsonima intermedia* that interact more frequently with the same set of floral visitor species in the community. The modularity index was calculated using the DIRTLPAwb + algorithm (Beckett 2016), which takes into account the frequency of interactions, using the *computeModules* function in the *Bipartite* package in the R program (Dormann et al. 2008). Therefore, with the specialization and modularity indices, it was possible to compare the network structure in the three studied *veredas*.

Since topological descriptors of networks can be influenced by the number of species or individuals interacting in the community and sampling effort (Fründ et al. 2016), we compared observed values with values generated by a null model. We used the Vaznull null model (Vázquez et al. 2005), which constrains connectance, network size, and the total number of interactions in each randomization. A 95% confidence interval was estimated for each metric from 10,000 simulated values, and the metric value was considered significant if it did not overlap with the confidence interval generated by the randomizations of the null model used.

In addition to these two network-level indices, four individual-level indices for *Byrsonima intermedia* were also evaluated, capturing distinct topological properties of an individual in the network: (1) degree, expressing the number of interaction partners (floral visitors) each individual of *Byrsonima intermedia* interacts with in the network; (2) weighted betweenness centrality, quantifying on average how often a species/individual lies on the shortest path between other pairs of species/individuals in the network, indicating the importance of a species/individual as a network connector; (3) weighted closeness centrality, which quantifies the closeness of a species/individual to all other species/individuals in the network. Individuals or species with high centrality values can quickly affect other individuals/species in the network and are useful for identifying important individuals of *Byrsonima intermedia* for network formation; (4) species-level specialization (d′), which quantifies how exclusive the interactions of a species/individual are relative to partner availability. All species-level indices were quantified using the *specieslevel* function in the *Bipartite* package in R (Dormann et al. 2008).

The network indices for the individuals of *Byrsonima intermedia* were analyzed using linear models. A comparison was made regarding the roles of species (calculated species level metrics) in each sampled *vereda*. Additionally, simple linear models were created for each *vereda* separately to assess whether the roles of individuals in the networks could vary with their attributes. In these models, the topological network indices of the individuals of *Byrsonima intermedia* were used as the response variable, with individual size (height), the number of flowers produced, and the average size of flowers (length and width) as explanatory variables. All constructed models were checked for residual dispersion and spatial autocorrelation (Moran's I test) using the *Dharma* package (Hartig 2020). All statistical analyses were conducted in the R program (R Development Core Team 2022).

Results

Floral visitors were recorded in 38 out of the 45 *Byrsonima intermedia* individuals sampled. In total, 24 species and 266 individuals of floral visiting bees were collected. The most abundant species were *Tetragonisca angustula* with 78 individuals, *Paratrigona lineata* with 51, *Tropidopedia flavolineata* with 29 and *Trigona spinipes* with 21. The other recorded species had an abundance of less than 20 individuals each.

The individual-based plant-visitor network constructed for the preserved *vereda* (Vereda das Pedras) revealed that out of the 15 sampled individuals, 14 received visits from 12 species of bees, resulting in a total of 108 interactions. In this *vereda*, *Tetragonisca angustula* accounted for nearly half of the observed interactions (46%), followed by *Tetragona clavipes* (16%; Fig. 2). Furthermore, 75% of all estimated interactions were observed, representing a greater sampling effort of interactions across all *veredas* (Observed = 40; Estimator = 53.60; Fig. 3). With respect to the intermediate *vereda* (Vereda da Almescla), the network was composed of 12 individuals of *Byrsonima intermedia* that received visits from 14 species of floral visitors, totaling 80 interactions (Fig. 2). The most frequent visitors were *Trigona hyalinata* (22.4%) and *Paratrigona lineata* (14.4%). The sampling effort for interactions was 56% of all estimated interactions (Observed = 42; Estimator = 74.50; Fig. 3). In the degraded *vereda* (Vereda do Peruaçu), 12 plant individuals received visits from 15 species of bees, totalling 79 interactions. The bees *Paratrigona lineata* (31.6%), *Tetragonisca angustula* (25%) and *Tropidopedia flavolineata* (20%) were the most representative (Fig. 2). The sampling effort represented 69% of sampling of all estimated interactions (Observed = 43; Estimator = 62.46; Fig. 3).

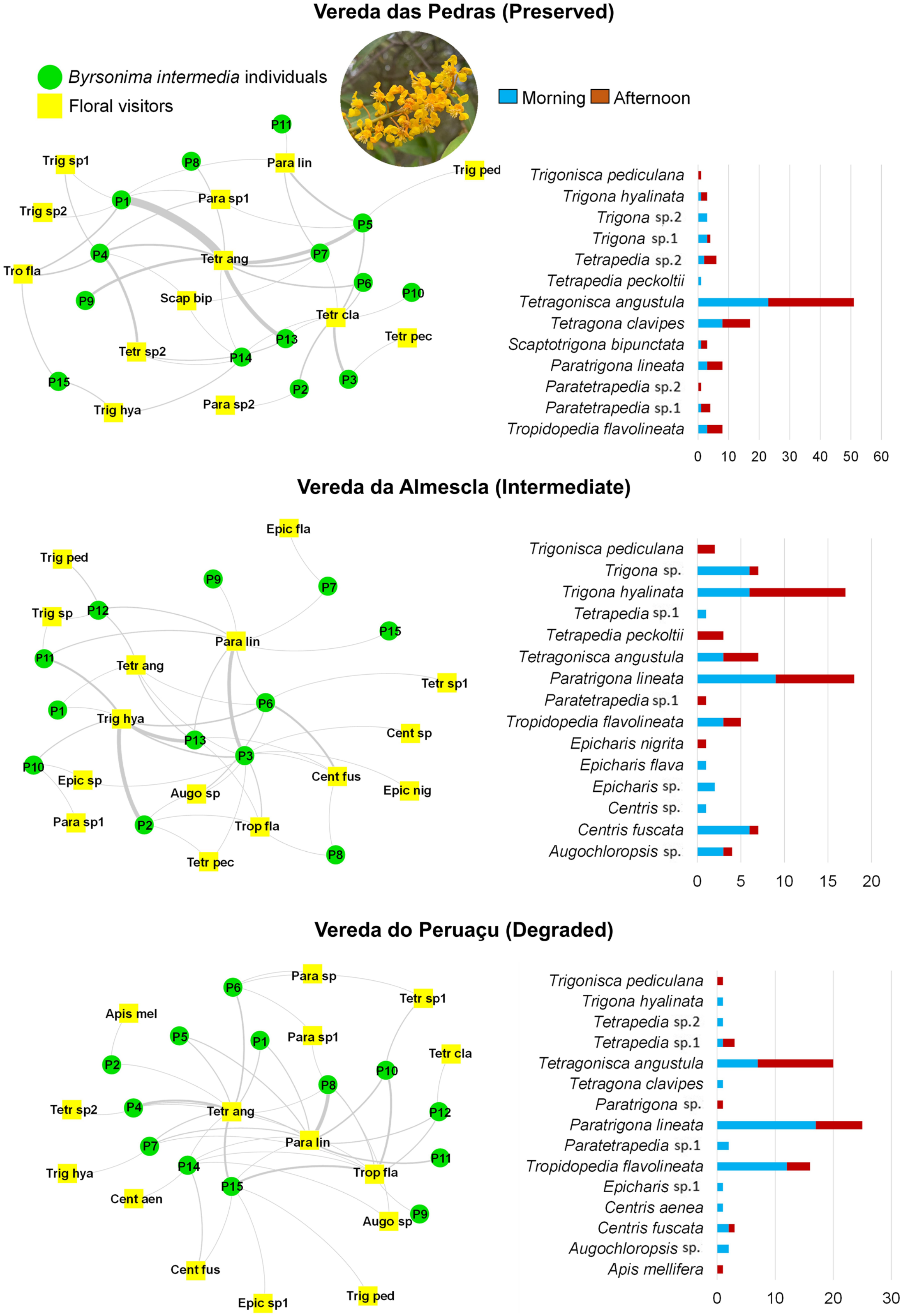
The networks of all sampled *veredas* were significantly modular (preserved *vereda*: $Q = 0.39$, $P < 0.005$; intermediate *vereda*: $Q = 0.34$, $P < 0.005$; degraded *vereda*: $Q = 0.34$, $P < 0.005$) and presented similar values, with the preserved *vereda* having the highest modularity value. The networks of the intermediate *vereda* and the degraded *vereda* presented five modules each and the preserved *vereda* presented four modules. Regarding specialization, all networks were significantly specialized (preserved *vereda*: $H2 = 0.38$, $P < 0.005$; intermediate *vereda*: $H2 = 0.26$, $P < 0.005$; degraded *vereda*: $H2 = 0.25$; $P < 0.005$), with the network of the preserved *vereda* being the most specialized.

Regarding the variation in species-level descriptors for the sampled plant individuals in the different *veredas*, for specialization ($F = 0.502$; $DF = 36$; $P = 0.61$), degree ($F = 0.35$; $DF = 36$; $P = 0.71$) and betweenness centrality ($F = 0.05$; $DF = 36$; $p = 0.94$; Fig. 4) there was no significant difference between the sampled areas. On the other hand, for closeness centrality the intermediate *vereda* had individuals with more important roles in the plant-visitor interaction network compared to the other sampled *veredas* ($F = 5.88$; $DF = 36$; $P = 0.006$; Fig. 4).

Considering the role of individuals in each *vereda* studied in relation to their attributes, in the preserved *vereda*, individuals with the highest number of flowers had a higher number of partners (degree) ($F = 10.40$; $P = 0.01$; Table 1). In the intermediate *vereda*, individuals who had the highest number of flowers had a higher degree ($F = 9.89$; $P = 0.01$; Table 1) and betweenness centrality ($F = 8.42$; $P = 0.01$) in the network. In addition, taller individuals also had greater closeness centrality ($F = 8.84$; $P = 0.02$; Table 1). In the degraded *vereda*, individuals with wider flowers had a higher degree in the interaction network ($F = 9.56$; $P = 0.01$).

Discussion

We found that individual-based plant-visitor networks on *Byrsonima intermedia* from *veredas* environments were composed by different species of bees and are significantly modular and specialized. Although the modularity of the networks was similar among them, our results also showed that the network of the preserved *vereda* had the highest observed specialization value. Besides, we also found that the role of individuals in the networks is strongly influenced by their attributes, especially the number of flowers, flower size, and plant height. The results show that the abundance of resources offered by each individual in the network, the size of the flower and the plant height are some factors that can determine its role in the network of interactions in the studied *veredas*. Therefore, our results indicate that the modular structure of visitor networks appears to be resilient to the observed disturbances, but the network specialization


Vereda das Pedras (Preserved)
Byrsonima intermedia individuals
Floral visitors
Morning
Afternoon
P11
Trig sp1
P8
Para lin
Trig ped
Para sp1
P1
Trig sp2
P5
P4
Tetr ang
P7
Tro fla
P6
P9
Scap bip
P10
Tetr cla
Tetr sp2
P13
Tetr pec
P14
P3
P15
P2
Trig hya
Para sp2
Trigonisca pediculana
Trigona hyalinata
Trigona sp.2
Trigona sp.1
Tetrapedia sp.2
Tetrapedia peckoltii
Tetragonisca angustula
Tetragona clavipes
Scaptotrigona bipunctata
Paratrigona lineata
Paratetrapedia sp.2
Paratetrapedia sp.1
Tropidopedia flavolineata
0
10
20
30
40
50
60
Vereda da Almescla (Intermediate)
Epic fla
Trig ped
P9
P7
Trig sp
P12
Para lin
P15
P11
Tetr ang
Tetr sp1
P1
P6
Trig hya
P13
Cent sp
P10
P3
Epic sp
Cent fus
Augo sp
Epic nig
Para sp1
P2
Trop fla
Tetr pec
P8
Trigonisca pediculana
Trigona sp.
Trigona hyalinata
Tetrapedia sp.1
Tetrapedia peckoltii
Tetragonisca angustula
Paratrigona lineata
Paratetrapedia sp.1
Tropidopedia flavolineata
Epicharis nigrita
Epicharis flava
Epicharis sp.
Centris sp.
Centris fuscata
Augochloropsis sp.
0
5
10
15
20
Vereda do Peruaçu (Degraded)
Para sp
P6
Tetr sp1
Apis mel
P5
P1
Para sp1
Tetr cla
P2
P10
P8
Tetr sp2
P4
Tetr ang
P12
P7
Para lin
P11
Trig hya
P14
Trop fla
Cent aen
P15
Augo sp
P9
Cent fus
Trig ped
Epic sp1
Trigonisca pediculana
Trigona hyalinata
Tetrapedia sp.2
Tetrapedia sp.1
Tetragonisca angustula
Tetragona clavipes
Paratrigona sp.
Paratrigona lineata
Paratetrapedia sp.1
Tropidopedia flavolineata
Epicharis sp.1
Centris aenea
Centris fuscata
Augochloropsis sp.
Apis mellifera
0
10
20
30

◂**Fig. 2** Interaction networks between individuals of *Byrsonima intermedia* and their floral visitors in the three studied *veredas* (Vereda das Pedras—preserved *vereda*, Vereda da Almescla—Intermediate *vereda*, and Vereda do Peruaçu—degraded *vereda*). In the network, green circles represent sampled individuals of *Byrsonima intermedia*, and yellow squares represent species of floral visitors. The width of the lines represents the visitation frequency. Next to each interaction network, a graph displays the visitation frequency of each species separated into morning and afternoon periods for the sampled *veredas*

and the roles of species respond to the drying level of the *veredas.*

The most abundant taxa recorded in the present study all belong to the Apidae family, predominantly from the Meliponini tribe, with a notable presence of the genera *Tetragonisca*, *Paratrigona*, *Trigona*, and *Tetragona*. The Meliponini tribe comprises species known as stingless bees, so named because they possess a reduced stinger. They are a group of bees considered responsible for 40 to 90% of the pollination of native Brazilian trees (Brown and Albrecht 2001). Bees within this tribe live in colonies and typically use pre-existing cavities to construct their nests, such as hollow trees and nests of other insects. They are generalist species, feeding on pollen and nectar, but may sporadically collect floral oils for use in nest construction (Ramalho and Silva 2002). Meliponines are sensitive to anthropogenic disturbances, especially deforestation, leading to environmental degradation and, consequently, smaller and fragmented populations (Brown and Albrecht 2001).

Among the main genera sampled, the only one that does not belong to the Meliponini tribe is the genus *Paratetrapedia*, which belongs to the Tapinotaspidini tribe. This tribe encompasses one of the most important and diverse groups of oil-collecting bees in the Americas, both in terms of numbers and biological habits (Aguiar and Melo 2011). They are a group of solitary bees, with the vast majority nesting on the ground, exposed soils, or surfaces covered by vegetation, often on flat or sloping terrain (Alves-dos-Santos et al. 2007). Species within this tribe are generally small in size (<10 mm) and possess specialized body structures for collecting, manipulating, and transporting oil (Ramalho and Silva 2002; Alves-dos-Santos et al. 2007; Aguiar and Melo 2011). This resource can be used along with pollen and nectar as food for larvae and/or adults and as waterproof nest lining. Some studies indicate a relationship between the flowers of plants in the Malpighiaceae family and species of the genus *Paratetrapedia*, suggesting an illegitimate relationship where the bees engage in oil and pollen thief, occasionally performing pollination during pollen collection (Sazima and Sazima 1989; Sigrist and Sazima 2004). However, Vogel and Machado (1991) mentioned that Malpighiaceae species with small flowers may have a legitimate relationship with *Paratetrapedia* species, making them effective pollinators (Sigrist and Sazima 2004). It's worth noting that other oil-collecting bee species that were sampled in lower abundance in this study often play a key role in interaction networks between plants and oil-collecting bees, such as *Centris* spp. and *Epicharis* spp. (Bezerra et al. 2009; Genini et al. 2010; Mello et al. 2013; Guimarães et al. 2021). However, we cannot rule out the possibility that our sampling method may have influenced this result. These bees tend to fly very quickly between flowers and do not linger for long on each plant individual (Buchmann 1987). Therefore, as we sampled each individual for a defined time interval and not throughout the day, some of these rapid visits may not have been captured regardless of the key role of these bees as pollinators for oil producing flowers. Nevertheless, in field observations, we noted limited activity of these species in the studied areas, same considering other plants in the vegetation. The low frequency of these visitors could impact the reproductive success of the plants in the medium and long term. Additionally, *Byrsonima* species are characterized by a stigma barrier (Sigrist and Sazima 2004). This barrier tends to be easily overcome by genus-specific pollinators but can be an effective barrier to the pollination by generalist bee species.

The networks in the three *veredas* had similar sampling efforts. Similarly, in all *veredas*, the sampled networks were significantly modular and specialized. As previously presented, modularity varied little among the *veredas*. Regarding modularity, the results indicates that in all *veredas* the *B. intermedia* individuals partition their interactions among themselves. Modular structure has also been reported in other studies on interaction networks involving Malpighiaceae and bees, considering different species within this family (Bezerra et al. 2009; Mello et al. 2013), as well as with other plant species that produce floral oil (Guimarães et al. 2021). However, Genini et al. (2010) did not identify this pattern in a floral visitor network of Malpighiaceae that included both pollinator and non-pollinator species. It's worth noting that results like found in this study, considering different individuals of the same Malpighiaceae species, are similar to persistent patterns identified when considering all species of oil-producing flowers and their floral visitors on a broader geographic scale (Bezerra et al. 2009; Mello et al. 2013). In all of these networks, modular structure corresponds to the characteristics of oil-flower families or the individual plants that make up these networks, and sometimes it is influenced by geographical location and species distribution (Bezerra et al. 2009; Genini et al. 2010; Mello et al. 2013; Guimarães et al. 2021). On the other hand, we found that the preserved *vereda* had the highest specialization. The high specialization of the network in the preserved *vereda* can be related to the fact that the most frequent bee species, *Tetragonisca angustula*, accounted for nearly half of the observed interactions (46%) there. The more specialized individuals and species are in their interactions, the

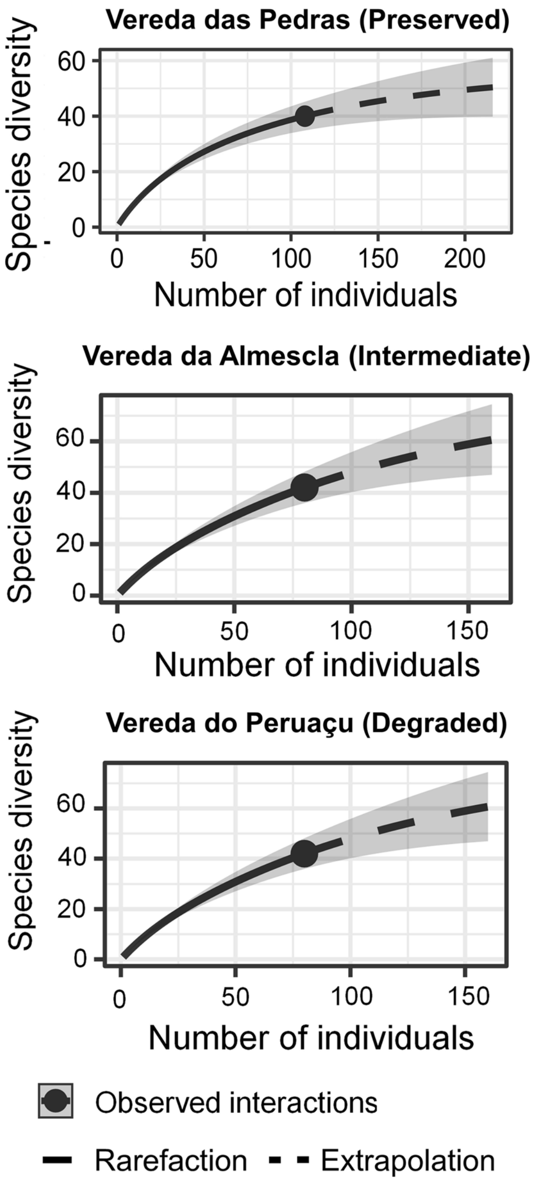


Fig. 3 Rarefaction and extrapolation curve for the network of individuals of *Byrsonima intermedia* and their floral visitors in the three studied *veredas* (Vereda das Pedras—preserved *vereda*, Vereda da Almescla – Intermediate *vereda*, and Vereda do Peruaçu—degraded *vereda*)

more specialized the entire network tends to be (Vázquez and Aizen 2003).

In the present study it was identified that resource availability, individual height, and flower size were important attributes for a plant individual's relevance in the interaction network. The results show that resource availability and individual height were factors that influenced individuals to have higher closeness centrality, as observed in the intermediate *vereda* compared to the other sampled *veredas* (meaning these individuals have a high degree of shared floral visitors with other individuals in the network). The greater height of plants can make them more conspicuous in the environment and more easily found by pollinators in the surroundings. On the other hand, the size of flowers is an attribute that directly indicates the quantity of resources available to visitors. These results suggest that taller plants with greater number of flowers play an important role in the cohesion of floral visitor networks in *veredas*. Higher centrality can result in higher pollen loads carried by effective pollinators, ultimately increasing individual fitness (Guimarães 2020; Arroyo-Correa et al. 2021). As previously mentioned, the *Byrsonima intermedia* species is typical of *vereda* environments, and in the studied areas, it exhibited a concentrated flowering, representing a sizeable amount of resources during that period. Furthermore, as we sampled interactions during a period of massive flowering, due to a dilution effect, visits from oil-collecting bees may have been diluted within the plant population.

High floral resource abundance was also a factor contributing to a higher individual interaction degree, as seen in the preserved and intermediate *veredas* (meaning a greater number of partners). On the other hand, the average flower length was the factor leading individuals to have a higher interaction degree (more partners) in the interaction network of the degraded *vereda*. These attributes have been mentioned previously as influential factors in mutualistic interaction networks between plants and pollinators (Dupont et al. 2011). Local variation among individuals within a population can also influence these mutualistic interactions (Guimarães 2020; Arroyo-Correa et al. 2021; Friedemann et al. 2022). Our study reinforces these relationships and contributes to the understanding of network structure among individuals in tropical areas, exploring the contribution

Conclusion

In this study, we observed that the networks of individuals of *Byrsonima intermedia* and their floral visitors were mainly composed of non-oil-collecting bees. Furthermore, the three studied networks exhibited similar patterns of modularity and specialization, with the preserved *vereda* showing the highest degree of specialization. Factors such as resource abundance provided by each individual in the network, flower size, and height are some of the factors that can determine their role in the interaction network in the studied *veredas*. These findings are important to understand pollination dynamics in *vereda* areas with varying degrees of anthropogenic impact on individual networks. Individuals within a population represent the basic units of interaction in ecological systems, and the role of these individuals in

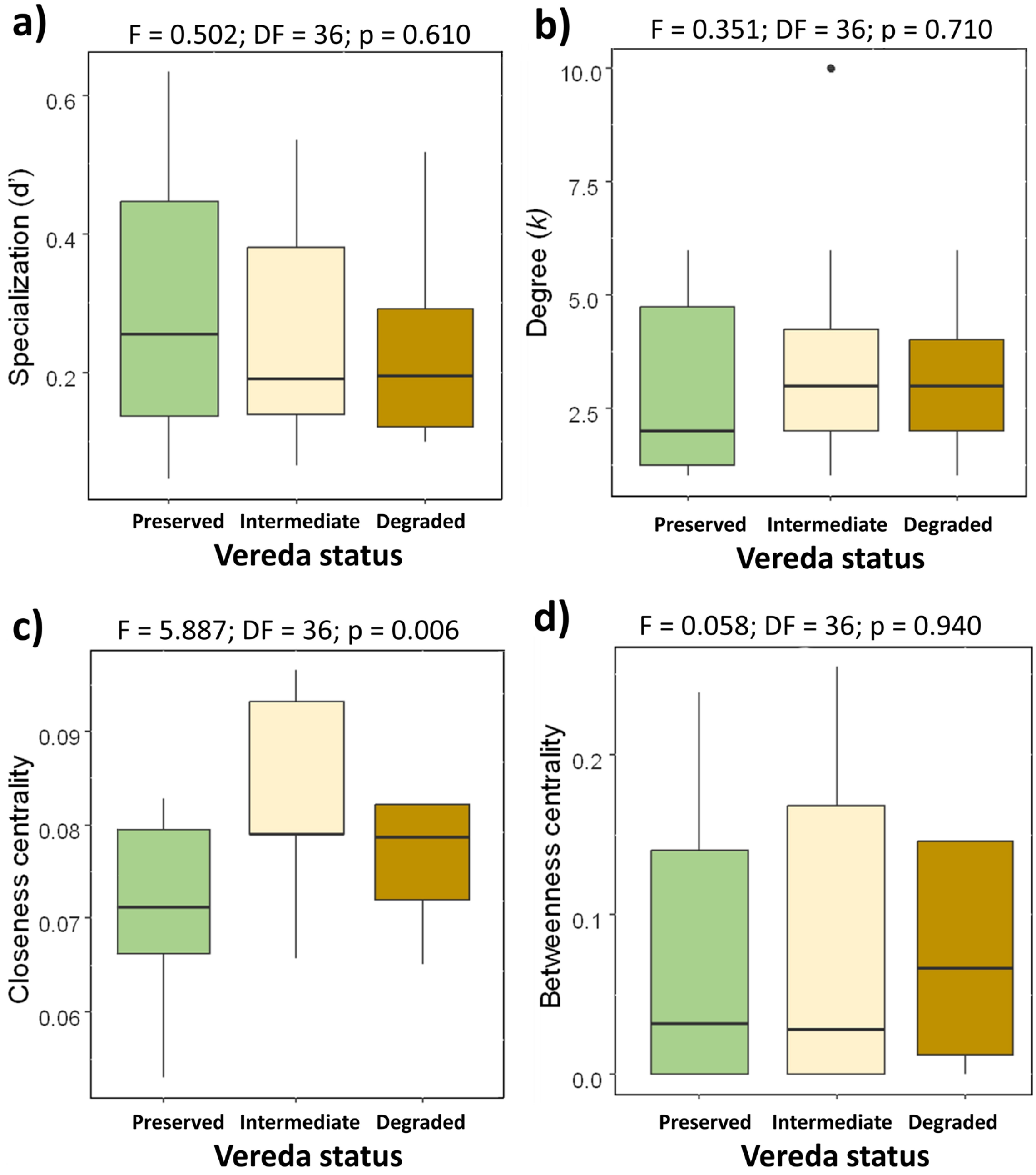


Fig. 4 Comparison of topological parameters (specialization, degree, closeness centrality, and betweenness centrality) among individuals of *Byrsonima intermedia* in the three sampled *veredas* (Vereda das Pedras—preserved *vereda*, Vereda da Almescla—Intermediate *vereda*, and Vereda do Peruaçu—degraded *vereda*)

different populations can affect the dynamics, stability, and organization of the entire community. Therefore, future studies should expand the available information to accurately assess the impact of anthropogenic effects on these individual-level interactions.

Table 1 Values from the simple linear models evaluating the role of the sampled individual's attributes in relation to their role in the interaction network of the three studied *veredas*. Values in bold indicate significant results ($p < 0.05$)

Variables	Preserved *vereda*		Intermediate *vereda*		Degraded *vereda*	
	F value	p value	F value	p value	F value	p value
Specialization (d′)						
Plant height	0.00	0.99	− 0.13	0.31	2.32	0.16
Number of flowers	0.63	0.45	− 0.52	0.61	0.73	0.41
Average flower width	0.88	0.37	0.87	0.13	0.81	0.39
Average flower length	0.03	0.86	1.11	0.30	7.71	0.23
Degree						
Plant height	1.31	0.28	3.26	0.11	0.22	0.65
Number of flowers	10.40	0.01	9.89	0.01	2.56	0.15
Average flower width	0.46	0.51	1.61	0.24	9.56	0.01
Average flower length	0.83	0.39	0.00	0.99	1.75	0.22
Weighted betweenness centrality						
Plant height	0.05	0.82	1.45	0.26	0.01	0.93
Number of flowers	1.07	0.33	8.42	0.02	0.94	0.36
Average flower width	0.11	0.75	3.06	0.12	1.51	0.25
Average flower length	1.43	0.26	0.03	0.85	2.70	0.14
Weighted closeness centrality						
Plant height	0.40	0.54	8.84	0.02	0.14	0.72
Number of flowers	1.50	0.25	4.58	0.05	1.49	0.26
Average flower width	0.94	0.36	3.32	0.11	0.68	0.43
Average flower length	1.71	0.22	0.13	0.73	1.08	0.33

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Author contributions All authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by SCOS, CSS, and WSA. The first draft of the manuscript was written by SCOS and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Declarations

Competing interest The authors declare no competing interests.

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